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Biology And Phylogeny Of The Cassidinae Gyllenhal Sensu Lato (Tortoise And Leaf-Mining Beetles) (Coleoptera: Chrysomelidae)

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BIOLOGY AND PHYLOGENY OF THE
CASSIDINAE GYLLENHAL SENSU LATO
(TORTOISE AND LEAF-MINING BEETLES)
(COLEOPTERA: CHRYSOMELIDAE)

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ABSTRACT

A parsimony analysis was undertaken to test subfamily and tribal group concepts of Cassidinae (ca. 2000 genera, ca. 6000 species). An integrated account of their biology was synthesized from the primary literature. A detailed morphological study of adults, using *Hemisphaerota palmarum* Boheman as a model, formed the basis for evaluating characters previously utilized and for defining novel characters. The data matrix comprised 210 characters (from adults and immature stages, ecology and behavior), 6 outgroups, and 98 ingroup exemplar species (representing 94 genera and 39 of the 43 recognized cassidine tribes). Results support the monophyly of Cassidinae and place it as sister to Galerucinae. The classical Hispinae s.str. is paraphyletic whereas the classical Cassidinae s.str. is monophyletic if some Imatidiine genera are included. Four tribes—Aproidini, Delocraniini, Hemisphaerotini, and Notosacanthini—are well supported by many autapomorphies. Multiple genera were sampled to test the monophyly of 14 cassidine tribes. Seven were recovered as monophyletic: Anisoderini, Cassidini, Dorynotini, Eugenysini, Hispini, Omocerini, and Spilophorini. Relationships and character support of all cassidine tribes are discussed and compared with phylogenies proposed by Borowiec (1995) and Hsiao and Windsor (1999).

The biological account and these phylogenetic results provide an opportunity for identifying some general trends and major innovations in the evolutionary history of Cassidinae. The alteration of the adult head from prognathous to hypognathous and the compaction of the body, legs, and various elytral-locking mechanisms are recurrent themes in adult morphology. Maternal care may have arisen once or twice. Seven trophic guilds are defined here for Cassidine larvae. They arise from two large radiations of leaf-mining and exophagous-feeding, a minor radiation in cryptic rolled-leaf feeding, and small generic and sub-generic specializations in stem mining, leaf scraping, petalophagy, and leaf-shelter chewers. Fecal shield construction and retention appear to be correlated with innovations in life history and in larval and pupal morphology, and they may have played an important role in cassidine diversification.

INTRODUCTION

The Chrysomelidae, or leaf beetles, comprise one of the largest animal families with more than 37,000 species arranged in approximately 2,000 genera and 19 subfamilies (Lawrence, 1982; Seeno and Wilcox, 1982; Jolivet et al., 1988; fig. 1). This remarkable diversity, coupled with a worldwide distribution and phytophagous diet, gives chrysomelids considerable ecological and economic significance. Despite their important role in global ecosystems, knowledge of intrafamilial relationships is surprisingly imprecise at all hierarchical levels (Reid, 1995).

The present research is focused on a distinct clade in Chrysomelidae, Cassidinae Gyllenhal. This clade was until recently regarded as two subfamilies, Cassidinae Gyllenhal *sensu stricto* (tortoise beetles) and Hispinae Gyllenhal *sensu stricto* (leaf-mining beetles). This separation and confusion of group names in Cassidinae stem from two factors: 1) failure to synthesize biological information, and 2) diverse opinions of phylogenetic concepts, ranks and nomencla-

ture (both formal and informal) (table 1). Biological knowledge and group concepts are intertwined, but in Cassidinae biological information must first be integrated before we can achieve taxonomic clarification.

Staines (2002b) reviewed the priority of group names and concluded that Cassidinae has priority over Hispinae since it appears first on page 434 in the same publication, Gyllenhal (1813), before Hispinae appears later on page 448. Borowiec and Świętojańska (2005) reviewed this name priority again, having concluded that Chen (1940) was the first revisor and that he fixed the group name as Cassidinae. My review of this issue also traced the first revision of Chrysomelidae to Chen (1940). As “First Revisor”, Chen (1940) gave precedence to the name Cassidinae. By ICZN article 24.2, terminology must follow Chen (1940). Cassidinae is therefore the correct name for the clade Hispinae + Cassidinae. Chen (1973) and Chen et al. (1986) used the names Cassididoidea and Hispidae for Cassidinae + Hispinae; however, Chen fixed the name earlier.

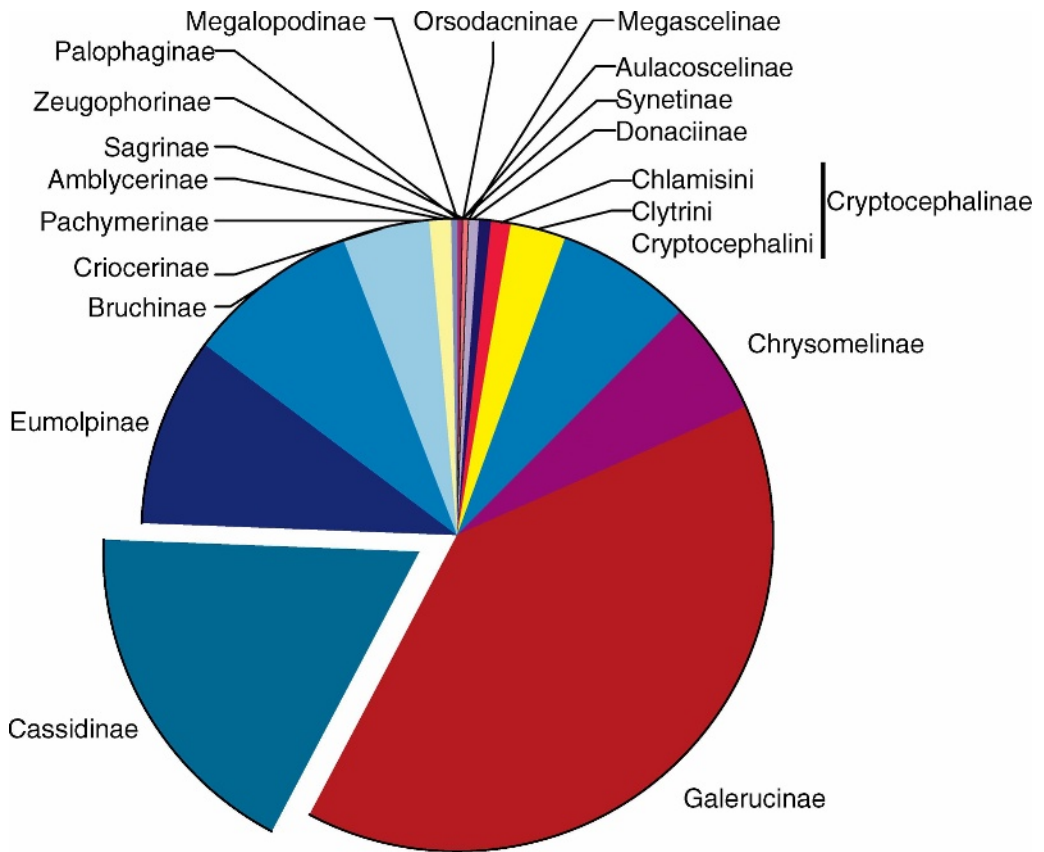


Fig. 1. Species diversity of subfamilies of Chrysomelidae.

TABLE 1
Historical Views of Position and Rank of Cassidinae

Related to Family Chrysomelidae:

Family Cassidiformes (Monrós, 1959)

Family Cassidiadae (Stephens, 1829)

Family Cassididae (Westwood, 1920; Chen, 1940)

Family Hispidae (Chen, 1964)

Superfamily Cassidoidea (Chen, 1973)

Two Families, Cassididae s.str. and Hispidae s.str. (Baly, 1869a, 1885, 1886; Baly and Champion, 1895; Weise, 1897; Sanderson, 1902; Böving and Craighead, 1931; Jolivet, 1954)

Within Chrysomelidae:

Section or division Cryptostoma (Chapuis, 1874, 1875; Weise, 1893, Jacoby, 1908; Maulik, 1919; Spett and Lewitt, 1926; Crowson, 1938; Gressitt, 1942; Chen, 1940–1985; Chûjo, 1953; Monrós and Viana, 1947; Monrós, 1959; Daccordi, 1980; Schmitt, 1989)

Section Fronticornis (Thomson, 1868)

Two Subfamilies, Cassidinae s.str. and Hispinae s.str. (Crowson, 1981; Monrós, 1955, 1959; Jolivet, 1959; Medvedev, 1971; Seeno and Wilcox, 1982; Lawrence, 1982; Verma, 1999; Santiago-Blay, 2004)

Two tribes, Cassidini and Hispini, of subfamily Clytrinae (Suzuki, 1988b)

Subfamily Hispinae s.l. (Crowson, 1953; Lawrence and Britton, 1994; Borowiec, 1995; Reid, 1995; Hsiao and Windsor, 1999; Flowers and Hanson, 2003; Vencl et al., 2004; Farrell and Sequeira, 2004)

Subfamily Cassidinae s.l. (Suzuki, 1974, 1980, 1988a, 1994; Staines, 2003, 2004)

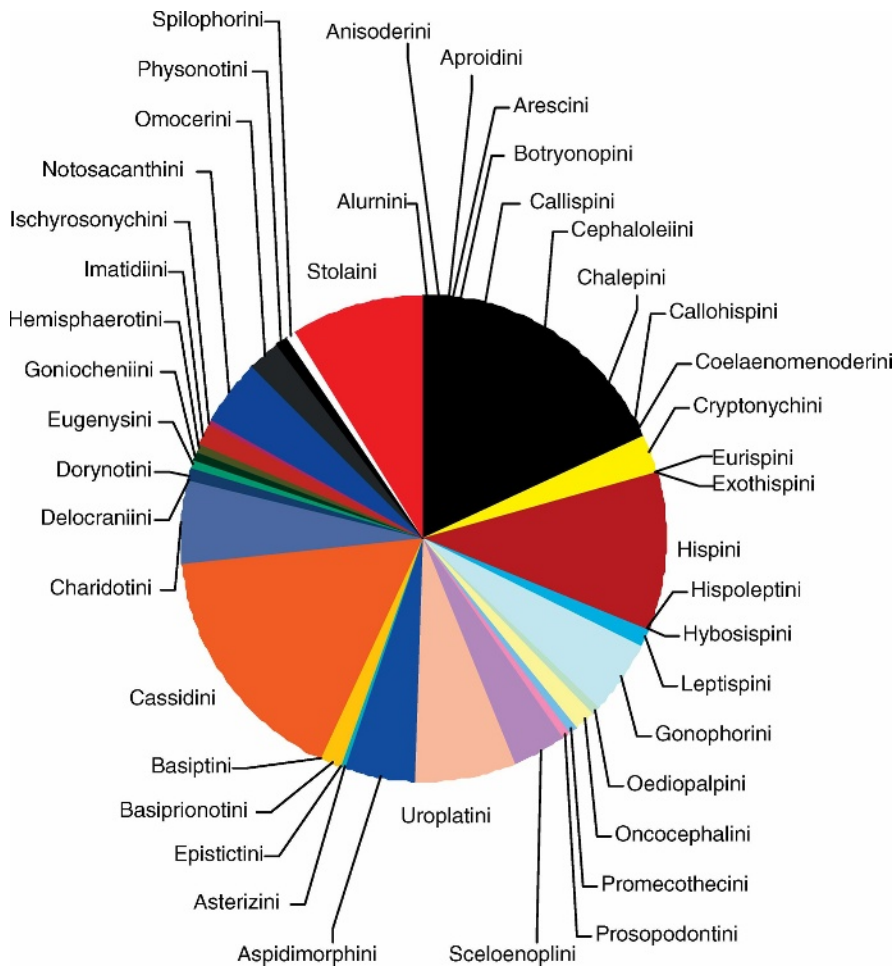


Fig. 2. Species diversity of tribes of Cassidinae.

Throughout this text, I use the name Cassidinae for the clade Cassidinae s.str. + Hispinae s.str. Cassidinae s.str. and Hispinae s.str. are the terms used in classical ideas and concepts of other researchers. These classical Cassidinae s.str. or cassidiform taxa correspond roughly with “tortoise beetles”, exophagous cassidines with shield-retaining larvae. The classical Hispinae s.str. or hispiform taxa have been called “leaf-mining beetles”. However, this umbrella term corresponds to at least six ecological guilds: leaf-shelter scrapers, leaf-tube scrapers, flower scrapers, stem miners, leaf miners and open-leaf feeders.

Cassidinae arose during the late Jurassic (Mann and Crowson, 1981a; Santiago-Blay,

1994) and have evolved into about 6,000 species classified into 43 tribes (fig. 2). They are found worldwide today but are particularly speciose in the Neotropics. Three unambiguous synapomorphies distinguish Cassidinae: (1) the mouth is positioned ventrally on the head (in other chrysomelids the mouth is anterior or anteroventral) (Chapuis, 1874, 1875; Crowson, 1953), and hence another one of their classical names is “Cryptostomes” (Chapuis, 1874, 1875; Jacoby, 1908; Gressitt, 1950; Crowson, 1953); (2) the antennal insertions are proximal and are positioned anteroventrally on the head (in most other chrysomelids they are widely spaced and positioned anterolaterally; in Galerucinae Latreille s.l. antennae are positioned ante-

romedially) (Schmitt, 1989); and (3) loss of tarsomere IV (present but reduced in other chrysomelids) (Chen, 1940, 1985; Chen et al., 1986; Riley et al., 2002). Gressitt (1950) pointed out that caudal furcae and shield retention are present in "cassidid" larvae but not in "hispid" larvae.

Cassidinae comprises approximately 16% of chrysomelid species diversity and forms the second largest sub-clade in Chrysomelidae after Galerucinae s.l. (figs. 1, 2). Cassidinae s.str. constitutes a moderately sized group of 2906 described species in 154 genera arranged into 19 tribes (Seeno and Wilcox, 1982) or 12 tribes (Borowiec, 1999). Hispinae s.str. is similarly speciose with 2980 described species (C. Staines, personal commun.) arranged in 170 genera and 24 tribes (Seeno and Wilcox, 1982; Staines, 2002b).

The position of Cassidinae within Chrysomelidae remains ambiguous and can only be addressed in higher level analyses of subfamily relationships; however, available phylogenies disagree (Lee, 1993; Reid, 1995, 1999; Hsiao, 1994a, 1994b, 1994c; Farrell, 1998; Duckett et al., 2004). Although this issue is addressed tangentially here (in the selection of outgroups), the sister clade of Cassidinae will be settled only as deeper chrysomelid relationships are resolved.

The present study focuses on two fundamental questions in cassidine systematics, monophyly and in-group relationships. Systematic debate regarding Cassidinae s.str. and Hispinae s.str. has been focused primarily on the ambiguous boundary between the two. Two recent studies (i.e., Borowiec, 1995; Hsiao and Windsor, 1999), concluded that they are paraphyletic and should be synonymized as a single clade, Hispinae s.l. Proposed cladograms (Borowiec, 1995; Hsiao and Windsor, 1999) differ on exactly how they are related. Unfortunately, new informal, redundant group terms were coined by these researchers and are now being used: "hispid Hispinae" (Borowiec, 1995; Hsiao and Windsor, 1999) and "cassidoid Hispinae" (Heron and Borowiec, 1997; Hsiao and Windsor, 1999; Vencl and Morton, 1999; Wilf et al., 2000; Vencl et al., 2004). These neologisms appear to correspond to the classical leaf-mining and open-leaf-feeding guilds but they are unnatural; that is, they

are not supported by synapomorphies. Additional informal terms will only exacerbate nomenclatural confusion in Cassidinae.

The historical focus on separating Cassidinae s.str. and Hispinae s.str. has inhibited studies that test tribal and generic concepts and relationships. Such studies are critical to stabilizing the classification and nomenclature within Cassidinae. Clarifying group concepts and relationships will also foster development of evolutionary hypotheses regarding the diverse array of morphologies, host plant associations, biogeographies, and unusual behaviors exhibited by these beetles.

My goal in this research was to document relationships at the taxonomic levels germane to the systematic problems outlined above. To achieve this goal, I carried out a detailed morphological study of adults with a sampling methodology that emphasized taxonomic and geographic diversity. I reviewed traditional phylogenetic characters, introduced novel characters, and tested all character hypotheses cladistically. The search for novel characters stimulated my attempt to synthesize biological information for Cassidinae from the primary literature. Phylogenetic results are used to identify monophyletic units within Cassidinae and to discuss macroevolutionary patterns in adult morphology, as well as behaviors such as maternal care and larval construction of defense shields with feces and exuviae.

The ultimate goals of systematic research are corroborated phylogenetic hypotheses, informative, predictive classifications and equally informative Linnaean names. These goals are achieved through iterative character refinement and expansion of the types of characters in the dataset to include morphology, molecules, behavior, and ecology. The present contribution is one step in that process.

TAXONOMIC HISTORY

POSITION OF CASSIDINAE WITHIN CHRYSOMELIDAE

Latreille (1802) first proposed the family name Chrysomelines for leaf beetles. Chapuis (1874) subdivided Chrysomelines into four

sections and 15 “tribes”, with his section IV, Cryptostomes, consisting of two tribes, Hispidae and Cassididae. Subsequent attempts to refine this arrangement include splitting or combining groups and altering ranks at all levels (Jacoby, 1908; Pierce, 1916; Chen, 1940, 1964; Gressitt, 1942b; Chûjo, 1953; Monrós, 1959; Gressitt and Kimoto, 1963), but Chapuis’ (1874) system and group concepts are still used today (Seeno and Wilcox, 1982).

Cassidinae s.str. and Hispinae s.str. have been traditionally regarded as forming a single clade, Cryptostomes, either most closely related to Chrysomelidae or as one or more groups within Chrysomelidae. Viewpoints on the position, rank, and formal names of Cassidinae s.str. and Hispinae s.str. are summarized in table 1.

A hypothesized relationship between Cassidinae s.str. and Coccinellidae (Gage, 1920; Westwood, 1920) never gained support. However, other authors have commented on the resemblance between cassidine and coccinellid larvae and pupae (Paterson, 1931, 1941); some cassidine species were even described in *Coccinella* (Fabricius, 1775).

When Cassidinae s.str. and Hispinae s.str. have been considered as a distinct clade most closely related to Chrysomelidae, they have been ranked as a family or superfamily, and termed Cassidiadae, Cassidiformes, Cassididae, or superfamily Cassidoidea. When treated as members of Chrysomelidae, Cassidinae s.str. and Hispinae s.str. have been ranked as the section Cryptostoma or division Fronticornis (Chapuis, 1875). They have also been ranked as a single subfamily (Hispinae or Cassidinae), as two distinct subfamilies, or as two distinct tribes called Cassididae s.str., Hispidae s.str., Cassidinae s.str., or Hispinae s.str. (these names were used before ICZN regulated the “ini” suffix for tribes). Based on larval data, Lee (1993) proposed a dissident view that Cassidinae s.str. and Hispinae s.str. are not each other’s closest relatives within Chrysomelidae.

Except for Reid (1995) and Hsiao and Windsor (1999), these views on phylogenetic concepts, ranks, and nomenclature have been universally based on limited taxon samples, few characters (table 2), personal views on hypothetical ancestral groundplans, and

a priori decisions on polarity (primitive versus derived). Many interpretations are essentially single character system phylogenies. For example, Verma’s view (1985, 1988, 1992, 1996) is based only on male genitalia, and Suzuki’s view (1969a, 1969b, 1970a, 1970b, 1994, 1996) is based on hindwing venation.

Current phylogenetic analyses emphasize a more comprehensive approach that uses extensive taxon samples, outgroup comparisons, multiple character sources (morphology, molecules, behavior and ecology), and global parsimony analysis (Kitching et al., 1998; Schuh, 2000). Modern character argumentation requires more rigorous homology assessment with consideration of outgroups (Nixon and Carpenter, 1993).

Recent higher level studies of chrysomelid phylogenetics (Lee, 1993; Hsiao, 1994a, 1994b, 1994c; Reid, 1995, 2000; Farrell, 1997; Duckett et al., 2004) provide a framework for addressing lower level problems. These studies are relevant to phylogenetic relationships in Cassidinae and are discussed briefly below.

Lee (1993) provided the first cladistic analysis of chrysomelid subfamily relationships. Thirty-four larval morphological characters were coded for 77 Japanese species (17 chrysomelid subfamilies; 0.21% species diversity) and a hypothetical ancestor. Monophyly of the hispine–cassidine clade was not supported, and Alticinae, Galerucinae, and Chrysomelinae were identified as possible relatives. Some problems of Lee’s (1993) analysis include a priori character polarization, ambiguous character state demarcations (e.g., states of characters 2, 15 and 22 overlap) and analysis with an obscure program by Sawada. Reanalysis of these data by Reid (1995) produced different topologies from those published by Lee (1993).

Hsiao (1994a) presented an unrooted chrysomelid phylogeny with the relationship ((Cassidinae s.str. + Hispinae s.str.) + Orsodacninae) + other subfamilies. His immediate goal was to draw attention to sequence data, namely 12S mtDNA, as a tool in chrysomelid systematics. Only 11 chrysomelid species (representing 11 chrysomelid subfamilies) were sampled and no outgroups were used. Hsiao (1994b) again promoted the use of 12S mtDNA and 16S mtDNA in chrysomelid

TABLE 2
Support for Relationships of Cassidinae s.str. and Hispinae s.str.

Study	Evidence	Position ^a
CLASSICAL STUDIES		
Chapuis and Candèze, 1855	Larvae	(Cassidinae + Criocerinae) + Hispinae
Chapuis, 1875	Opisthognathy	(Cassidinae + Hispinae) + others
Sanderson, 1902	Caudal process (= faecifork)	(Cassididae + Hispididae) + others
Gage, 1920	Larvae	(Cassidinae + Coccinellidae) + others
Westwood, 1920	Larvae	(Cassidinae + Coccinellidae) + others
Zia, 1936	Male genitalia	(Cassidinae + Hispinae + Eumolpinae) + others
Böving and Craighead, 1931	Larvae	(Cassidinae + Hispinae) + others
Powell, 1937	Male genitalia	((Cassidinae + Hispinae) + Eumolpinae) + others
Chen, 1940	Antennal proximity, opisthognathy, incomplete tegmen near median foramen, internal sac shorter than median lobe	(Cassidinae + Hispinae) + (Eumolpinae + (Lamprosominae + Chlamydiae))
Iablokoff-Khnzorian, 1966	Male genitalia	(Cassidinae + Hispinae) + Eumolpinae
Crowson, 1938	Metendosternite	(Cassidinae + Hispinae) + Lamprosominae + Eupoda
Barber, 1946	Male ejaculatory tube	(Cassidinae + Hispinae) + Eumolpinae
Suzuki, 1969a, 1969b, 1970a, 1970b, 1994, 1996	Hind-wing venation	(Cassidinae + Hispinae) + others
Jolivet, 1954	Hind-wing venation	(Cassidinae + Hispinae) + others
Jolivet, 1959, 1988	Host plant usage	(Cassidinae + Hispinae) + others
Chen, 1964	Opisthognathy; abdomen with five sternites and eight tergites	(Hispidae s.l.) + other chrysomelids
Chen, 1985	Opisthognathy; tarsal segmentation; bifid tarsal setae; antennal proximity; tegmen incomplete and near foramen	(Hispidae s.l.) + Eumolpinae) + others
Stork, 1980	Bifid tarsal setae	(Cassidinae + Hispinae) + Donaciinae + Criocerinae + Bruchidae
Mann and Crowson, 1981a	Bifid tarsal setae; larva with three segmented antenna, one segmented labial palp, and multiple ocelli	(Cassidinae + Hispinae) + Criocerinae + Donaciinae) + (Bruchinae + Sagrinae) + other chrysomelids
Mann and Crowson, 1983a	Male genitalia	Cassidinae + Hispinae + Criocerinae + Donaciinae + Sagrinae + Bruchinae
Mann and Crowson, 1996	Male genitalia	Cassidinae + Hispinae + Criocerinae + Donaciinae + Sagrinae
Pajni et al., 1987b	Female genitalia	Cassidinae + Hispinae + Chrysomelinae + Eumolpinae)
Suzuki, 1988	Male genitalia	(Cassidinae + Hispinae) + (Lamprosomatinae + Cryptocephalinae)
Verma, 1985, 1988, 1992	Male genitalia	(Cassidinae + Hispinae) + others
Verma, 1996	Male genitalia	((Cassidinae + Hispinae) + (Donaciinae + Criocerinae)) + (Bruchidae + Sagrinae)
Schmitt, 1989	Bifid tarsal setae; egg bursters absent	((Cassidinae + Hispinae) + ((Criocerinae + Sagrinae) + Donaciinae)) + others
Petitpierre, 1989	Karyotype 2n = 16–18	((Cassidinae + Hispinae) + Criocerinae) + others
Suzuki, 1994a	Hind-wing venation	(Cassidinae + Hispinae) + others
Cox, 1994a	Egg bursters absent	Cassidinae + Hispinae + Donaciinae + Galerucinae
Samuelson, 1996	Elytral microtrichia	Cassidinae + Hispinae + Eumolpinae + Chrysomelinae

TABLE 2
(Continued)

Study	Evidence	Position ^a
CLADISTIC STUDIES		
Lee, 1993	34 larval morphological characters	(((Chrysomelinae + Cassidinae) + (Alticinae + Galerucinae)) + Hispinae) + others
Hsiao, 1994a, c	12S mtDNA sequence; Neighbor-joining and Parsimony topologies	((Cassidinae + Hispinae) + Orsodacninae) + others
Hsiao, 1994b	12S, 16S mtDNA sequences; Neighbor-joining and Parsimony topologies	(((Galerucinae + Alticinae) + (Chrysomelinae + Criocerinae)) + ((Orsodacninae + Megalopodinae) + Syntetinae)) + Cassidinae + Hispinae) + others
Reid, 1995	71 morphological characters 22 larval morphological characters Combined adult and larval characters General morphological features	(Hispinae s.l. + Eumolpini) + others (Criocerini + Hispinae s.l. + (Chrysomelini + Timarchini)) + others (Hispinae s.l. + (Galerucinae + (Chrysomelini + Timarchini))) + others ((Criocerini + Hispinae s.l.) + Sagrinae) + others
Farrell, 1998	Morphological (Reid, 1995; Kuschel, 1995) + 18S nuclear DNA; 115 species	(Cassidinae + Hispinae) + (Donaciinae + Criocerinae + Pachymerinae + Amblycerinae + Bruchinae) (Chrysomelidae + Curculionidae)
Hsiao and Windsor, 1999	12S mtDNA sequence; 49 species (48 ingroup, 1 outgroup); Parsimony; Neighbor-joining	(Cassidinae + Hispinae) + Donaciinae
Wilf et al., 2000	Results of Hsiao and Windsor, 1999	Hispinae s.l. + (((Bruchinae + Amblycerinae) + Pachymerinae) + Sagrinae) + (((Haemoniini + Donaciini) + Plateumarini) + Criocerini)
Reid, 2000	56 morphological characters	(Hispinae s.l. + (Synetini + Cryptocephalinae)) + others (Hispinae s.l. + Criocerinae) + others Additional topologies under different treatments
Duckett et al., 2004	Small subunit ribosomal DNA + 18S nuclear DNA (Farrell, 1995) + morphological data (Reid, 1995, 2000)	(cassidine <i>Imatidiini</i> + Cryptocephalinae) + Cassidinae
Farrell and Sequeira, 2004	Molecular characters (parsimony) Molecular characters (Bayesian) Morphological characters (parsimony) + Morphological characters (Bayesian) + Combined (majority rule)	(((cassidine <i>Imatidium</i> + Cryptocephalinae) + Hispinae s.l.) + Eumolpinae) + others ((cassidine <i>Imatidium</i> + Cryptocephalinae) + Eumolpinae + Hispinae s.l.) + others (Hispinae s.l. + Criocerinae) + others (((Hispinae s.l. + others)) + Criocerinae) + Donaciinae (((Hispinae s.l. + others)) + Criocerinae) + Donaciinae

^aTerminals of Cassidinae + Hispinae are in boldface type. "Others" indicates chrysomelid subfamilies.

systematics. His sample of 13 Chrysomelid genera included 2 cassidine genera but no outgroups; under both parsimony and neighbor-joining analyses, these cassidines were

placed as sister taxa, basal to a large clade that included Galerucinae s.l., Chrysomelinae, Criocerinae, Syntetinae, Megalopodinae and Orsodacninae.

Reid's analysis (1995) marked a significant advance in the quality of chrysomelid phylogenetic analyses. He used outgroups (Curculionoidea and Cerambycoidea) for the first time, sampled all chrysomelid subfamilies, reviewed traditional morphological characters, introduced many new character systems (71 characters total), sampled an unprecedented number of taxa (ca. 0.2% species diversity [C. Reid, personal commun.]), and used current phylogenetic methods consistently (i.e., repeating the analysis recovered published topologies [Schmitt, 1996; Chaboo, unpubl. data]). Reid did not design his 1995 study to address the historical controversy surrounding (1) Cassidinae s.str. + Hispinae s.str. and (2) Alticinae s.str. + Galerucinae s.str., and he assumed them to be single monophyletic terminals (Hispinae s.l. and Galerucinae s.l., respectively) prior to analysis. Weighted analysis of the adult dataset resulted in the relationship Eumolpini + Hispinae s.l. Weighted analysis of the larval dataset resulted in a tritomy (Criocerini + Hispinae s.l. + Chrysomelinae). The unweighted analysis of combined adult and larval datasets resulted in Hispinae s.l. appearing as sister to the clade Galerucinae s.l. + Chrysomelinae. Various permutations of weighted characters were used on the combined data, with three results for Hispinae: sister to Galerucinae s.l. + Chrysomelinae, sister to Chrysomelinae, or sister to Criocerinae. Reid (1995) proposed that Hispinae s.l. and Criocerinae were probable sister taxa, but he did not present strong evidence. Reid (2000) re-analyzed his dataset by omitting non-chrysomeloid outgroups, correcting mis-scored characters, adding missing data, and exploring the effects of partitioning and weighting. The position of Hispinae s.l. remained inconclusive in all analyses of larval, adult and combined data. Criocerinae was suggested as the sister group based on plesiomorphic support.

Farrell (1998) presented a combined analysis of morphological data of Chrysomelidae (Reid, 1995) and Curculionidae (weevils) (Kuschel, 1995) with his own 18S nuclear ribosomal DNA data for 115 species (ca. 0.09% of Phytophaga species diversity). Species from six genera of Cassidinae were sampled (ca. 0.02% generic diversity). The preferred

topology suggested the relationship Cassidinae + (Donaciinae + Criocerinae + Pachymerinae + Amblycerinae + Bruchinae). Reid (2000) critically discussed problems of taxon and character sampling, theory, analysis, and interpretation in Farrell's (1998) work. Additionally, Farrell (1998) stated that sequences were aligned using Sequencher 3.0 (Genecodes, 1995); however, this program only shows raw chromatographs. One could produce coarse alignments using Sequencher 3.0, but more rigorous programs like Clustal (Thompson et al., 1997), MALIGN (Wheeler and Gladstein, 1994, 1994–2000), or POY 3.0 (Wheeler et al., 2002) are commonly used for alignment. Farrell and Sequeira (2004) subsequently expanded Farrell's (1998) study by adding 11 sequences for eight new in-group genera and four more outgroup genera, further refining the morphological characters of Reid (1995, 2000) and incorporating the morphological dataset of Svacha et al. (1997). Various analyses were performed with mixed results for the sister taxon and placement of Cassidinae (table 2). A most surprising result was the separation of *Imatidium* from other cassidines under Bayesian analyses of the molecular data.

In another higher level chrysomelid analysis, Duckett et al. (2004) combined sequence data from small subunit ribosomal DNA, 18S nuclear ribosomal subunit DNA (Farrell, 1999) with the morphological data of Reid (1995, 2000). Seven cassidine species from four tribes were included in their 100 species sample. Results suggested that Cassidinae was paraphyletic with respect to Cryptocephalinae. The placement of the cassidine *Imatidiini* as sister to Cryptocephalinae appears to corroborate Farrell and Sequeira (2004).

Genomic data are a powerful tool in evolutionary biology, and recent chrysomelid studies have used 12S mtDNA sequences (Hsiao and Windsor, 1999), 18S nuclear DNA (Farrell, 1995), and small subunit ribosomal DNA (Duckett et al., 2004). These are the earliest explorations of a wide pool of potential molecular markers, and it is premature to determine what each sequence together or in combination reveals about chrysomelid phylogenies or at what level they are most effective. In some other insect

groups, where molecular systematics is more advanced, it is evident that certain sequences work better at lower or higher taxonomic levels because of differential rates of evolution. For example, Danforth et al. (2004) have found that mitochondrial sequences are not the best choice for recovering deep divergences in bees.

All of the recent cladistic studies help narrow the range of phylogenetic hypotheses for higher-level chrysomelid relationships. They collectively provide a context for lower level research, as evidenced by studies of Galerucinae s.l. (Lingafelter and Konstantinov, 2000; Kim et al., 2003; Gillespie et al., 2003; Duckett et al., 2004; Gillespie et al., in press), new world Criocerinae (Vencl and Morton, 1999; Vencl et al., 2004), Cryptocephalinae (Gómez-Zurita et al., 1999; Termomia et al., 2006), Cassidinae (Borowiec, 1995; Hsiao and Windsor, 1999; McKenna and Farrell, 2005), and Eumolpinae (Gómez-Zurita et al., 2005).

MONOPHYLY OF CASSIDINAE

A large body of evidence points to monophyly of Cassidinae s.str. + Hispinae s.str. The fundamental synapomorphies of Cassidinae mentioned above are the ventral position of mouth, loss of tarsomere IV (tarsal formula 4-4-4), and close anteroventral insertions of antennae in adults.

Other characters have been proposed in support of Cassidinae, but comparisons with extensive taxon samples have not been conducted to demonstrate precisely their distribution within Cassidinae and Chrysomelidae. Adult characters include: stridulatory file on head (Schmitt, 1989); procoxae not markedly projected (shared with Galerucinae s.l. and Chrysomelinae) (Chen, 1940); tarsomere III deeply-lobed (Schmitt, 1989); tarsomeres I–III with basal pads and bifid tarsal setae (shared with Bruchinae, Sagrinae, Criocerinae, and Donaciinae), although not on the same segments (Stork, 1980; Mann and Crowson, 1981a; Schmitt, 1989); hindwing with vein Cu_1 continuous or almost continuous with second anal cell (Chen, 1940; Suzuki, 1994) and with vein cu_{1b} forming $2Cu_c$ (shared with Cryptocephalinae, Lamprosomatinae, and Eumolpinae)

(Suzuki, 1994); shape of the furcal arms of the metendosternite (shared with Lamprosomatinae) (Crowson, 1938, 1945, 1946); abdominal ganglia 5 separated from the fused ganglia of abdominal segments 6, 7, and 8 (Mann and Crowson 1983b); abdominal sterna III–IV connate (Riley et al., 2002); male genitalia with tegmen dorsoventrally flattened (shared with Eumolpinae) (Chen, 1940); male internal sac shorter than the median lobe (Chen, 1940); male internal sac with bulges (number and arrangement shared with Sagrinae) (Mann and Crowson, 1996a); an elongate, stout flagellum enveloped in supporting folds (shared with Sagrinae, Donaciinae, and Criocerinae) (Mann and Crowson, 1996b); ejaculatory tube in addition to the ejaculatory duct (shared with Eumolpinae) (Barber, 1946); vagina bell-shaped and with a long tubular spermathecal gland (Kasap and Crowson, 1980); Xy_p sex chromosome system (shared with Criocerinae and Donaciinae) (Petitpierre, 1989); karyotype $2n = 16-18$ (shared with Criocerinae) (Petitpierre, 1989); and support from 12S mtDNA and 18S mtDNA (Hsiao, 1994a, 1994b, 1994c; Hsiao and Windsor, 1999).

Larval characters argued as support for a monophyletic Cassidinae include multiple lateral stemmata (Mann and Crowson, 1981), three-segmented antenna (Mann and Crowson, 1981), mandible dentate, with two to five teeth (Böving and Craighead, 1931) (shared with Bruchinae) (Lee, 1993), maxilla with two palpomeres (Böving and Craighead, 1931), and the first instar lacking egg-bursters or hatching spines (shared with Galerucinae, Synetinae, and Donaciinae) (Lee, 1993; Cox, 1994). These character hypotheses need reevaluation with examination of many species. Some are clearly not homologous; for example, egg-bursters refer to setae, spines, and tubercles located on diverse body segments (van Emden, 1946).

For my study of sister-subfamily and internal relationships of Cassidinae, I use Seeno and Wilcox's (1982) arrangement as the starting point since this was the most recent and most commonly used comprehensive treatment of the subfamily, tribal and generic arrangement of Chrysomelidae. Under this scheme, Cassidinae s.str. includes 159 genera arranged into 19 tribes, and Hispinae

s.str. includes 168 genera arranged into 24 tribes with *Cladophora* Dejean as incertae sedis. The attribution of these group names may need reevaluation to ensure their accordance with the ICZN code. Because researchers have traditionally focused exclusively on either Cassidinae s.str. or Hispinae s.str., the historical literature is separated and is therefore reviewed separately in the following two sections.

MONOPHYLY AND CLASSIFICATION OF CASSIDINAE S.STR.

Linnaeus (1758) first named *Cassida* (Latin for helmet). This was followed by a period of descriptions of new species and genera by Fabricius (1801), Chevrolat (1837), Hope (1840), Chevrolat and Duponchel (1843), Sturm (1843), Guérin (1835), and Erichson (1847). Boheman's four monographs (1850–1855) were significant because they synthesized information from the previous century. Because he presented the first classification of genera, Chapuis (1875) has been designated the "Father of Cassidinae" (Seeno and Wilcox, 1982). Another period of new genera and species descriptions followed, especially in works by Weise (1893–1921) and Maulik (1916–1948b).

Franz Spaeth's 124 publications on Cassidinae s.str. during 1898–1943, being comprised primarily of species lists and new descriptions, underlie our understanding of cassidine diversity (Hincks, 1950a, 1950b; Borowiec, 1995; Staines, 2005). His catalogue (Spaeth, 1914) recognized three cassidine tribes but he subsequently followed Chapuis' tribal groupings. Unfortunately, his large integrative manuscript was lost during a 1942 bombing in Vienna (Hincks, 1950b, 1952; Riley, 1986). The University of Manchester bought an incomplete manuscript, along with his extensive specimen collection (Hincks, 1951). Hincks (1952) distilled Spaeth's manuscript as a diagnostic key to tribes; this treatment did not adequately establish tribal boundaries because diagnoses were brief, being based on a limited number of characters, and were sometimes incorrect (e.g., Borowiec [1995] pointed out the morphological inaccuracy of the first couplet). In his review of Spaeth's body of work, Staines

(2005) found that many species names proposed by Spaeth are unacceptable. All species and group names in Cassidinae must be reevaluated in future revisionary works.

Since the 1950s, individual tribal treatments have been produced for Aspidimorphini Hincks (Borowiec, 1992, 1997b), Eugenysini Hincks (Viana, 1968), Goniocheniini Hincks (Viana, 1964b), Hemisphaerotini Hincks (Spaeth, 1929; Monrós and Viana, 1951; Chaboo and Nguyen, 2004), and Omocerini Hincks (Viana, 1964a). Some included keys to genera and species.

The generic and tribal arrangement published by Seeno and Wilcox (1982) was modified with the synonymy of Aspidimorphini Chapuis (Borowiec, 1994a), Charidotini Hincks, and Cassidini Gyllenhal (Riley, 1986). Cassidini is currently the largest cassidine tribe with approximately 1000 species (one third of cassidine diversity), and it is the only tribe whose members are found worldwide. The Seeno and Wilcox (1982) arrangement was further modified with the synonymy of Ischyrosonychini Chapuis and Asterizini Hincks with Physonotini Hincks (Borowiec, 1999; Riley et al., 2002); however, no character argumentation was presented and two different tribal names are currently used, Physonotini Hincks (Borowiec, 1999) and Ischrysonoychini Chapuis (Riley et al., 2002). Medvedev and Eroshkina (1988) transferred Notosacanthini Hincks to Hispinae s.str. based on its mining larvae, but this has been subsequently ignored (e.g., Borowiec, 1999).

Faunal studies of Cassidinae s.str. have been documented at several geographic scales. The North American fauna is moderately well known due to low species diversity and the attention of several specialists (Drury, 1879; Blatchley, 1910; Barber, 1916; Fattig, 1948; Wilcox, 1954, 1964; Arnett, 1968; Balsbaugh and Hayes, 1972; Riley and Enns, 1979; Riley et al., 2002; Riley et al., 2003). Blackwelder (1946) is still a valuable checklist for the Caribbean and South and Central American fauna. Central and South American cassidine faunistics exist for Central America (Champion, 1893, 1894) as well as for the individual countries of Argentina (Burmeister, 1870; Viana, 1964, 1968), Costa Rica (Chaboo, 2003; Flowers and Hanson,

2003), Cuba (Zayas, 1939, 1952, 1988), French Guiana (Borowiec and Moragues, 2005), Haiti (Wolcott, 1927), Mexico (Noguera, 1988), Nicaragua (Maes and Tellez Robleto, 1988; Maes and Staines, 1991), Panama (Windsor et al., 1992), Paraguay (Fiebrig 1910), Puerto Rico (Wolcott, 1923, 1936), Trinidad and Tobago (Chaboo and Borowiec, 2003), and Venezuela (Freude, 1949).

Old World faunal studies are available for Afghanistan (Gruev, 1988), Arabia (Bryant, 1957), Africa (Bryant, 1959; Heron and Borowiec, 1997; Boroweic, 1994, 1997b, 2002; Świętojańska, 2001; Rice, 2003; Heron, 2003, 2004a), Bengal (Sumana and Raychaudhuri, 1997), Cambodia (Baly, 1866; Kimoto and Gressitt, 1979; Kimoto, 1998), Canary Islands (Wollaston, 1864, 1865), Central Asia (Lopatin, 1977), China (Gressitt, 1952; Gressitt and Kimoto, 1963; Chen et al., 1986), Greece (Gruev, 1990), India (Maulik, 1919; Ghate and Rane, 2002), Indonesia (Spaeth, 1900; Kimoto, 1998), Iraq (Gruev, 1995), Israel (Borowiec, 1997a), Japan (Kimoto and Takizawa, 1994), Kazakhstan (Lopatin, 1977), Korea (Gressitt and Kimoto, 1961a, 1961b), Laos (Kimoto and Gressitt, 1979; Kimoto, 1988), Malaysia (Mohamedsaid, 2004), Micronesia (Gressitt, 1955), Nepal (Medvedev, 1990), New Guinea (Masters, 1889; Weise, 1917), Pakistan (Abdullah and Qureshi, 1969), Philippines (Baer, 1886), Korea (Gressitt and Kimoto, 1963; An et al., 1985a, 1985b; Gruev, 1990), South Africa (Borowiec, 2005), Taiwan (Kimoto and Takizawa, 1997), Thailand (Baly, 1866; Kimoto and Gressitt, 1979; Kimoto, 1998), Turkey (Aslan and Özbek, 1997), Vietnam (Kimoto and Gressitt, 1979; Medvedev, 1982; Kimoto, 1988), parts of Asia (Gressitt, 1939, 1952, 1963; Bryant and Gressitt, 1957; Borowiec, 2001), parts of the former Soviet Union (Palij and Klepikova, 1957), and Java (Kimoto et al., 1995).

At present, Lech Borowiec (Poland) is systematically recording cassidine distributions and describing new species. His (1999) catalog of Cassidinae s.str. minus Imatidiini summarized the literature to date, known species distributions, and known host records, and he presented novel tribal synonymies. This catalog and its frequently up-

dated website (Borowiec and Świętojańska, 2005) should catalyze a new level of research.

MONOPHYLY AND CLASSIFICATION OF HISPINAE S.STR.

Linnaeus (1758) coined the name *Hispa* (Latin for prickly). Chevrolat (1834–1837), Chevrolat and Duponchel (1843), Fabricius (1775–1904), Guérin (1835–1855), Gyllenhal (1813), Hope (1840), Perty (1832), Thompson (1856–1868), and Thunberg (1805) all contributed genera and species during the next 100 years. Baly (1858) made the first attempt to integrate this information, having described 25 new genera. This work was extended through catalogs and faunistic works (Chapuis, 1875; Gemminger and Harold, 1876; Bryant, 1885; Champion, 1894; Donckier, 1899).

Weise (1911–1913) monographed 60 hispine genera and subgenera, and he laid the foundation for the modern tribal classification of Hispinae s.str. Würmli (1975) provided an illustrated key to the 14 Old World tribes, 84 genera, and 9 subgenera and revised the Old World tribe Botryonopini Weise (Würmli, 1976a). Weise (1911), Baly (1885, 1886) and Würmli (1975) remain the most comprehensive publications in Hispinae s.str.

Faunal treatments of New World hispines are available for the entire region (Uhmann, 1957a), North America (Staines, 2006), Central America (Baly, 1885, 1886), South America (Uhmann, 1932), Argentina (Monrós and Viana, 1947), Brazil (Uhmann, 1935a), Costa Rica (Uhmann, 1930; Flowers and Hanson, 2003; Staines, 1997b), Nicaragua (Staines, 1996b, 2002b), Paraguay (Uhmann, 1935b), West Indies (Sanderson, 1967), and Trinidad and Tobago (Callan, 1954). North American regional works are also available (Drury, 1879; Horn, 1882; Blatchley, 1910; Arnett, 1963; Staines, 1997a; Riley, 1986; Riley et al., 2002; and Wilcox, 1955).

Old World Hispinae s.str. faunistics have been studied in Afghanistan (Gruev, 1988), Arabia (Bryant, 1957), Africa (Bryant, 1959), Cambodia (Kimoto and Gressitt, 1979; Kimoto, 1988), Canary Islands (Wollaston, 1864), Central Asia (Lopatin, 1977), China

(Gressitt, 1939, 1942, 1950, 1952, 1953; Gressitt and Kimoto, 1963; Uhmman, 1955a), Congo (Uhmman, 1967), Greece (Gruev, 1990), India (Maulik, 1919, 1937), Indonesia (Uhmman, 1955b; Kimoto, 1998), Japan (Kimoto and Takizawa, 1994), Kazakhstan (Lopatin, 1977), Korea (Gressitt and Kimoto, 1963), Laos (Kimoto and Gressitt, 1979; Kimoto, 1988), Madagascar (Gestro, 1909; Uhmman, 1960), Malaysia (Mohamedsaid, 2004), Micronesia (Gressitt, 1955), Nepal (Medvedev, 1990), New Guinea (Masters, 1889; Weise, 1917), Pakistan (Abdullah and Qureshi, 1969), Philippines (Baer, 1886), Taiwan (Kimoto and Takizawa, 1997), Thailand (Kimoto and Gressitt, 1979; Kimoto, 1998), Togo (Kraatz, 1895), Vietnam (Kimoto and Gressitt, 1979; Kimoto, 1988), and the South Pacific and New Guinea (Gressitt, 1957, 1960, 1963).

Tribal treatments are available for Alurnini Weise (Fischer, 1935), Aroidini Weise (Samuelson, 1989), Botryonopini (Würmli, 1975a), and Sceloenoplini (Staines, 2002a). Butte (1968a, 1968b, 1968c, 1969) and Ramos (1996) revised genera of Chalepini Weise. Chalepini and Uroplatini Weise have been recently synonymized as Uroplatini (Riley et al., 2001; Staines, 2002b). Oediopalpini Monrós and Viana was also synonymized with Spilophorini Chapuis (Staines, 2002b), and Imatiidini Hincks has been synonymized with Cephaloleiini Weise (Staines, 2002b). These synonymies were necessitated by ambiguous morphological character diagnoses. Altogether, Staines (2002b) listed 11 tribes and 100 genera for the New World hispines. Species treatments are available for *Alurnus* Fabricius, *Cephaloleia* Chevrolat (Staines, 1996; McKenna and Farrell, 2005), *Chaeridiona* Baly (Würmli, 1976b), *Coraliomela* Jacobson, *Mecistomela* Jacobson, *Oychalepus* Uhmman (Ramos, 1998), *Microrhopala* Dejean (Clark, 1983), and *Pseudocalaspidea* Jacobson (Fischer, 1935).

Discussion of tribal relationships has been limited. Weise (1905) pointed out the division of Old and New World faunas and suggested that American tribes are more advanced than Old World tribes. Alurnini has been regarded as the most primitive tribe, based on the presence of sensory bristles on the pronotal

angles and presumed vestigial nervation of the elytra (Weise, 1910; Fischer, 1935; Monrós and Viana, 1947).

CASSIDINAE S.STR. AND HISPINAE S.STR.: TWO DISTINCT CLADES?

The boundary is ambiguous between Cassidinae s.str. and Hispinae s.str. because a number of taxa exhibit intermediate features (Chapuis, 1875; Maulik, 1919; Crowson, 1953, 1955, 1967), particularly in the immature stages (Sanderson, 1902; Böving and Craighead, 1931; Gressitt and Kimoto, 1961a, 1961b; Lawrence, 1982, 1991; Jolivet and Hawkeswood, 1995). In these publications, cassidine larvae were considered as external leaf-feeders, whereas hispine larvae were considered as miners or cryptic feeders. The larval eight abdominal spiracles were considered vestigial in Cassidinae s.str. but developed in Hispinae s.str. Sanderson (1902) stated that cassidine larvae have the last abdominal tergum modified with a caudal process whereas hispine larvae lack this modification, and cassidines retain fecal shields on these processes whereas hispine larvae carry no shields. These distinctions were conceptualized early in the history of Cassidinae and have not been reevaluated or have become invalid as more taxa have become known.

Placement of certain taxa is controversial because their adults and larvae display a combination of these classical cassidine and hispine features. Such enigmatic taxa include the hispoid *Oediopalpa negligens* (Weise) whose larvae are free-living and retain a shield (Bruch, 1906). Notosacanthini (broadly flattened animals) was long classified in Cassidinae s.str. based on adult morphology; discovery of their mining larvae led to the tribe's transfer to Hispinae s.str. (Medvedev and Eroshkina, 1988). Borowiec (1999) nonetheless maintained Notosacanthini under Cassidinae s.str. *Plautyauchenia* Sturm was placed in Cassidinae s.str., but larval morphology suggests its position in the hispine Alurnini Weise (Maulik, 1933). Placement of *Delocrania* Guérin-Ménéville in Cassidinae s.str. has also been questioned (Maulik, 1919, 1933), although all subse-

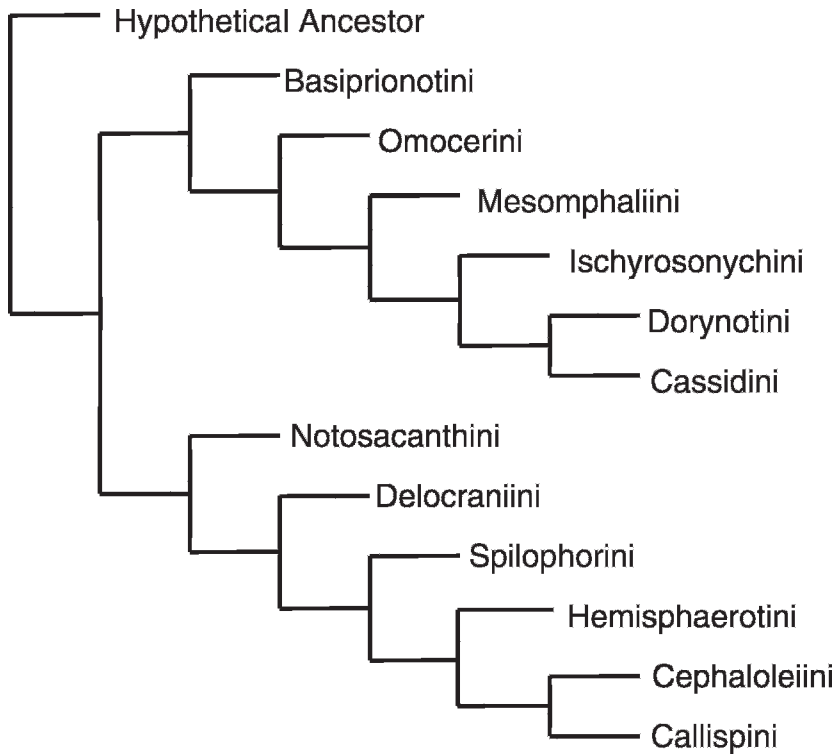


Fig. 3. Phylogenetic hypothesis for Cassidinae proposed by Borowiec (1995) based on analysis of 12 tribal terminals, a hypothetical ancestor as outgroup, and 19 characters (5 autapomorphies, 11 binary and 3 multi-state).

quent classifications of Cassidinae s.str. have included *Delocrania*.

Borowiec (1995) presented the first modern phylogenetic analysis of Cassidinae. This study used 19 binary characters—14 adult morphological characters, 3 larval morphological characters, 1 larval behavioral character, and 1 host plant character. The morphological characters, derived mostly from Hincks (1952), were scored for nine cassidine tribes, two hispinae tribes and an all-zero hypothetical ancestor. The use of higher taxa as terminals does not test monophyly of those groups and limits the range of characters that could be sampled. The single published tree (fig. 3) indicated that Cassidinae s.str. and Hispinae s.str. were paraphyletic with respect to each other. Five of the 19 characters were uninformative autapomorphies, which do not resolve relationships (Hennig, 1966). Borowiec (1995) synonymized Cassidinae s.str. and Hispinae s.str.

as Hispinae s.l. without discussing the name priority. In his subsequent world catalog of Cassidinae s.str., Borowiec (1999) reerected the traditional name Cassidinae sensu Seeno and Wilcox (1982), omitted the tribe Imatidiini, and rearranged the 15 remaining tribes into 12 tribes. No argument was made for his novel arrangement nor any explanation offered for the obvious contradictions with his earlier phylogenetic concept and nomenclature.

Hsiao and Windsor (1999) used 12S mtDNA in their phylogenetic analysis of 48 species representing 18 tribes of Cassidinae s.str. and Hispinae s.str., and they presented two alternative hypotheses of Cassidine relationships (fig. 4A, B). They concluded that Cassidinae s.str. and Hispinae s.str. were each paraphyletic and synonymized them as Hispinae s.l. This study initiated the use of molecules for cassidine systematics; however, problems in analysis and taxon sampling

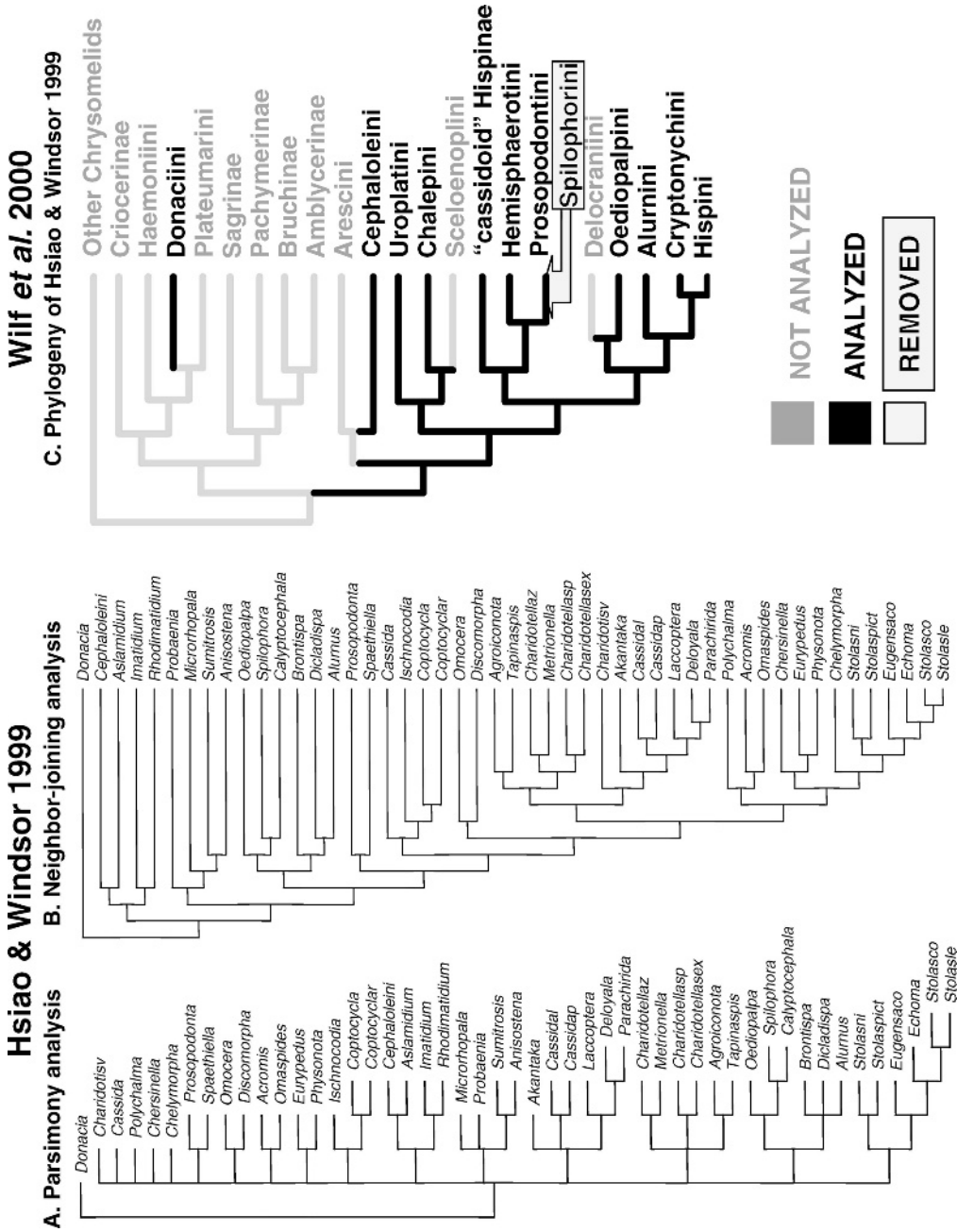


Fig. 4. **A, B.** Phylogenetic hypotheses for Cassidinae proposed by Hsiao and Windsor (1999) based on 48 taxa, Donaciinae as outgroup, and 12s mtDNA data. **C.** Phylogeny presented by Wilf et al. (2000).

undermine the proposed hypothesis. Of the ca. 450–535 aligned bases used it is unclear how many were actually informative. A single outgroup, Donaciinae, was included, despite the equal likelihood of multiple possibilities from other cladistic studies (e.g., Lee, 1993; Reid, 1995; Farrell, 1998) and the apparent contradiction with Hsiao's (1994a) earlier study that resolved Orsodacninae as sister to Cassidinae s.str. + Hispinae s.str. Outgroup selection influences polarity of ingroup states, so a different selection or, even better, an expanded set of outgroups could change their topology. By selecting only the aquatic Donaciinae, Hsiao and Windsor (1995) constrained their analysis to support a conclusion of an aquatic ancestor of Hispinae s.l. + Donaciinae. The ingroup taxon sample comprised one Old World species and 47 Panamanian species, including four *Stolas* Billberg species, three *Charidotella* Weise species, and three *Cassida* species. These latter three genera were found to be polyphyletic, a result suggesting that the sequence choice may not be conservative enough to be phylogenetically meaningful at tribal levels. The sampling of 18 of the 43 recognized tribes, and the bias towards Panamanian taxa, missed important taxonomic and geographic diversity. Both parsimony and neighbor-joining were used to develop tree topologies. The consensus derived by parsimony was poorly resolved with a large basal polytomy (fig. 4A). Instead of reevaluating their data, Hsiao and Windsor (1999) did a neighbor-joining analysis and selected that result as the basis of their phylogenetic and evolutionary discussions (fig. 4B). Farris et al. (1996) have already demonstrated inadequacies in the neighbor-joining method (e.g., finding only one exact solution) and the existence of better methods (jackknifing).

Wilf et al. (2000) altered the Hsiao and Windsor (1999) neighbor-joining topology by adding terminals to represent six chrysomelid outgroup subfamilies and four Cassidine tribes, Delocraniini, Chalepini, Sceloenoplini, and Uroplatini (fig. 4C). These taxa were inserted into the topology of Hsiao and Windsor (1999) based on opinion, and no sequence data were submitted to Genbank (as of 2007). Although no reanalysis was

done, phylogenetic structure was found among outgroups. The host plant evolutionary scenario constructed by Wilf et al. (2000) is intriguing, and it is unfortunate that this *Science* cover story was built on a contrived dataset.

Borowiec (1995) and Hsiao and Windsor (1999) provided two alternative phylogenetic hypotheses:

1. Hispinae s.str. as monophyletic, nested among traditional cassidine tribes (Borowiec, 1995).
2. Hispinae s.str. as polyphyletic, with three clades nested among plesiomorphic cassidine (Hsiao and Windsor, 1999).

Currently, there are several competing classification schemes for Cassidinae s.str. and Hispinae s.str.: the classical one (Seeno and Wilcox, 1982), two recent schemes based on weakly supported phylogenetic hypotheses (Borowiec, 1995; Hsiao and Windsor, 1999), and the scheme proposed in the catalog of Cassidinae s.str. (Borowiec, 1999).

FUNDAMENTAL NOMENCLATURE ISSUES

The lack of a well-supported phylogenetic hypothesis has created many nomenclatural problems. Borowiec (1995) and Hsiao and Windsor (1999) arrived at different topologies, but agreed that Cassidinae s.str. and Hispinae s.str. were paraphyletic, and that the unified clade should be called Hispinae s.l. Borowiec (1995) provided no argumentation for selecting the name Hispinae s.l. over Cassidinae. Hsiao and Windsor (1999) justified their choice as a convention supposedly established by Crowson (1955), Lawrence and Britton (1994) and Reid (1995). (Crowson [1955] is a collection of papers that appeared in the *Entomologist's Monthly Magazine* during the 1950s; chrysomelid relationships were discussed in Crowson [1953] and that text was reproduced exactly in Crowson [1955, 1967]). Crowson (1953) used the name Hispinae for Cassidinae + Hispinae, but in subsequent publications he recognized both Cassidinae s.str. and Hispinae s.str. as distinct entities (Crowson, 1981; Mann and Crowson, 1981, 1983, 1986). In any case, the first revisor of Chrysomelidae was Chen (1940) and we must follow his convention (article 24.2, ICZN [2000]).

Lawrence and Britton (1994) recognized Cassidinae, but Lawrence (1982, 1991) recognized Cassidinae s.str. and Hispinae s.str. Reid's (1995) use of Hispinae s.l. for Cassidinae s.str. + Hispinae s.str. was for convenience of analysis (C. Reid, personal commun.). "Cryptostomes" appears to be the closest to a conventional name for the clade Cassidinae s.str. + Hispinae s.str.

Several group terms are currently in use: Cassidinae s.str.; Hispinae s.str.; "hispid Hispinae" (Borowiec, 1995; Hsiao and Windsor, 1999); "cassidoid Hispinae" (Heron and Borowiec, 1997; Hsiao and Windsor, 1999; Wilf et al., 2000). Use of the terms "hispid Hispinae" and "cassidoid Hispinae" is not recommended as these lack any apomorphic support and are not natural groups. The "-oid" suffix is also poorly since as it implies superfamily rank. As stated earlier, Cassidinae is used here after Chen (1940) for the clade Cassidinae s.str. + Hispinae s.str.

TRIBAL RELATIONSHIPS OF CASSIDINAE

Ambiguous tribal boundaries have been discussed: Cassidini Hincks, Charidotini Hincks, Aspidimorphini Hincks, and Basipitini Hincks (Riley, 1986; Borowiec, 1999; Riley et al., 2002); Goniocheniini Hincks and Omocerini Hincks (Viana, 1968; Seeno and Wilcox, 1982); Physonotini Hincks, Asterizini Hincks, and Ischyrosynychini Hincks (Seeno and Wilcox, 1982; Borowiec, 1999; Riley et al., 2002); Stolaini Hincks and Eugenysini Hincks (Seeno and Wilcox, 1982); Aprodini Weise and Eurispini Weise (Würmli, 1975a; Samuelson, 1968, 1989); Alurnini Weise (Maulik, 1933a, 1933b); Cephaloleiini Weise and Arescini Weise (Strong, 1977a); Notosacanthini Hincks and Aspidimorphini Hincks (Hawkeswood, 1989); Notosacanthini Hincks, Epistictini Hincks, and Basiprionotini Hincks (Zaitzev and Medvedev, 1982; Borowiec and Świątojańska, 2004); Delocraniini Hincks, Notosacanthini Hincks, Hemisphaerotini Hincks, and Spilophorini Hincks (Monrós and Viana, 1951); and Imatidiini Hincks and Cephaloleiini Weise (Spaeth, 1914, 1938; Bondar, 1940c; Blackwelder, 1946; Monrós and Viana, 1947, 1951; Papp, 1953; Aslam, 1965; Uhmman, 1957; Seeno and Wilcox,

1982; Windsor et al., 1992; Borowiec, 1995, 1999; Hsiao and Windsor, 1999; Borowiec, 2000; Wilf et al., 2000; McKenna and Farrell, 2005). Only the synonymy of Aspidimorphini, Charidotini and Cassidini appears to be generally accepted. Duckett et al.'s (2004) finding of Imatidiini as sister to Cryptocephalinae and separated from other cassidines needs reconsideration.

Confusion about the monophyly, positions, relationships and taxonomic names of groups stems from several factors. Historically there has been no more than one specialist of Hispinae s.str. per generation; the retirement of Charles Staines, the principal current authority, has resulted in his greater productivity. Expertise on Cassidinae s.str. has been marginally better, and currently there are several active taxonomic researchers. In general, a new generation of specialists must be trained, as in any other taxonomic group. Morphological systematics in Cassidinae has been limited and few phylogenetic characters have been proposed. Molecular systematics is a novel and rapidly evolving field but promises an explosion of genomic data. Ecological and behavioral data await exploration. The research tradition has been separated along subfamily lines and/or along geographic lines (Old World versus New World) and thus characters have not been optimized across the entire group, much less across all relevant outgroups. Consequently, traditional characters tend to become ambiguous as more taxa are compared. Expanding and refining the character dataset is critical to resolving systematics issues.

BIOLOGY OF CASSIDINAE

Biological information on Cassidinae has historically been treated separately for the two subfamilies, Cassidinae s.str. and Hispinae s.str. Information is widely scattered in a primary literature largely consisting of single species accounts. Given growing support for a single monophyletic clade, it is appropriate to develop an integrated, synthetic account of cassidine biology. In the following discussion I use group concepts as outlined in the Introduction; that is, Cassidinae refers to the classical Cassidinae s.str.

(tortoise beetles) + Hispinae s.str. (hispines; leaf-mining beetles). Because many species are discussed, genus and species names are provided throughout, with authors cited at first mention only. Species names are consistent with the most recent catalogs: Borowiec (1999) for Cassidinae s.str.; Papp (1975) for New World Hispinae s.str.; and Würmli (1975) and Weise (1911a) for Old World Hispinae s.str. Recent synonymies of names are indicated in brackets. Plant names conform to the online plant catalogue, W3Tropicos, maintained by the Missouri Botanical Garden (2004).

Some aspects of cassidine biology were summarized in recent multiauthored volumes on Chrysomelidae (Jolivet, 1988d, 1989, 1997; Jolivet and Cox, 1996; Jolivet et al., 1998, 1994, 2004; Cox, 1999; Clark et al., 2004), and in general reviews of eggs and oviposition patterns (Hinton, 1981; Hilker, 1994; Selman, 1994), British larvae (Cox, 1982), pupae (Cox, 1996a), and predators and parasites (Mariau, 1988; Cox, 1996b; Noguera-de-Sá and Vasconcellos-Neto, 1988). Insect leaf miners, including some cassidine miners, have been discussed by Needham et al. (1928), Frost (1942), Hering (1951), Hespeneheide (1991) and Hespeneheide and Dang (1996).

Maulik's (1919) account of Indian Cassidinae s.str. and Hispinae s.str. is still one of the best introductions to cassidine biology. Kosior's (1975) monograph, based on a 5-year study of nine *Cassida* species and one *Hypocassida* Weise species in Poland, is a useful introduction to temperate species. For Neotropical species of Cassidinae s.str., Buzzi (1998) provided brief summaries for 21 species, Windsor et al. (1992) focused on Panamanian species, and Noguera-de-Sá et al. (2004) summarized their investigations on eight Brazilian species. Borowiec (1999) and Borowiec and Świętojańska (2004) cataloged Cassidinae s.str., including distributions, host plant data, and keys to the literature.

A composite biology of Cassidinae can be distilled from scattered accounts of single species such as Taylor's (1937) detailed account of *Promecotheca reichei* Baly and Garthwaite's (1939) account of *Craspedonta leayana* (Latreille). Extensive data have accumulated on the widespread Old World

genus *Aspidimorpha* Hope through research conducted in many countries spanning the last century (Maulik, 1919; Corbett and Dover, 1927; David and Muthiah, 1960; Thompson, 1964; Atkins et al., 1966; Baltazar, 1970; Verma and Kumar, 1972; Hoque and Monawar, 1976; Kumar and Attah, 1977; Mohan and Verma, 1981; Hawkeswood, 1982; Bhattacharya and Verma, 1982; Verma and Shrivastava, 1985, 1989; Nakamura, 1989; Nakamura and Abbas, 1987a, 1987b, 1989; Nakamura et al., 1989, 1994; Miah et al., 1992; Noerdjito et al., 1992; Chattopadhyay and Sukul, 1994; Borowiec, 1997b; McBride et al., 2000).

Biological information on *Cassida*, one of the largest cassidine genera, has also accumulated (Engel, 1932, 1936; Manolache et al., 1938; Nietzke, 1939; Maw, 1976; Ward and Pienkowski, 1978; Al-Ali and Abbas, 1981; Tipping, 1983; Singh and Siddhu, 1992; Ang and Kok, 1995; Ang et al., 1994, 1995; Spring and Kok, 1997; Bacher et al., 1999). Information on certain American genera is growing as several researchers are currently examining these from different angles. Ongoing research on *Physonota* Boheman and *Chelymorpha* Chevrolat (Britten et al., 2003; K. Olmstead, personal commun.) are revealing much about the ecology of those genera. *Acromis* Chevrolat has attracted attention because of its fascinating extended maternal care, extreme sexual dimorphism, and male fighting (Fiebrig, 1910; Buzzi, 1980; Windsor, 1987). A cladistic analysis (Chaboo, 2002) along with research in ontogeny (A. Trillo, personal commun.) and shield chemistry (F. Vencel, personal commun.) will lead to further understanding of this interesting genus.

Some researchers have focused on particular genera and species of Cassidinae; for example, *Coelaenomenodera* (Mariau, 1975; Mariau and Bescombes, 1971; Berti and Mariau, 1999; Mariau and Lecoustre, 2000, in press; Mariau and Morin, 1971, 1972, 1974; Mariau and Philippe, 1983), *Mecistomela marginata* Latreille (Macêdo et al., 1994), *Octuroplata octopustulata* Baly (Texeira et al., 1999), *Gratiana* Spaeth (Siebert, 1975; Friero, 1982; Friero-Costa, 1984; Hill, 1999; Hill and Hulley, 1995), and *Eurypedus nigrosignatus* Boheman (Gómez, 1997, 2004;

Gómez et al., 1999). Zundir Buzzi and his collaborators have altogether published a body of information for certain Neotropical genera; for example, *Anacassis* Spaeth (Aravena, 1959; Buzzi, 1975a, 1975b, 1983, 1996; Buzzi and Garcia, 1976; McFayden, 1987), *Dorynota* Chevrolat (Buzzi, 1976a, 1976b; Buzzi and Cruz, 1976, 1991), and *Drepanocassis* Spaeth (Buzzi and Winder, 1986a, 1986b).

In addition to these individual species and generic studies, valuable information on cassidine biology has come from studies of the ecological interactions of species. Unfortunately, Carroll's (1978) promising research with *Stolas* Billberg species on *Ipomoea* Linnaeus (Convolvulaceae; morning glories) has not developed further. Rausher et al. (Rausher, 1983, 1984; Simms and Rausher, 1989) have followed *Deloyala guttata* (Olivier) and *Charidotella* (*Charidotella*) *sexpunctata* (Fabricius) (= *Metriona bicolor* Weise; = *Charidotella bicolor* Fabricius), and they provided the first demonstration of how herbivorous insects can influence genetic diversity of host plants (*Ipomoea* in this case). The implication of this finding in host race and sympatric species formation could be further explored (Jolivet and Hawkeswood, 1995). Root and colleagues (Messina and Root, 1980; Root and Cappuccino, 1992) have followed the evolutionary ecology of diverse insects over many years, including the cassidine leaf miner, *Microrhopala* Chevrolat, on *Solidago* Linnaeus species (Asteraceae; golden rods). The biology of rolled-leaf cassidines, Arescini Weise and Cephaloleiini Weise, with their host plants, Musaceae Juss., Zingiberaceae Adans., and Heliconiaceae (A. Richard) Nakai, has become a well-studied model in tropical insect-plant associations (discussed below).

Hespenheide and Dang (1999) provided a unique perspective on the ecology of tropical cassidine leaf miners. They found that plants mined by beetles were primarily mined by larval buprestids, and secondarily by larval cassidines. These cassidines can use several hosts, contradicting a general perception of monophagy of miners, and they can share host plants with other beetle species.

A few community ecology studies on cassidines (e.g., Hespenheide and Dang,

1999), provide significant insights. Cassidines are suitable models for studying herbivore-herbivore interactions, herbivore-predator interactions (e.g., Schenk and Bacher, 2002), herbivore-parasite interactions (e.g., Morrison and Strong, 1981), and plant-insect interactions (e.g., Gómez et al., 1999). Guild structures have only been studied in those cassidines that inhabit *Heliconia* Linnaeus (e.g., Seifert, 1982). As research animals, cassidines seem easy to work on due to their relatively sedentary habits and restricted host plant choices. Larvae can be easily marked in the field (Garcia and Paleari, 1990) and age of shield-retaining larvae can be determined simply by counting exuviae within shields (Olckers and Hulley, 1989; Chaboo, 2002).

DIVERSITY

Cassidinae is the second largest clade of Chrysomelidae after Galerucinae sensu Lingafelter and Konstantinov (2000) (ca. 10,000 species) (fig. 1), and it has been classified into 43 tribes, 324 genera, and ca. 6000 species (fig. 2). Cassidine morphological, ecological and behavioral diversity are remarkable. Adults (figs. 5, 14) range in size from tiny *Oxylepus* Desbrochers (ca. 3 mm long) to the elongate *Alurnus* Fabricius (fig. 5D, >30 mm long). Larvae show a similar size range, from 1 to 40 mm long, with *Alurnus* larvae reaching >40 mm (Mariau, 2004). These large cassidines are considered among the largest herbivorous insects (Crowson, 1981). The name *Cassida* and the popular name "tortoise beetles" refer both to the rounded body shape, in which the pronotum and elytra are flared or explanate, and to the retraction of the head into the pronotum. Adults of Eugensini are the widest cassidine species, having greatly expanded elytral margins. The word "hispa" means rough and refers to the many species with spiny dorsal surfaces. More poetic names, such as "living jewels" (Maulik, 1919), reflect the diverse and attractive colors of Cassidinae.

Immature stages of insects are poorly known in general (Stehr, 1991), and cassidines are no exception. Descriptions and some biological information are available for ca. 350 species in 170 genera (appendix 2; Chaboo, unpubl. data). Eggs (fig. 15) may be

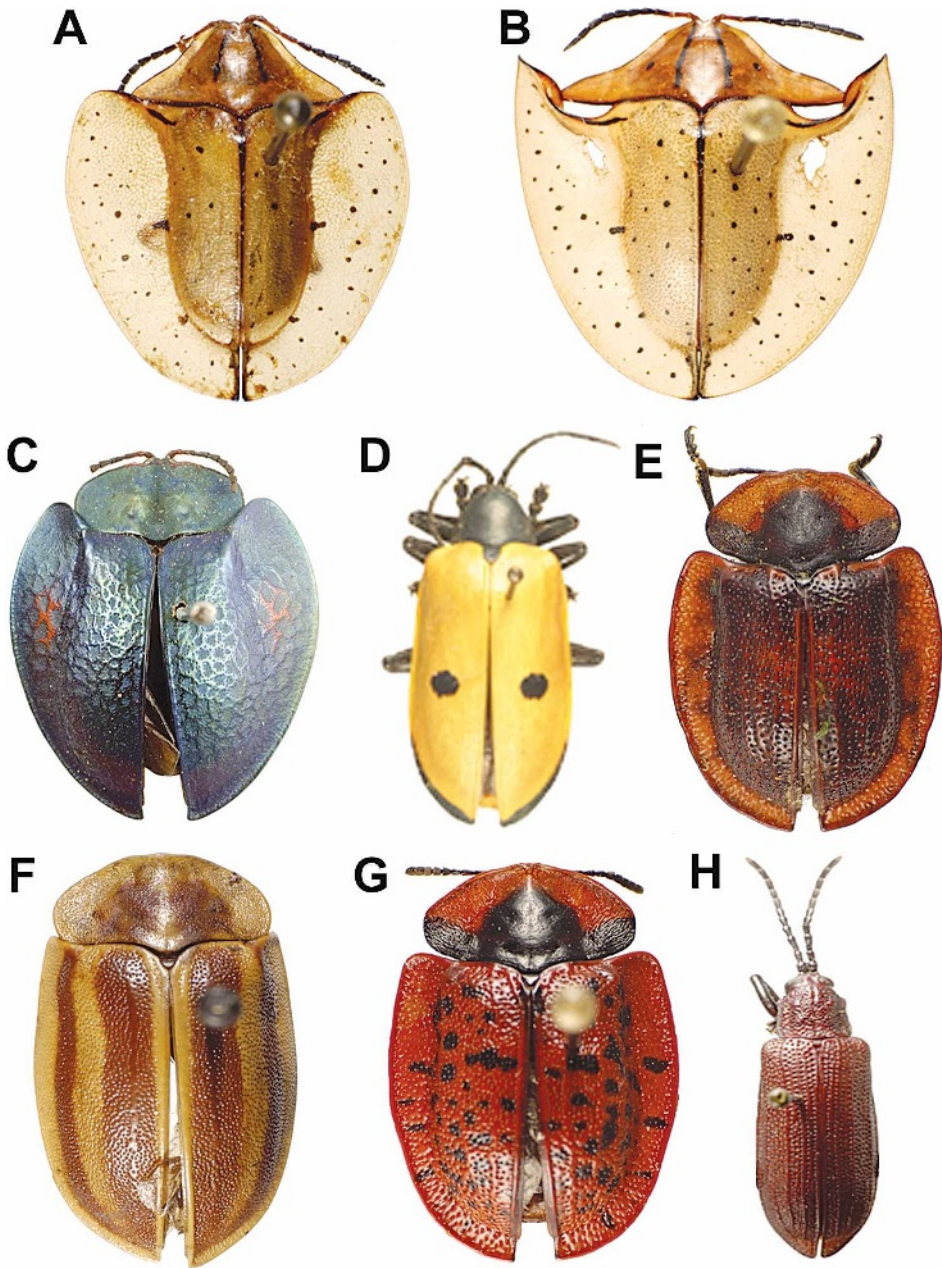


Fig. 5. Cassidinae, adults, dorsal aspect. **A.** *Acromis sparsa*, female. **B.** *Acromis sparsa*, male. **C.** *Agenysa caedemadens*. **D.** *Alurnus bipunctatus*. **E.** *Amythra reticulata*. **F.** *Anacassis fuscata*. **G.** *Anepsiomorpha deplanata*. **H.** *Anisodera guerini*.

solitary or laid in groups of widely variable numbers, and they may be naked or have elaborate oothecal coverings (Hilker, 1994), chewed plant fragments (Taylor, 1937), or adhesive coatings that help attach soil and

debris (Stammer, 1936b; Crowson, 1981). The female may coat the upper pole of each egg with gut symbionts; newly hatched larvae consume these symbionts and are thus infected (Stammer, 1936b; Peterson and

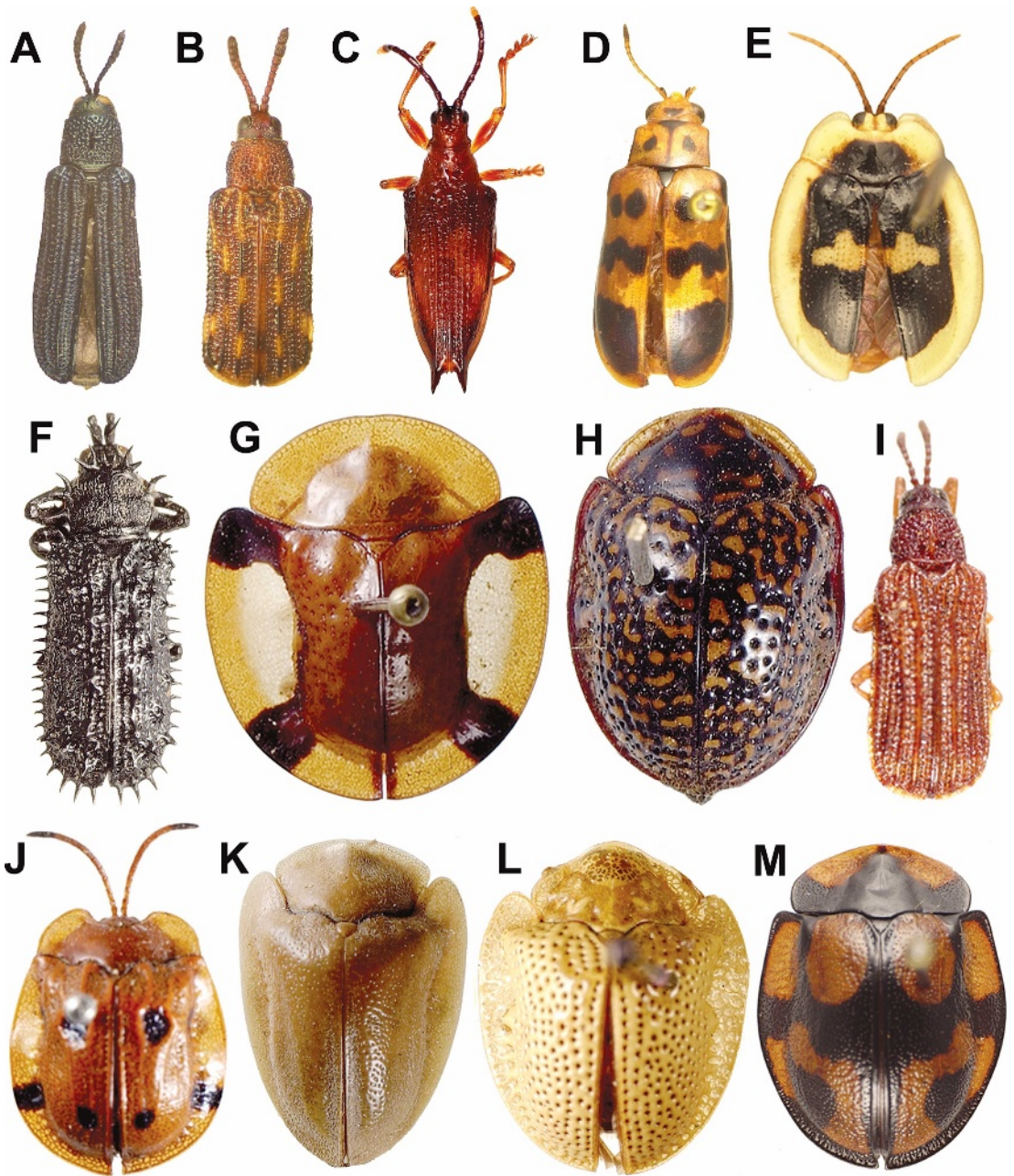


Fig. 6. Cassidinae, adults, dorsal aspect. A. *Anisostena perspicua*. B. *Anoplites inaequalis*. C. *Aproidea balyi*. D. *Arescus* sp. E. *Aslamidium* sp. 4 (Costa Rica). F. *Asamangulia cuspidata*. G. *Aspidimorpha quadrinodosa*. H. *Asteriza flavicornis*. I. *Baliosus californicus*. J. *Basiprionota quadriimpressa*. K. *Basipta glauca*. L. *Batonota lerouxii*. M. *Botanochara angulata*.

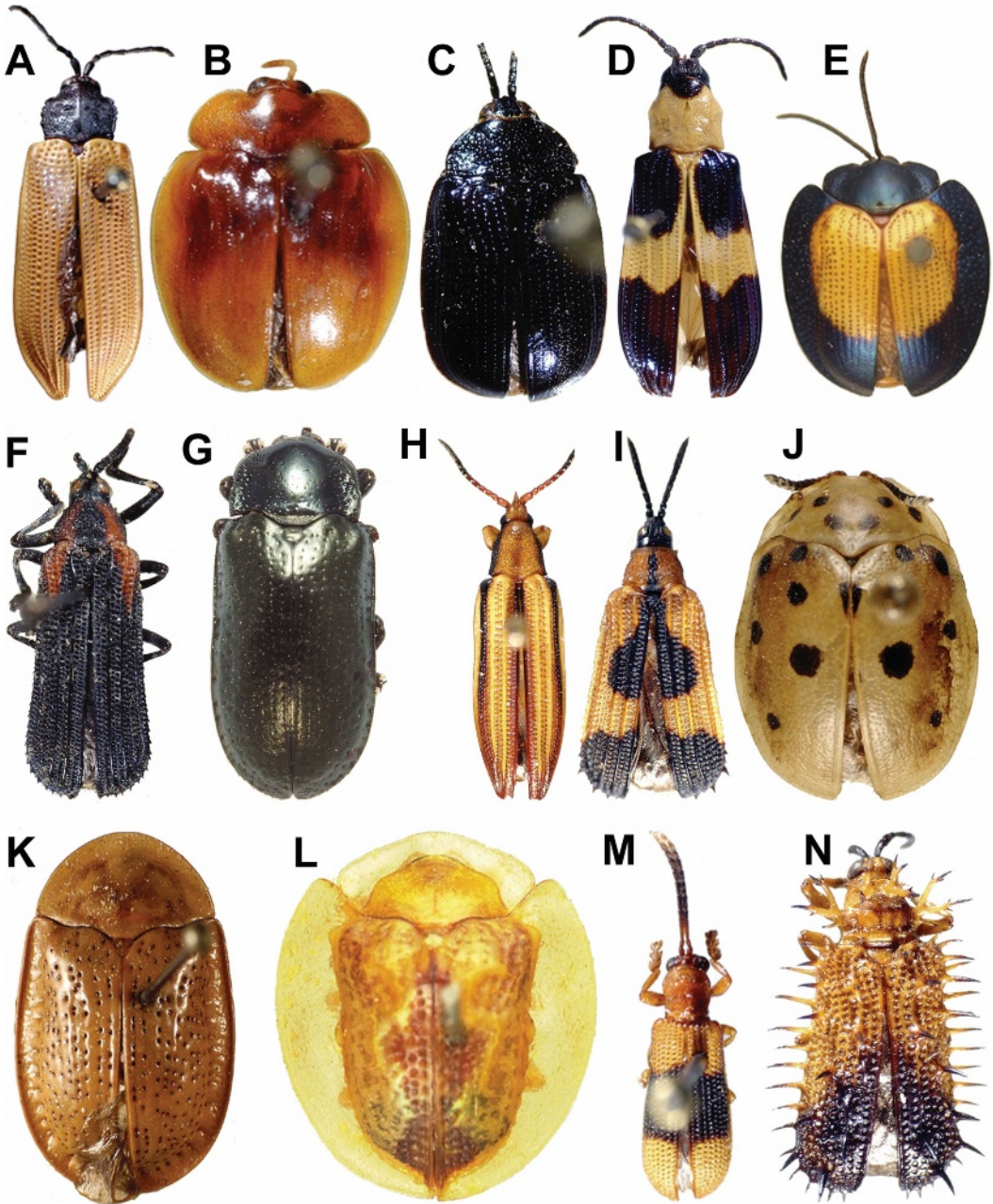


Fig. 7. Cassidinae, adults, dorsal aspect. A. *Botryonopa foveicollis*. B. *Calliaspis rubra*. C. *Callispa bowringi*. D. *Callistola speciosa fasciata*. E. *Calyptocephala discoidea*. F. *Cephalodonta* sp. G. *Cephaloleia* sp. H. *Ceratispa palmicola*. I. *Chalepus* sp. J. *Chelymorpha cassidea*. K. *Conchylotenidia hybrida*. L. *Coptocycla dorsoplagiata*. M. *Cyperispa thoracostachyi kolombangana*. N. *Dactylispa angusta*.

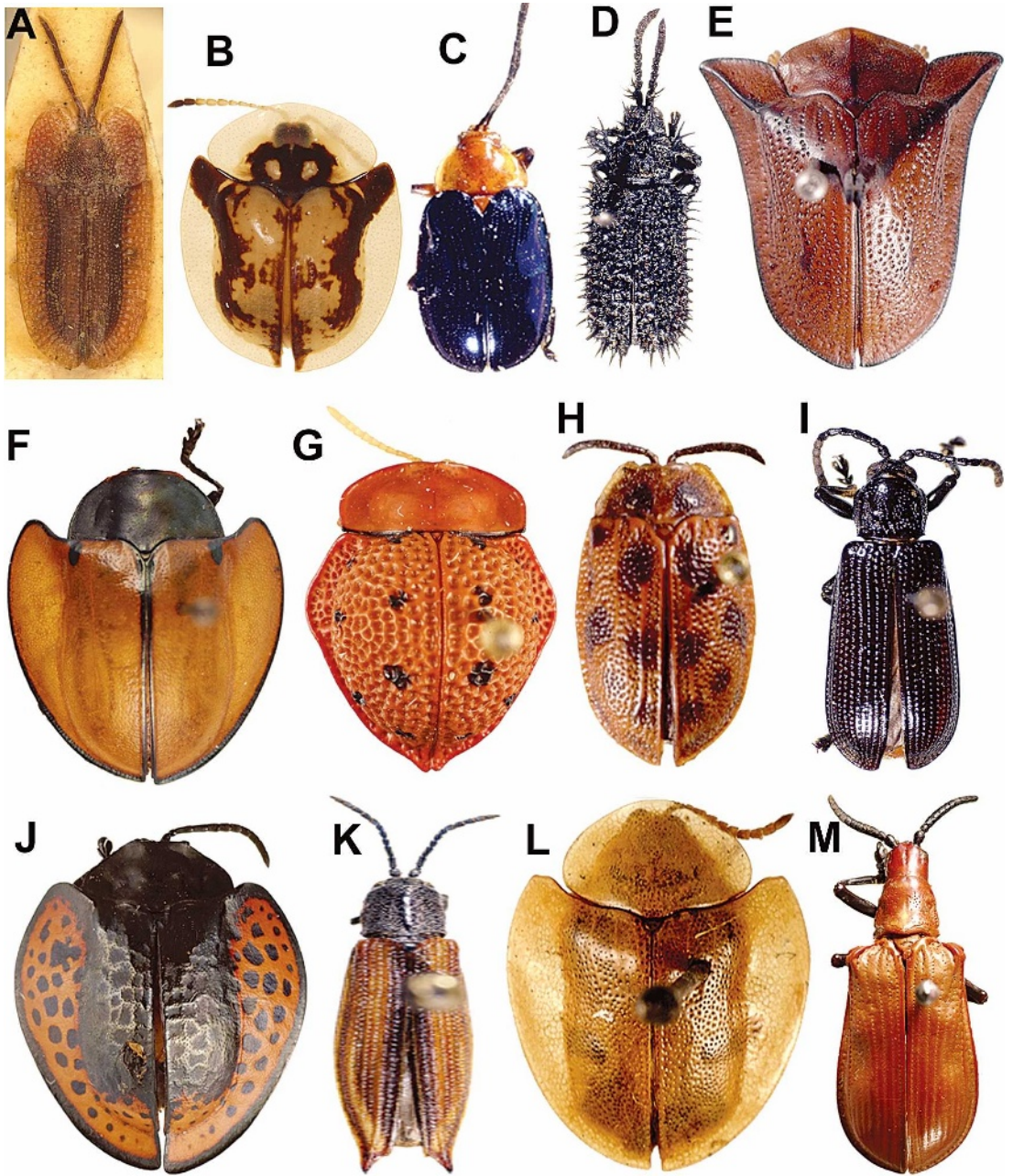


Fig. 8. Cassidinae, adults, dorsal aspect. A. *Delocrania latipennis*. B. *Deloyala guttata*. C. *Demotispa* sp. D. *Dorcathispa* sp. E. *Dorynota pugionota*. F. *Echoma marginata*. G. *Elytrogonia quatuordecimmaculata*. H. *Epistictina viridimaculata*. I. *Estigmaena chinensis*. J. *Eugenysa coscaroni*. K. *Eurispa vittata*. L. *Eurypepla jamaicensis*. M. *Exothispa reimeri*.

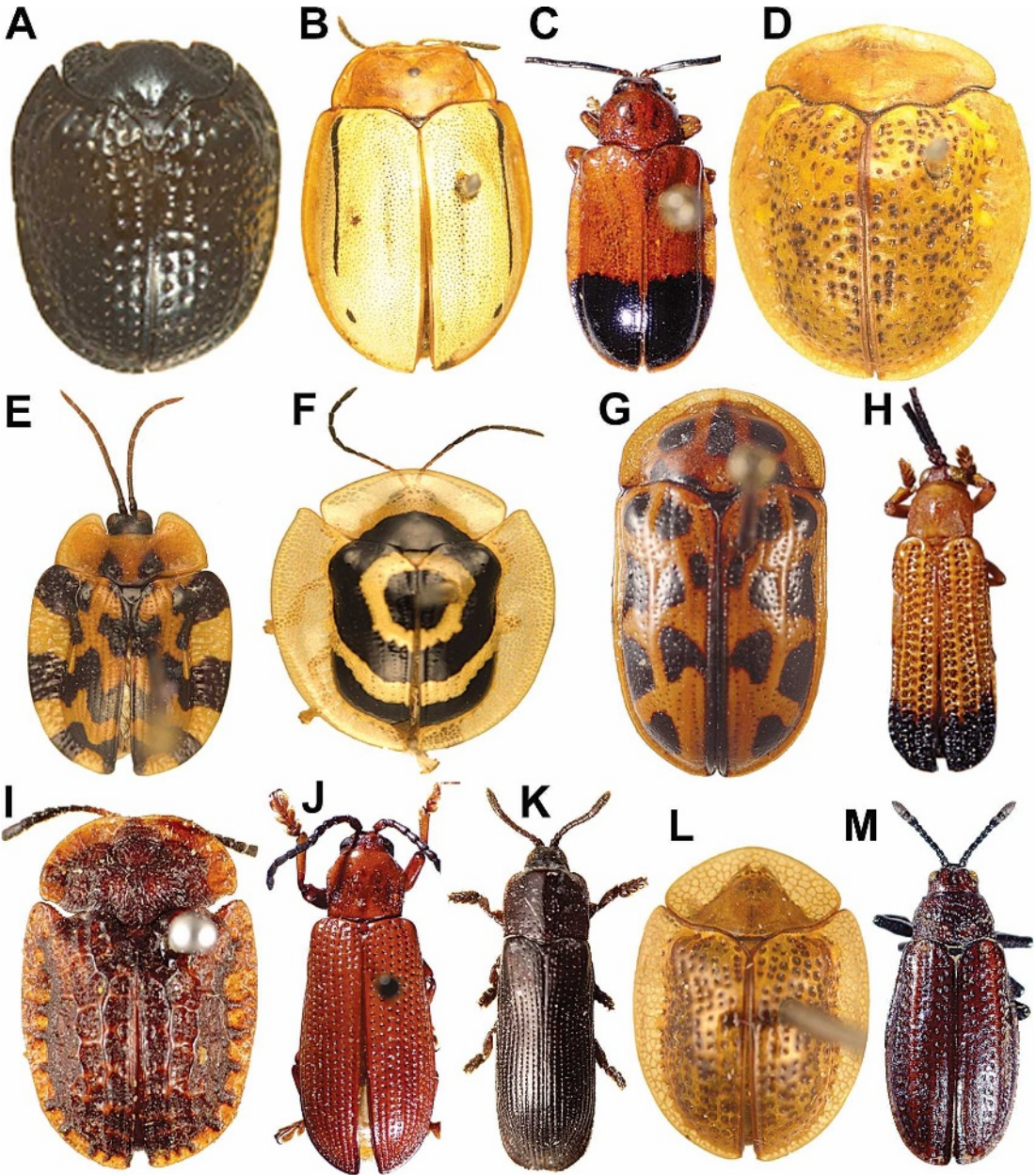


Fig. 9. Cassidinae, adults, dorsal aspect. A. *Hemisphaerota cyanea*. B. *Hilarocassis exclamationis*. C. *Hispodonta chapuisi*. D. *Hybosa* sp. E. *Imatidium capense*. F. *Ischnocodia annulata*. G. *Ischyrosomyx oblonga*. H. *Klitispa opacicollis*. I. *Laccoptera cicatrosa*. J. *Lasiochila gestroi*. K. *Leptispa denticulata*. L. *Metriona vilis*. M. *Microrhopala vittata*.

Schalk, 1994). The diversity of morphology (figs. 16, 19) and ecology displayed by larvae and pupae parallels that of adults. Larvae eat leaves as miners, strip-miners, scrapers,

skeletonizers, and chewers. Most species are either miners or open folivores. Three tribes, Arescini, Callispini, and Cephaloleiini, include cryptic feeders within young unrolled

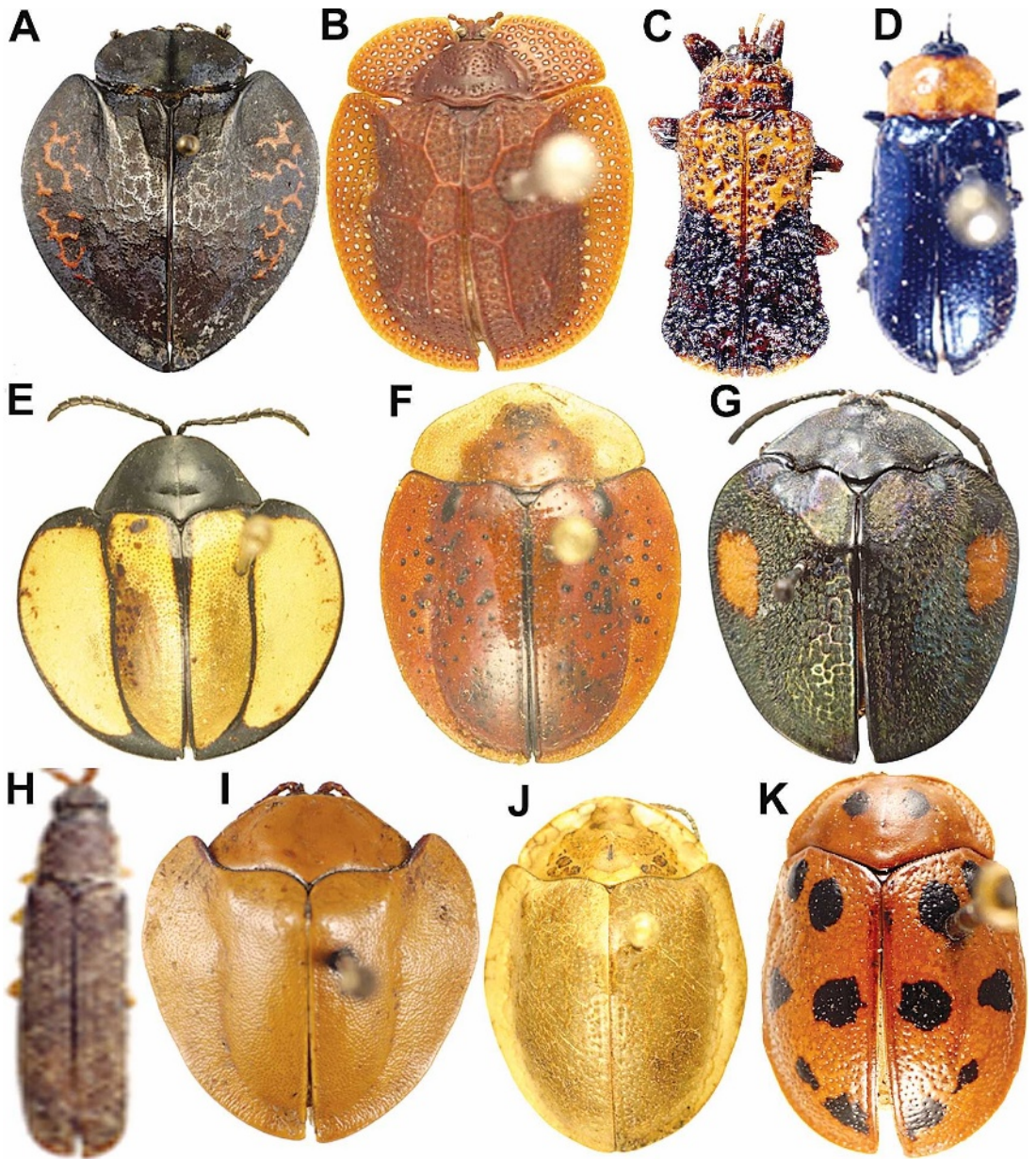


Fig. 10. Cassidinae, adults, dorsal aspect. **A.** *Miocalaspis gentilis*. **B.** *Notosacantha badia*. **C.** *Octotoma marginicollis*. **D.** *Oediopalpa guerini*. **E.** *Omaspides bistriata*. **F.** *Orexita wagneri*. **G.** *Oxynodera biplagiata*. **H.** *Palmispa parallela*. **I.** *Paraseleis flava*. **J.** *Phyonota* sp. **K.** *Phytodectoidea quatuordecimpunctata*.

leaves or within flowers (Maulik, 1937; Seifert, 1982; Mariau, 2004; Staines, 2004). Larvae in the Asian genus *Leptispa* Baly (Leptispini) live cryptically by constructing a leaf shelter (Froggatt, 1914; Maulik, 1919; Gressitt, 1950; Chen et al., 1986; Vorovna

and Medvedev, 1982; Chaboo and Divakaran, unpubl. data).

Diverse life histories are the most likely explanation for the remarkable morphological diversity in Cassidinae, particularly in immature stages. With data available for only

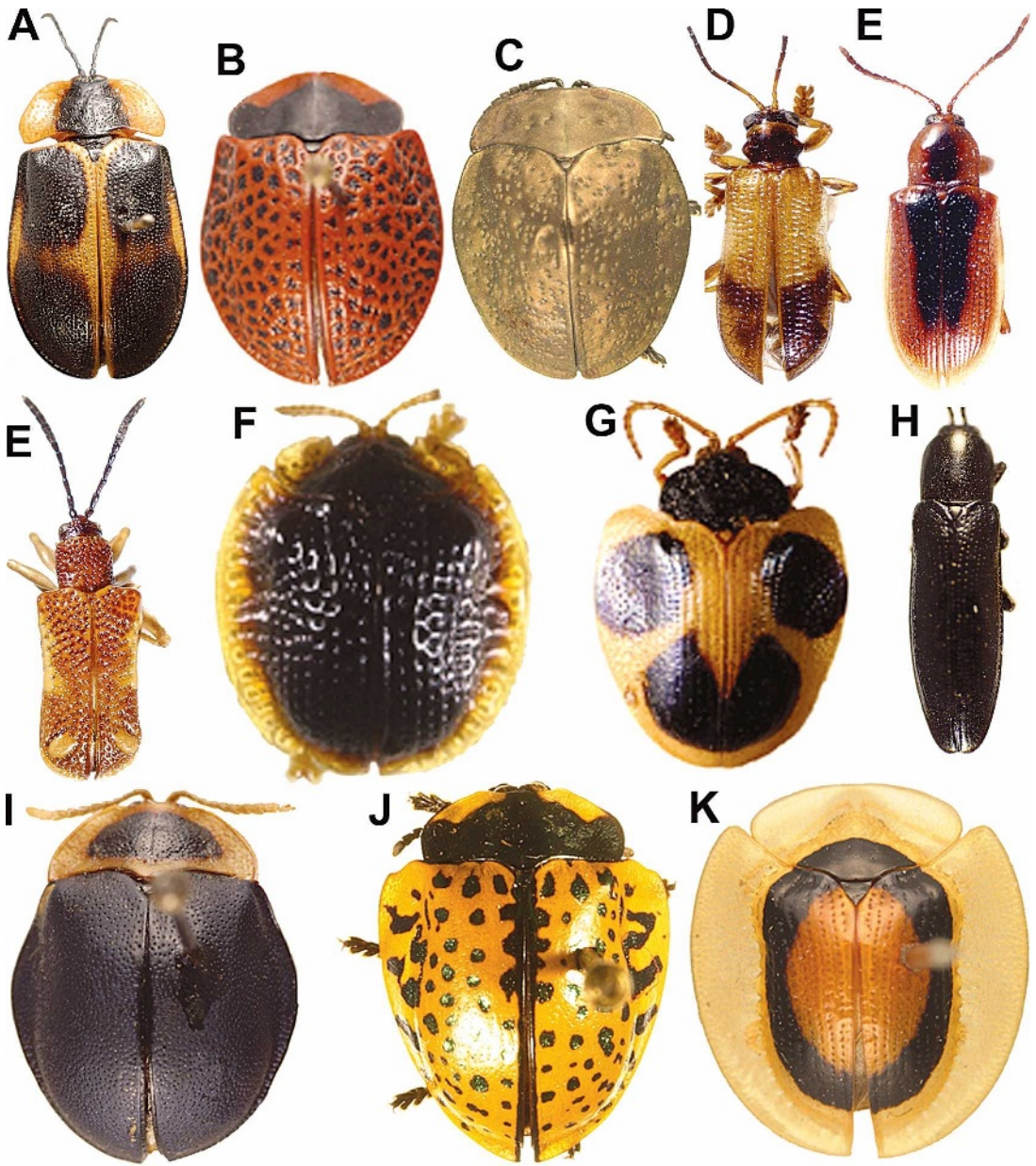


Fig. 11. Cassidinae, adults, dorsal habitus. A. *Plautyauchenia deyrollei*. B. *Poecilaspis impressa*. C. *Polychalca* sp. D. *Promecothecha papuana*. E. *Prosopodonta dorsata*. F. *Scoloenopla mantecada*. G. *Spaethiella* sp. H. *Spilophora aequatoriensis*. I. *Stenispia metallica*. J. *Stoiba fascicollis*. K. *Tapinaspis atroannulus*.

about 6% of the known species, the lack of information for more than 5600 species poses an enormous gap in our biological understanding of cassidines.

BIOGEOGRAPHY

Cassidines are cosmopolitan but primarily tropical, with most species being found in the

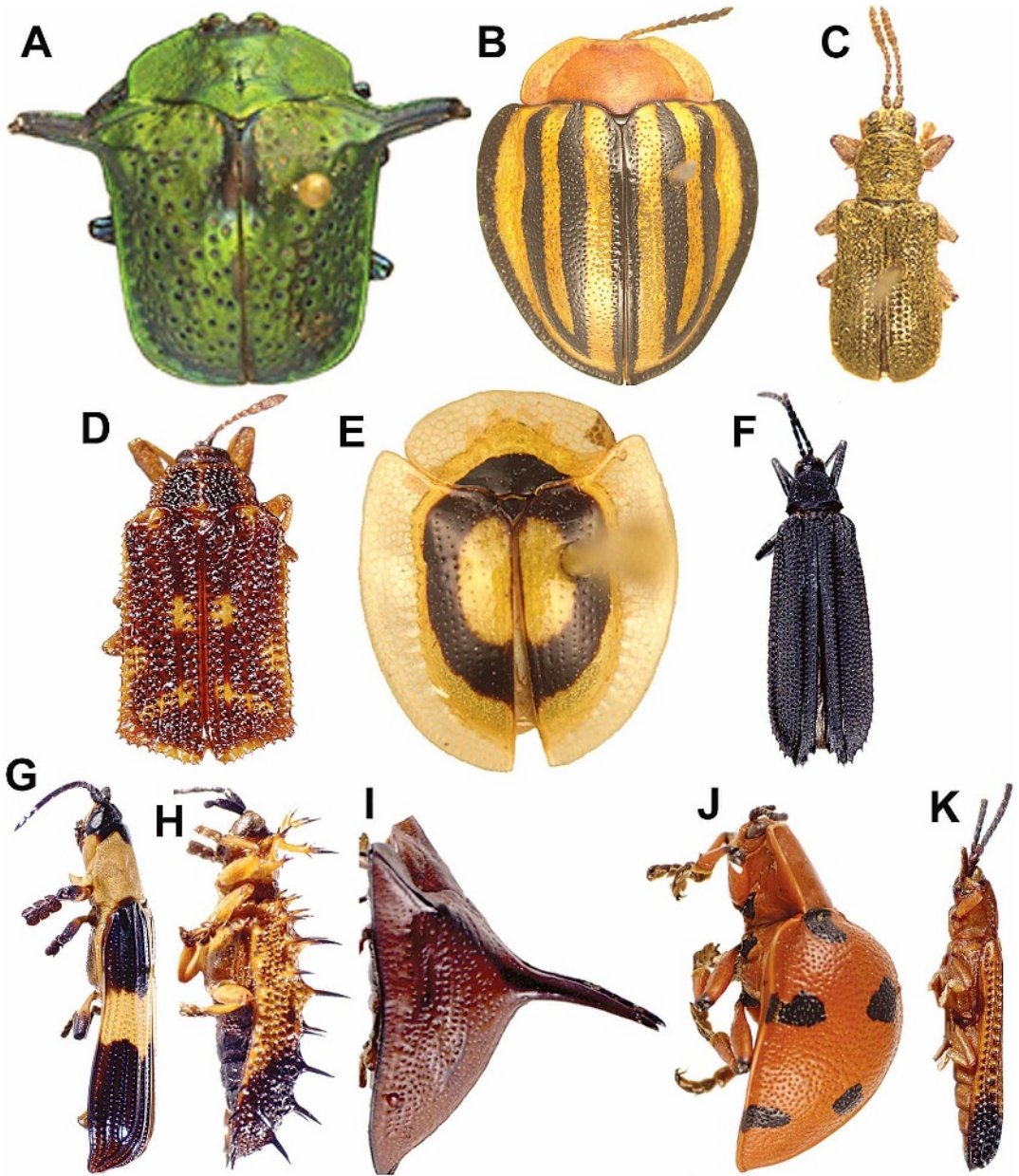


Fig. 12. Cassidinae, adults. A–F. Dorsal aspect. A. *Tauroma caeruleopunctata*. B. *Terpsis quadrivittata*. C. *Trichispa* sp. D. *Uroplata girardi*. E. *Xenocassis ambita*. F. *Xenochalepus* sp. G, K Lateral aspect. G. *Callistola speciosa fasciata*. H. *Dactylispa* sp. I. *Dorynota pugionota*. J. *Elytrogona bulla*. K. *Klititspa* sp.

Neotropical region. They are notably absent from New Zealand (Crowson, 1981; Leschen and Reid, 2004). Biogeography has been little discussed; even basic narrative hypotheses (e.g., Gondwanan explanations) are lacking. Tribes are either Old World or New World

with little overlap in faunas (table 3) (Monrós and Viana, 1947; Gressitt, 1952; Borowiec, 1999) and it has been suggested that this disjunct pattern is due to host plant distributions (Maulik, 1931a, 1937). Würmli (1975) suggested that this could be an evolutionary

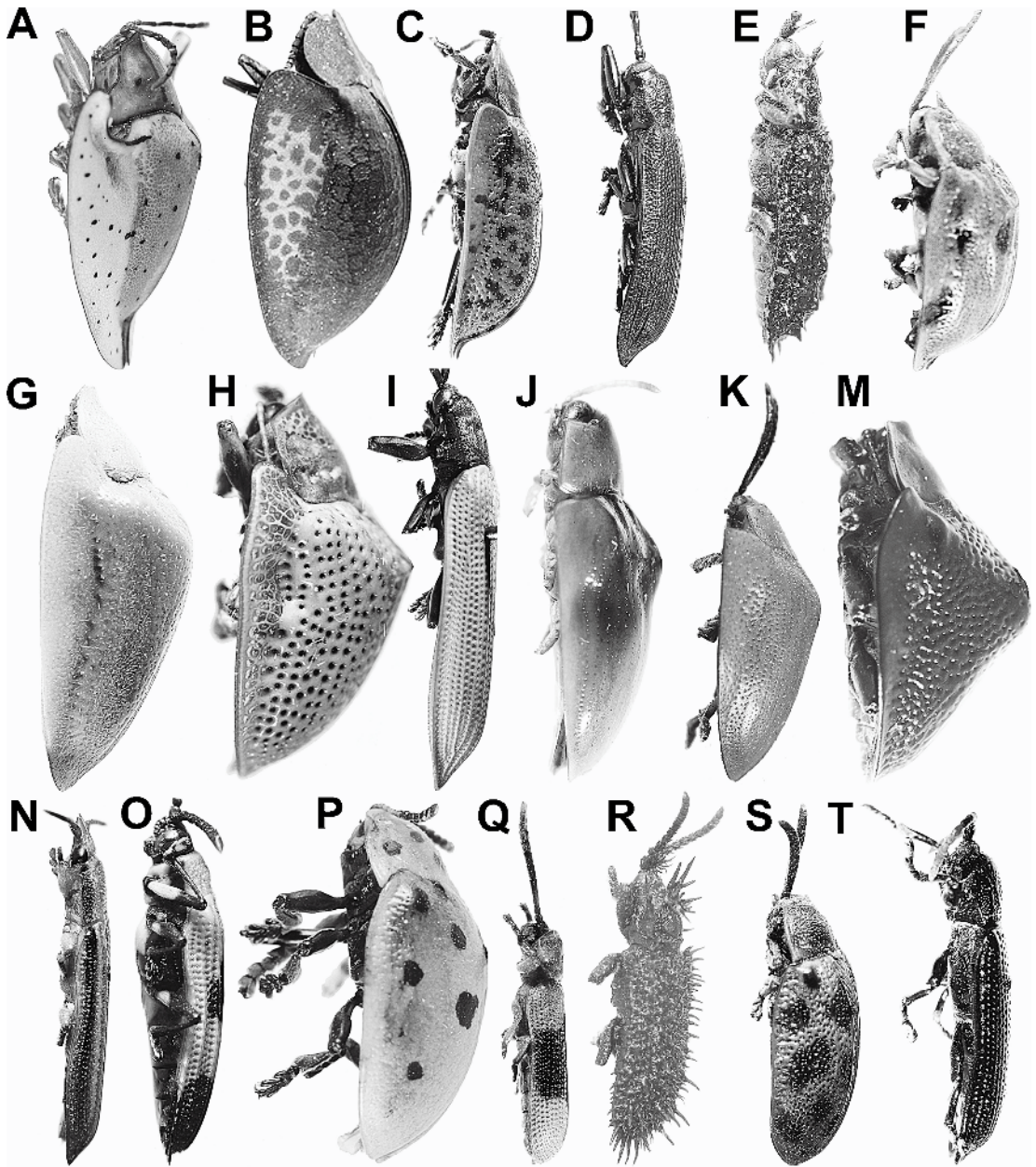


Fig. 13. Cassidinae, adults, lateral aspect. **A.** *Acromis sparsa*, male. **B.** *Agenysa caedemadens*. **C.** *Anepsiomorpha deplanata*. **D.** *Anisodera guerini*. **E.** *Asamangulia* sp. **F.** *Basiprionota quadrinodosa*. **G.** *Basipta glauca*. **H.** *Batonota lerouxi*. **I.** *Botryonopa foveicollis*. **J.** *Calliaspis rubra*. **K.** *Callistola speciosa*. **L.** *Calyptocephala nigrans*. **M.** *Canistra plagosa*. **N.** *Ceratispa palmicola*. **O.** *Chalepus* sp. **P.** *Chelymorpha cassidea*. **Q.** *Cyperispa thoracostayi kolombagara*. **R.** *Dorcathispa* sp. **S.** *Epistictina viridimaculata*. **T.** *Estigmene chinensis*.

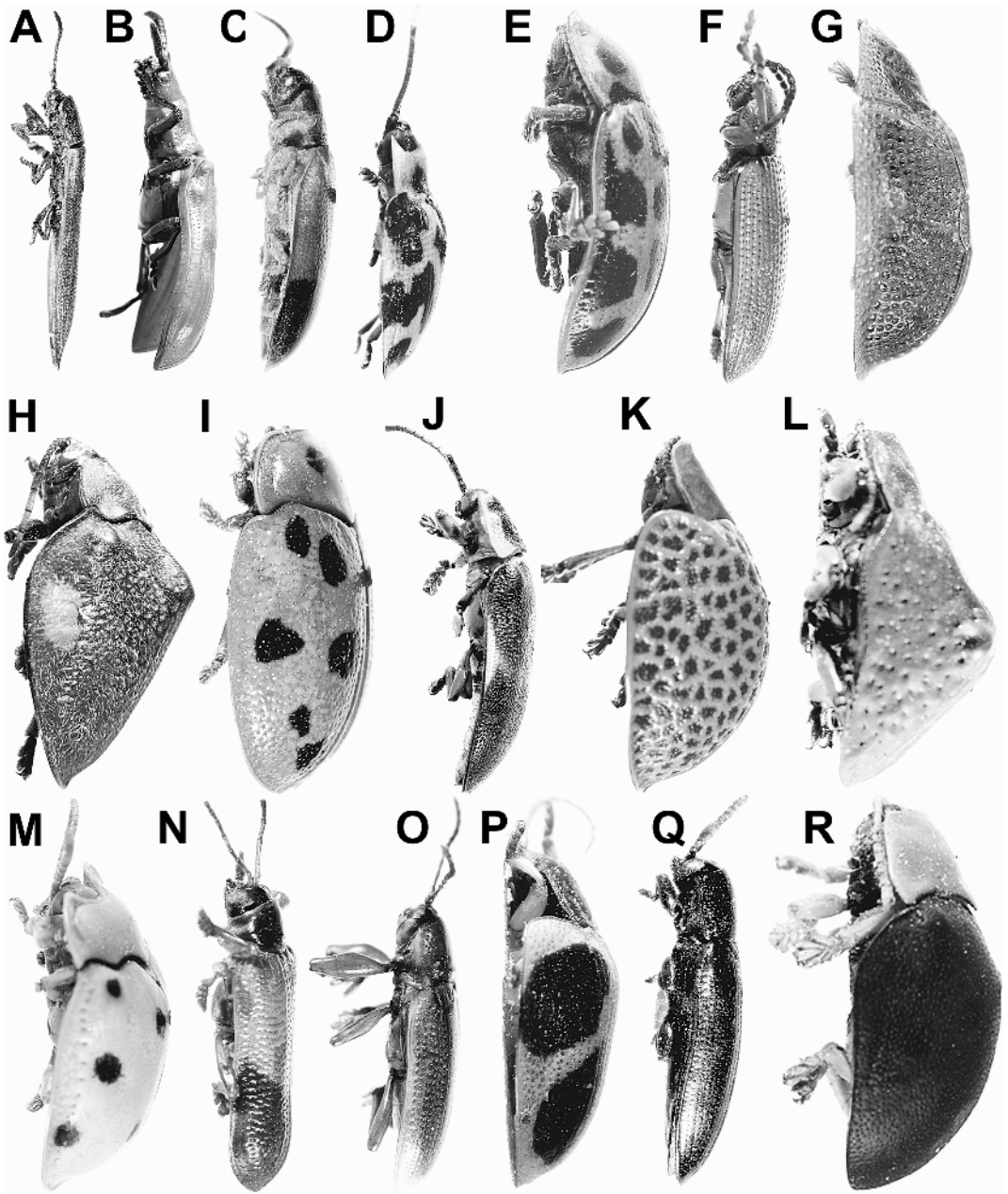


Fig. 14. Cassidinae, adults, lateral aspect. **A.** *Eurispia vittata*. **B.** *Exothispa reimeri*, abdomen removed. **C.** *Hispodonta chapuisi*. **D.** *Imatidium fasciata*. **E.** *Ischyrosomyx oblonga*. **F.** *Lasiochila gestroi*. **G.** *Notosacantha badia*. **H.** *Oxynodera biplagiata*. **I.** *Paraselensis flava*. **J.** *Plautyauchenia deyrollei*. **K.** *Poecilaspis impressa*. **L.** *Polychalma platynota*. **M.** *Prioptera sinuata*. **N.** *Promecotheca papuana*. **O.** *Prosopodonta dorsata*. **P.** *Spilophora aequatoriensis*. **Q.** *Stenispia metallica*. **R.** *Stoiba indivisa*.

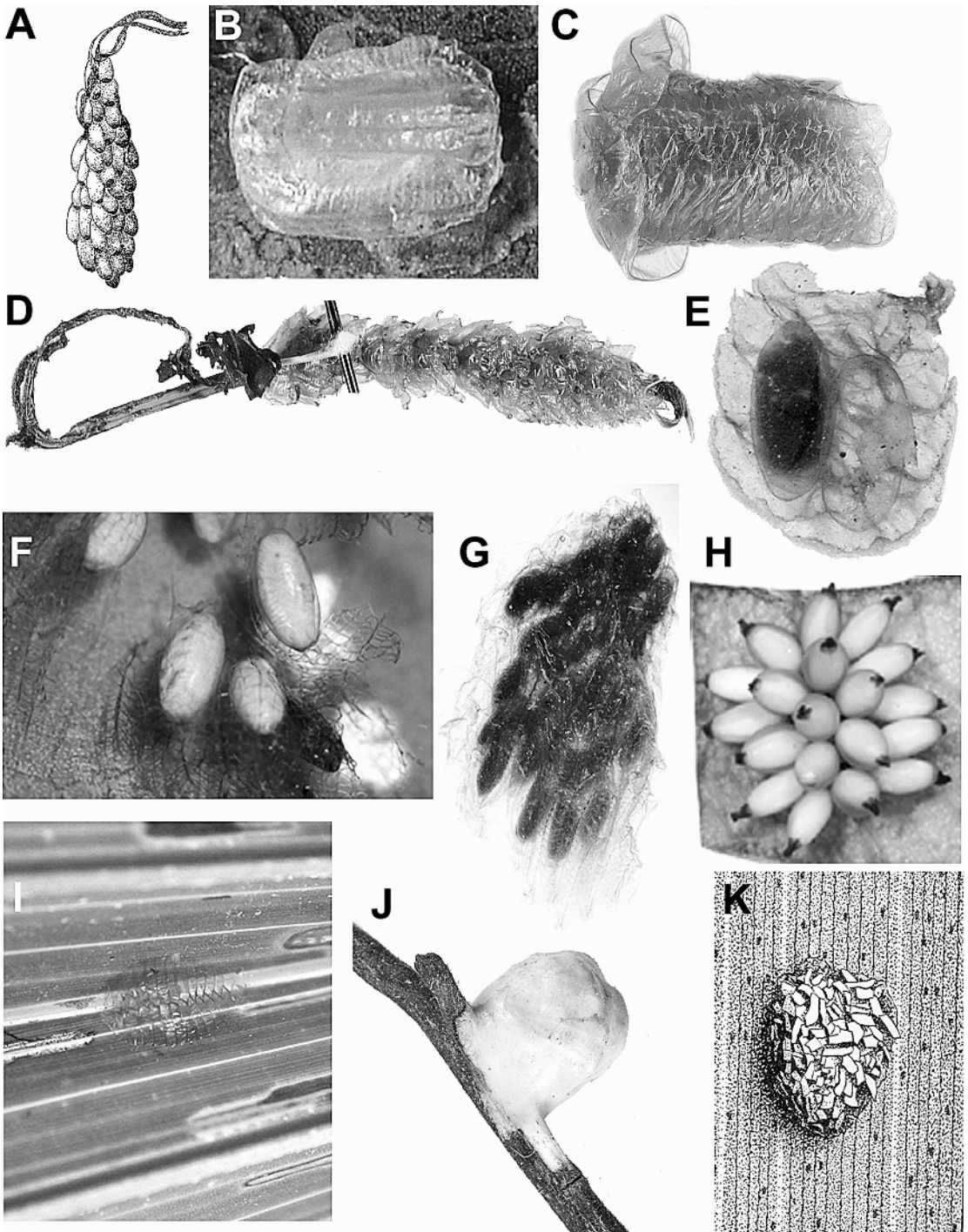


Fig. 15. Eggs of Cassidinae. A. *Acromis sparsa*. B. *Aspidimorpha furcata*. C. *Aspidimorpha miliaris*, ootheca. D. *Callispa bowringi*. E. *Charidotis* sp. (Argentina), pinned. F. *Craspedonta mouhouti*. G. *Epistictina* sp. H. *Eurypedus nigrosignatus*. I. *Hemisphaerota palmarum*. J. *Physonota* sp. (Mexico), mass attached to stem. K. *Promecotheca reichei*, after Taylor (1937).

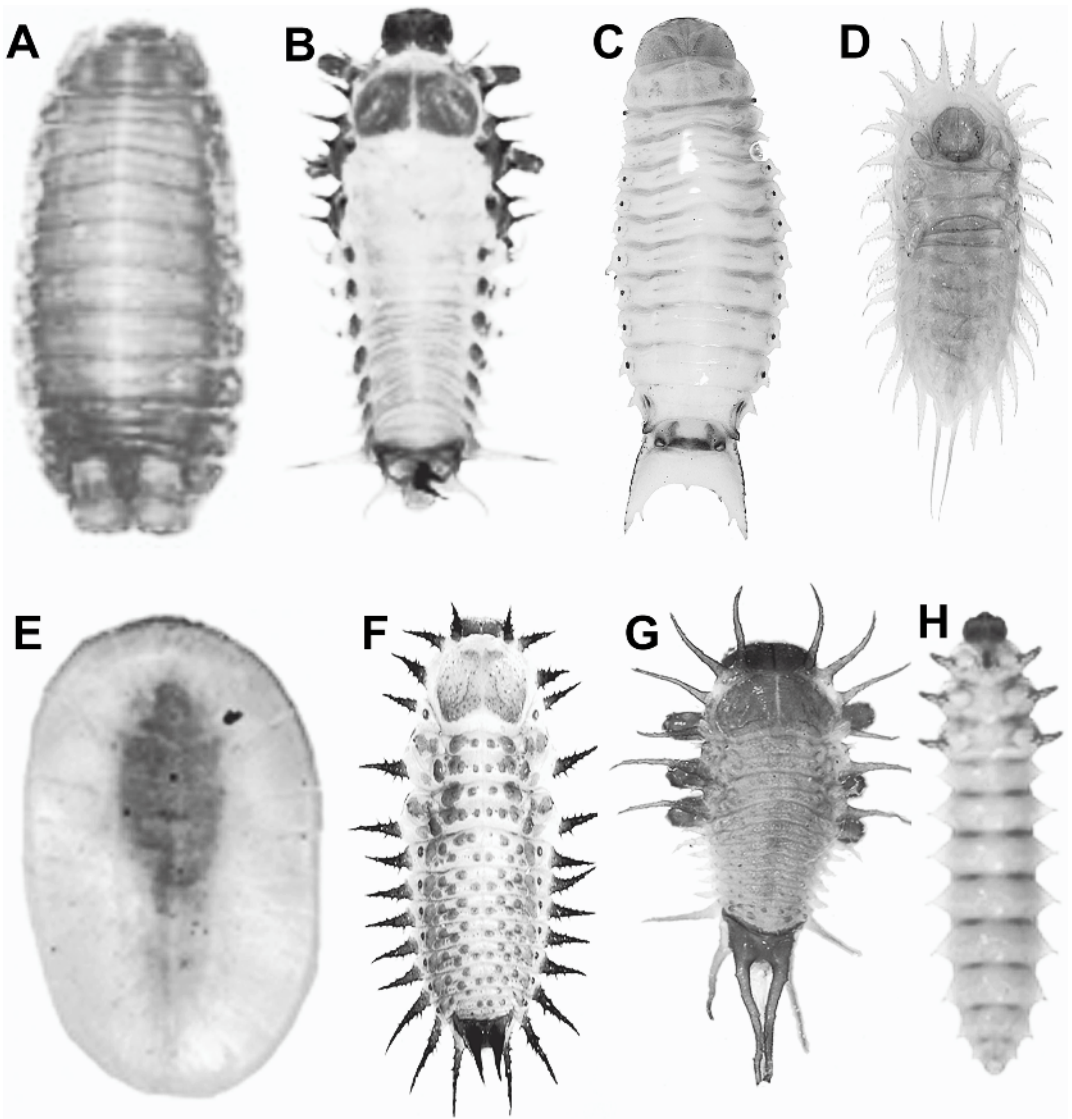


Fig. 16. Larvae of Cassidinae. A. *Alurnus humeralis*. B. *Basiprionota* sp. C. *Botryonopa* sp. D. *Callispa bowringi*. E. *Cephaloleia* sp. F. *Chelymormpha argus*. G. *Craspedonta mouhoti*. H. *Microrhopala rubra*.

pattern but that it may also reflect the interests of collectors and collections or even be an artifact of poor taxonomy. Crowson (1981) also pointed out the “unfortunate tendency” to separate Old and New World faunas and indicated that the study of Cassidinae was an “extreme manifestation” of this poor method. Murray (1870) outlined broad distribution patterns of Coleoptera based on ecology and listed Cassidinae as a macrotypal group (i.e., largely tropical). Crowson (1981) considered

this climatic-ecological grouping of some merit and perhaps evolutionarily significant. Gressitt (1950) briefly discussed influences on the Chinese hispinae fauna, indicating endemics and regional distribution patterns.

Fossil History

The cassidine fossil record includes 41 adult body fossils in shales (from Solhoven, Germany; Florissant, Colorado, USA) and in

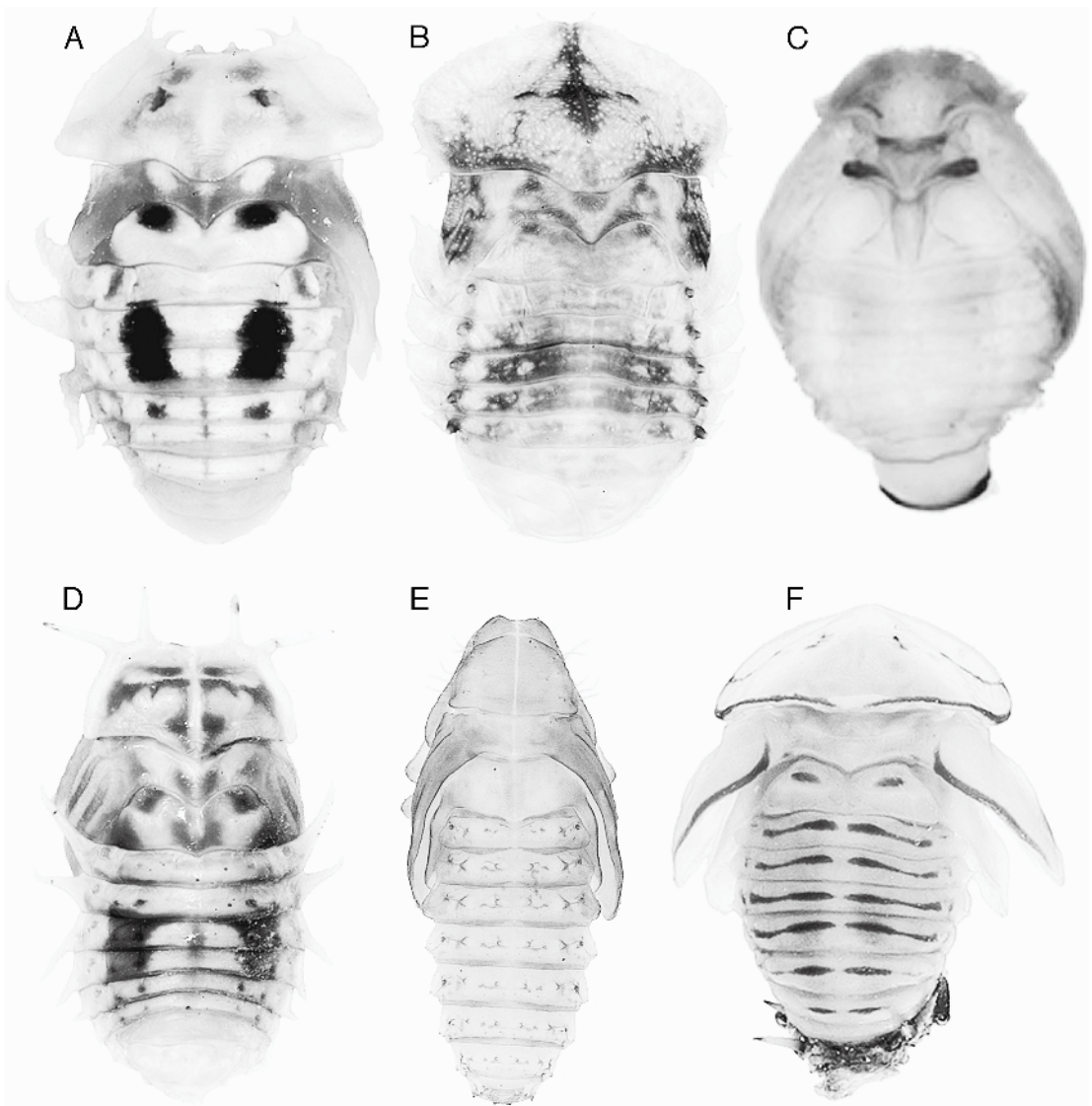


Fig. 17. Pupae of Cassidinae, dorsal aspect. **A.** *Basiprionota cerata*, shield status unknown. **B.** *Eugenysa columbiana*, shield removed. **C.** *Hemisphaerota palmarum*, shield removed. **D.** *Megapyga* sp., fifth larval exuviae removed. **E.** *Microrhopala rubra*, no shield retained. **F.** *Physonota helianthi*, fifth larval exuviae in situ.

ambers (Dominican and Baltic) (Santiago-Blay, 1994), two larvae in amber (Dominican and Baltic) (Poinar, 1999), and four compressed fossilized feeding patterns (Wyoming and North Dakota) (Wilf et al., 2000). These specimens have been identified in the genera *Anisodera* Chevrolat (Santiago-Blay et al., 1996; Santiago and Craig, 1999; Staines and Samuelson, 2000), *Callistaspis* Haupt

(Haupt, 1950), *Cassida* (Poinar, 1999), *Cephaloleichnites* Wilf et al. (Wilf et al., 2000), *Chalepus* Thunberg (Spahr, 1981), *Delocrania* Guérin (Farrell et al., 1992; Santiago-Blay et al., 1996), and *Sceloenopla* Chevrolat (Santiago-Blay et al., 1996; Santiago and Craig, 1994; Staines and Samuelson, 2000). Two larval cassidines from Dominican and Baltic ambers remain undescribed (Poinar, 1999).

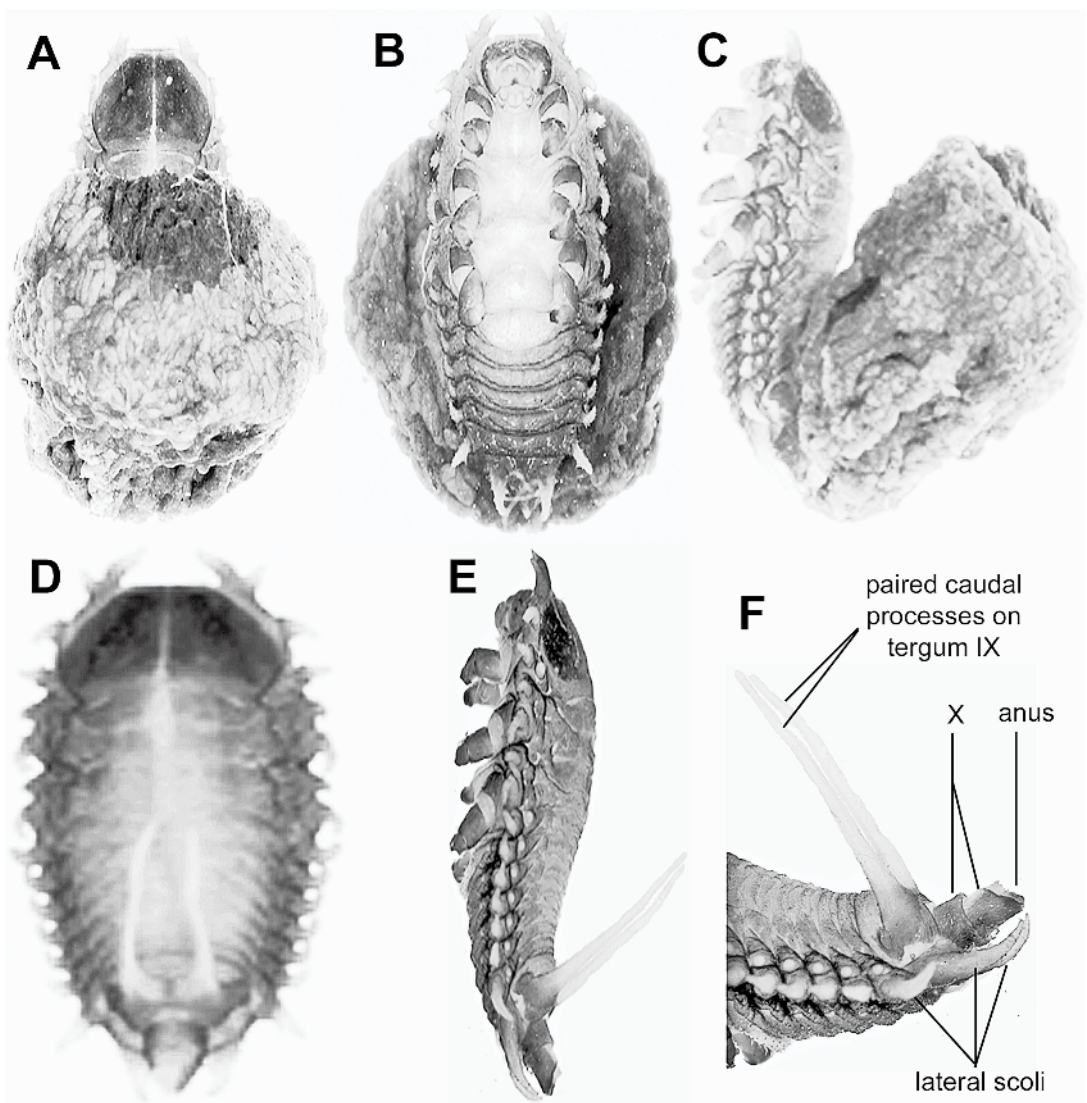


Fig. 18. *Acrocassis gibbipennis*, mature larva. **A.** Dorsal view, shield in situ. **B.** Ventral view. **C.** Lateral view. **D.** Dorsal view, shield removed. **E.** Lateral view. **F.** Hind end, lateral view, showing abdominal segment X, elongate anus, caudal processes and lateral scoli.

Dating the maximum age of cassidines is controversial. Mann and Crowson (1981a) plotted ages of known chrysomelid fossils, including three cassidine amber fossils from the Tertiary, on their phylogenetic hypothesis of Chrysomelidae. They argued that the minimum age of origin of the clade ((Cassidinae s.str. + Hispinae s.str.) + (Bruchinae + Sagraeae + Donaciinae + Criocerinae)) to be in the latest Cretaceous. Solhofen shales have

been dated to the Late Jurassic; however, limited preservation of these compression deposits prevents a definitive identification of most beetle families, including chrysomelids (D. Grimaldi, personal commun.) and raises doubts on the attribution of Jurassic fossils to Chrysomelidae. Based on his concept of the most primitive cassidines and on Uhmann's (1939) study of cassidine fossils in Baltic amber, Crowson (1981) hypothe-

TABLE 3
Tribal Diversity, Distribution, and Host Plants of Cassidinae

Genera and species numbers were derived from recent catalogs. Host plant data were derived from many sources (Jolivet and Hawkeswood, 1995; Flowers and Janzen, 1997; Ghate et al., 2003; Staines, 2004; Clark et al., 2004; Borowiec and Świętojańska, 2005. Distribution data were derived from Seeno and Wilcox, 1982, and Borowiec and Świętojańska, 2005.

Tribes	Genera	Species	Plant family	Distribution
Alurnini Weise	6	29	Arecaceae, Heliconiaceae, Sterculiaceae	Neotropical
Anisoderini Weise	3	75	Costaceae, Musaceae, Poaceae, Zingiberaceae	Asia, Indonesia, Philippines
Apruidini Weise	1	3	Convolvulaceae, Philesiaceae	Australia
Arescini Weise	4	17	Heliconiaceae, Marantaceae, Musaceae	Neotropical
Aspidimorphini Hinck	7	281	Amaranthaceae, Asteraceae, Convolvulaceae, Lamiaceae, Verbenaceae	Africa, India, Madagascar, Asia
Asterizini Hincks	1	2	Unknown	West Indies
Basiprionotini Hincks	5	81	Verbenaceae	Asia, Madagascar, Philippines
Basiptini Hincks	1	5	Asteraceae	Africa
Botryonopini Weise	2	40	Arecaceae	India, Madagascar, Philippines
Callispini Weise	6	173	Arecaceae, Musaceae, Orchidaceae, Poaceae, Zingiberaceae	Africa, India, Indonesia, Philippines
Callohispiini Uhmman	1	1	Unknown	Madagascar
Cassidini Hincks	76	964	Amaranthaceae, Asteraceae, Bignoniaceae, Caryophyllaceae, Chenopodiaceae, Convolvulaceae, Fabaceae, Lamiaceae, Meliaceae, Passifloraceae, Rhamaceae, Rutaceae, Solanaceae, Verbenaceae	Worldwide
Cephaloleiini Weise	9	311	Agavaceae, Arecaceae, Bromeliaceae, Costaceae, Cyperaceae, Musaceae, Orchidaceae, Poaceae, Solanaceae, Zingiberaceae	Neotropical
Chalepini Weise	25	342	Agavaceae, Aristolochaceae, Betulaceae, Carpinaceae, Cecropiaceae, Celastraceae, Commelinaceae, Cornaceae, Ericaceae, Fabaceae, Malvaceae, Mimosaceae, Pandanaceae, Piperaceae, Poaceae, Polygonaceae, Sapindaceae, Tiliaceae	New World
Charidotini Hincks	6	312	Bignoniaceae, Convolvulaceae, Orchidaceae, Poaceae, Rubiaceae, Verbenaceae	Neotropical
Coelaenomenoderini Weise	8	73	Arecaceae, Costaceae, Cyperaceae, Zingiberaceae	Australia, New Guinea
Cryptonychini Weise	24	138	Arecaceae, Costaceae, Cyperaceae, Fabaceae, Flagellariaceae, Heliconiaceae, Juncaceae, Ophioglossaceae, Pandanaceae, Poaceae, Zingiberaceae	Africa, Australia, Madagascar, Philippines
Delocraniini Guérin-Ménéville	1	3	Arecaceae	Neotropical
Dorynotini Hincks	6	47	Bignoniaceae	Neotropical
Epistictini Hincks	3	11	Bignoniaceae, Meliaceae	Asia
Eugensini Hincks	3	35	Asteraceae, Convolvulaceae	Neotropical
Eurispini Weise	3	14	Cyperaceae	Australia, India, New Guinea
Exothispini Weise	1	1	Unknown	Africa

TABLE 3
(Continued)

Tribes	Genera	Species	Plant family	Distribution
Goniocheniini Hincks	5	30	Ehretiaceae, Lamiaceae, Sterculiaceae	Neotropical
Gonophorini Weise	10	290	Araceae, Arecaceae, Costaceae, Marantaceae, Musaceae, Orchidaceae, Pandaceae, Poaceae, Zingiberaceae	Australia, India, Indonesia, New Guinea, Philippines
Hemisphaerotini Hincks	2	42	Arecaceae, Heliconiaceae, Sterculiaceae	C. & S. America
Hispiini Weise	20	611	Acanthaceae, Anacardiaceae, Arecaceae, Asteraceae, Bombaceae, Brassicaceae, Caesalpinaceae, Campanulaceae, Carpinaceae, Cistaceae, Commelinaceae, Costaceae, Cyperaceae, Euphorbiaceae, Fabaceae, Fagaceae, Lamiaceae, Malvaceae, Marantaceae, Myricaceae, Onagraceae, Poaceae, Rhamaceae, Rosaceae, Solanaceae, Sterculiaceae, Tiliaceae, Verbenaceae, Zygophyllaceae	Africa, Asia, Australia, S. Europe
Hispoleptini Uhmann	1	4	Arecaceae	S. America
Hybosispini Weise	1	5	Unknown	S. America
Imatidiini Hincks	8	78	Arecaceae, Fabaceae, Heliconiaceae, Marantaceae	Neotropical
Ischyrosomychni Hincks	2	18	Unknown	Neotropical
Leptispini Weise	1	67	Poaceae	Africa, Asia, Australia
Notosacanthini Hincks	2	254	Apocynaceae, Arecaceae, Euphorbiaceae, Rhizophoraceae	O. World (not Europe)
Oediopalpini Monrós and Viana	1	37	Poaceae	Neotropical
Omocerini Hincks	7	139	Boraginaceae, Ehretiaceae, Lamiaceae	Neotropical
Oncocephalini Weise	3	72	Convolvulaceae, Dioscoraceae, Orchidaceae, Poaceae, Zingiberaceae	Africa, Asia, Australia
Physonotini Hincks	6	46	Asteraceae, Ehretiaceae, Lamiaceae,	New World
Promecothecini Weise	2	34	Arecaceae, Flagellariaceae, Heliconiaceae, Pandanaaceae, Poaceae, Musaceae, Zingiberaceae	Asia, Australia, Madagascar
Prosopodontini Weise	1	26	Arecaceae, Heliconiaceae	Neotropical
Sceloenoplini Uhmann	5	219	Arecaceae, Bromeliaceae, Cecropiaceae, Fabaceae, Rutaceae, Sapotaceae	Neotropical
Spilophorini Hincks	2	30	Arecaceae, Dioscoraceae, Poaceae	Neotropical
Stolaini Hincks	16	528	Asteraceae, Convolvulaceae, Cuscutaceae, Ehretiaceae, Solanaceae	Neotropical
Uroplatini Weise	32	396	Annonaceae, Asteraceae, Bignoniaceae, Caesalpinaceae, Celastraceae, Ehretiaceae, Fabaceae, Fagaceae, Lamiaceae, Lauraceae, Malpighiaceae, Malvaceae, Mimosaceae, Oleaceae, Pedaliaceae, Poaceae, Polygonaceae, Rubiaceae, Sapindaceae, Sterculiaceae, Tiliaceae, Verbenaceae, Vivianaceae, Xanthorrhoeaceae	New World

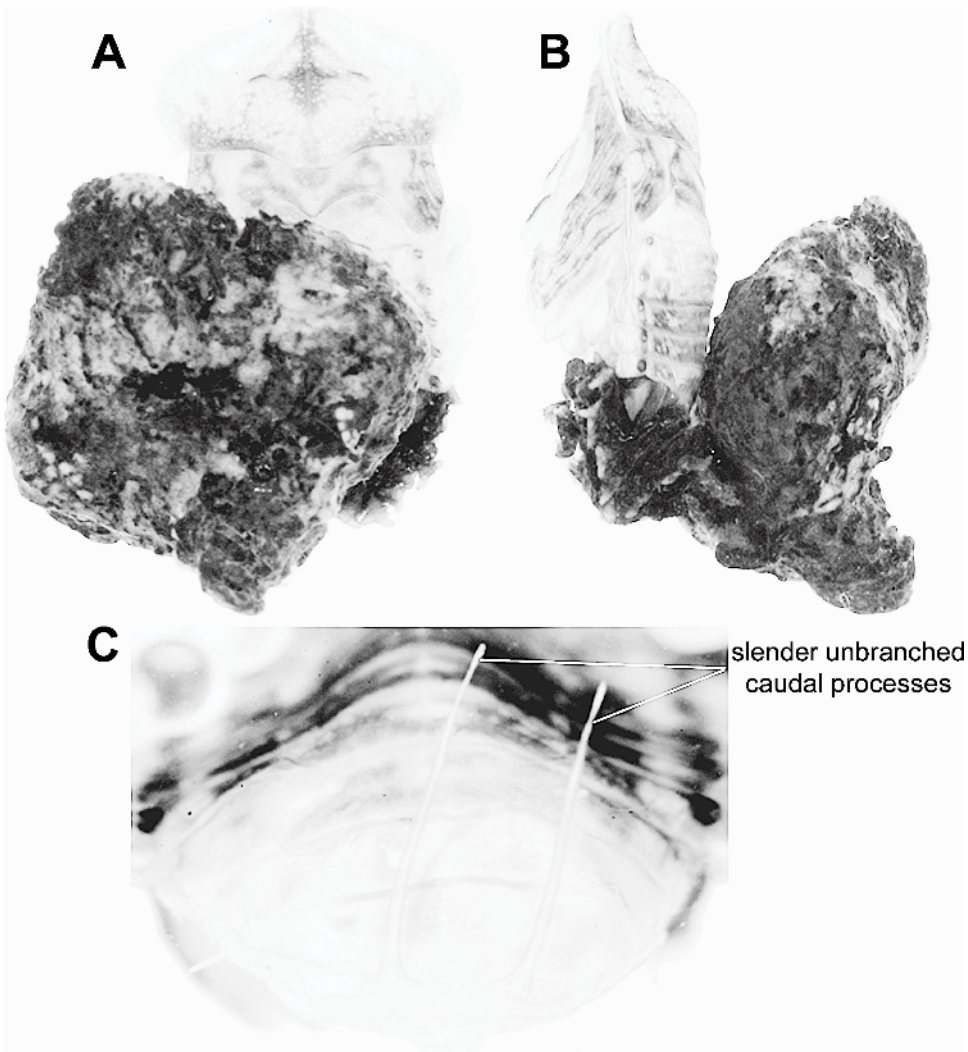


Fig. 19. *Acrocassis gibbipennis*, pupa. **A.** Dorsal view, shield in situ. **B.** Ventral view, shield in situ. **C.** Hind end, dorsal view, shield removed.

sized that cassidines were present in South America before the latter became an island continent at the beginning of the Tertiary period.

HOST PLANTS

Host records for Cassidinae have accumulated through species reports and regional host lists. Hosts are known for about 200 (ca. 63%) genera (Jolivet and Hawkeswood, 1995; Borowiec, 1999), a remarkable record among herbivorous insects. The taxonomic variation

in plant family selection (table 3) has led to the view that Hispinae s.str. prefers monocots whereas Cassidinae s.str. prefers dicots (Crowson, 1981). Cassidinae shows a wide variation in preference, from polyphagous to narrowly oligophagous (to plant genera) or monophagous to plant species. Palms (Arecaceae) and grasses (Poaceae) account for a large proportion of the records (Maulik, 1937; Gressitt, 1942b and subsequent publications; Jolivet and Hawkeswood, 1995; Borowiec, 1999). Seven cassidine tribes utilize palms, and many are serious pests of

economically important palms (Mariau, 2004). At least 14 cassidine tribes feed on members of the Zingiberales, mining their stems, or living cryptically within rolled-leaf tubes and within floral bracts (reviewed by Staines, 2004).

The evolution of cassidine host plant associations has attracted some attention. Steinhausen (1950) considered tortoise beetles specializing on Caryophyllaceae and Chenopodiaceae as “basal”, and Convolvulaceae specialists as “derived”. Crowson (1953) suggested a step-wise evolution in host use from an aquatic ancestor close to Donaciinae to semiaquatic forms in phytotelmata, such as the rolled-leaf feeders, then multiple origins of open folivory and mining. Wilf et al. (2000) discussed host choice in Cassidinae, using the phylogenetic hypothesis of Hsiao and Windsor (1999) and presented an evolutionary scenario with an ancestor on an aquatic or semiaquatic dicot host plant, with a switch to monocot hosts with the rolled-leaf feeders becoming specialized for semiaquatic terrestrial feeding within rolled leaves of Zingiberales. This scenario fits Crowson’s (1953) hypothesis, but see discussions of some analytical problems in the Introduction with regard to Hsiao and Windsor (1999) and Wilf et al. (2000).

Cassidines tend to be restricted in their host plants, often even to plant species. Some cassidines exhibit host-switching across widely separated families of plants. Most species of Alurnini, Hemisphaerotini, and Imatidiini feed on members of the monocotyledonous families Arecaceae, Heliconiaceae, and Marantaceae (table 3). At least one alurnine, *Plautyauchenia latrellei* Castelnau, also feeds on the eudicot *Theobroma* (Sterculiaceae: cocoa) (Maulik, 1933). Two species of *Imatidium* feed on *Inga* (Fabaceae) (Gilbert et al., 2001). One hemisphaerotine, *Spaethiella tristis* (Boheman), feeds on the palms *Cocos nucifera* Linnaeus (coconut) and *Elaeis guineensis* Jacq. (oil palm) (Arecaceae), as well as on cocoa, *Theobroma grandiflorum* (Wildenow ex Sprengel) Schumann (Sterculiaceae) (Garcia et al., 1996; Borowiec, 1999; Barbosa et al., 1999; Chaboo and Nguyen, 2004). The variations in taxonomy, leaf morphology, and chemistry of these alternate hosts, and their implications for mouth

morphology and nutrition warrant further study.

CASSIDINES AS PLANT PESTS

Phytophagy on diverse cultivated plants makes chrysomelid beetles one of the most significant pest groups. Eating leaves damages plants to some degree; high population densities, including cyclic outbreaks, can make cassidine adults and larvae serious pests of timbers (hardwoods and bamboos), oil palm crops, food crops, and ornamentals. Mining activity can lead to blisters, brown patches, drying of leaves, and even loss of the entire leaf. Blotch mines result in virtually mined-out leaves (Jones and Brisley, 1925; Boldt and Staines, 1993). Stem mining (Beeson, 1941) and leaf chewing (Chen, 1928, 1929) can significantly damage bamboo forests in Asia. Leaf mining, scraping, or chewing offers an indirect route for fungal infections, thus further threatening a plant (Barbosa et al., 1999); for example, fungal infection via leaf scraping by *Spaethiella* Barber and Bridwell (Garcia et al., 1996).

Massive outbreaks of Cassidinae are known; for example, *Promecotheca cumingi* Baly (Ding Siew Ming, 1976) and *Coelaenomenodera elaeidis* Maulik (Cotterell, 1925). Such populations can reach pest levels on certain host plants. Palms are among the most susceptible, and damage is particularly costly considering the economic significance of palms in tropical economies as food, building materials, and ornamentals (Maulik, 1930, 1931b, 1931c; Ford and Cavey, 1985). Specific cassidine pests of palms and other economically important plants are given in table 4. Cotterell (1925) described “the air as thick with” *Coelaenomenodera* Blanchard adults during periodic outbreaks on the African Gold Coast.

Cassidines attack Asian and African food crops including corn, rice, sugarcane, bamboo, date palm, and coconut (Maulik, 1919). Members of *Aspidimorpha* are among the most intensively studied cassidines (see citations above), probably due to their conspicuous size, gregarious larvae, and economic impact on the food crops sweet potato and kangkong (table 4).

TABLE 4
Cassidine Pests of Some Economically Important Plants

Host plant	Pest (region)	Source
<i>Cocos nucifera</i> (coconut)	<i>Promecotheca</i> Blanchard (Pacific)	Taylor, 1937; Jones, 1913; Burkill, 1918; Froggatt, 1939
<i>Elaeis guineensis</i> Jacq. (oil palm)	<i>Coelaenomenodera elaeidis</i> Maulik (central Africa)	Maulik, 1920; Cotterell, 1925; Cachan, 1957; Philippe et al., 1979; Hesperheide, 1991
	<i>Promecotheca</i> (Pacific)	Froggatt, 1914
	<i>Calyptocephala brevicornis</i> Boheman (Brazil)	Moura, 1984
	<i>Imatidium nevei</i> Bondar (Brazil)	Bondar, 1941
	<i>Spaethiella tristis</i> (Boheman) (Neotropics)	Genty et al., 1978; Garcia et al., 1996
	<i>Delocrania</i> Guérin spp. (Neotropics)	Genty et al., 1978
	<i>Alurnus humeralis</i> Rosenberg (Neotropics)	Merino and Vasquez, 1963; Villacis Santos, 1968; Genty et al., 1978
Ornamental palms: <i>Sabal</i> Adans.	<i>Hemisphaerota cyanea</i> (United States)	Jackman, 1975
<i>Sabal casuarum</i> (O. F. Cook) Becc.	<i>Hemisphaerota palmarum</i> (Caribbean)	Chaboo and Nguyen, 2004
Ornamental palms	<i>Coraliomela brunnea</i> Thunberg	J. Pech, personal commun.
<i>Gmelina arborea</i> Roxb. ex Sm. (white teak, Asian bushbeech, white beech, or grey teak)	<i>Craspedonta leayana</i> (Latreille) (Myanmar)	Atkinson, 1928; Beeson, 1941
<i>Ipomoea</i> spp. Linnaeus (sweet potato; kangkong)	<i>Aspidimorpha</i> (southeast Asia)	Schultze, 1908; Maulik, 1919; Corbett and Dover, 1927; Dammerman, 1929; Kalshoven, 1981; Kimoto et al., 1984; Noerdjito and Adisoemarto, 1986; Nakamura and Abbas, 1987a, b; Nakamura et al., 1989; Noerdjito et al., 1992; Noerdjito and Nakamura, 1999; Verma and Shrivastava, 1985, 1989
	<i>Chelymorpha cassidea</i> (Fabricius) (USA)	Chittenden, 1924
	Cassidini species (Brazil)	Monte, 1932
	<i>Cassida</i> (New Guinea)	Kimoto et al., 1984
<i>Glycine max</i> (L.) Merr. (soybean)	<i>Odontota horni</i> Smith (United States)	Kogan and Kogan, 1979
<i>Saccharum officinarum</i> L. (sugarcane)	<i>Craspedonispa saccharina</i> Maulik (Trinidad)	Callan, 1954
<i>Bambusa</i> spp. (bamboo)	11 cassidine species (Old World)	Maulik, 1937
	<i>Anoplites heringi</i> Uhmann (Costa Rica)	Callan, 1954
	<i>Clinocarispa bisbicarinata</i> Uhmann (Trinidad)	Callan, 1954
<i>Oryza sativa</i> L. (rice)	<i>Diclidispa armigera</i> Olivier (Asia)	Sen and Chakravorty, 1970; Vadadia et al., 1989
	<i>Hispa oenescens</i> Baly (Asia)	Maxwell-Lefroy, 1906
	<i>Leptispa</i> Baly (Asia)	Maxwell-Lefroy, 1906; Maulik, 1919
<i>Cordia sebestena</i> Linnaeus	<i>Eurpepla calochroma</i> (Blake) (Florida)	Chaboo, 2004

Past recommended treatments of cassidine pests include old-fashioned washes with tobacco and soap (Froggatt, 1914) and lead arsenate (Lever, 1934; Frost, 1942), as well as infection with *Beauveria globulifera* Picard (Reyes, 1932). The insecticide thiocyclam hydrogen oxalate has been effective in controlling adults of *Coelaenomenodera* (Philippe, 1990). By injecting stems of hosts or soil (for root uptake by hosts) with this insecticide, adults and larvae can both be controlled (Mariau and Philippe, 1983). *Pediobius (Pleurotropis) parvulus* Ferr., a eulophid parasite, has been successfully used to control *Promecotheca* on some Pacific Islands (Philippe et al., 1979).

The case history of *Craspedonta leayana* (Latreille) (= *Calopepla leayana* Hope) illustrates the great impact of some cassidines. This species occurs throughout China, India, Laos, Myanmar, and Thailand (Borowiec, 1999). It is a natural herbivore of *Gmelina arborea* Roxb. ex Sm. (Verbenaceae) (Atkinson, 1928; Beeson, 1941), an important tropical pulpwood commonly called white teak, Asian bushbeech, white beech, or grey teak (D. Little, personal commun.). Plantations of *Gmelina* Linnaeus were initiated in 1924 in northern Myanmar to supply wood locally. Increasing levels of defoliation by *Craspedonta* Chevrolat were noted subsequently (Atkinson, 1928), and a pest control study was initiated. Control methods included hand collection (e.g., 428,000 individuals collected in August 1935), introduction and mass rearing of various natural parasitoids, destruction of potential dormancy sites (e.g., felling dead trees and clearing land around plantations by burning vegetation), various traps, changes in silvicultural methods, and application of calcium cyanide washes. None of these methods proved successful in controlling dense beetle populations. By the late 1930s, *Gmelina* plantations were abandoned due to *Craspedonta* impact (Garthwaite, 1939; Beeson, 1941).

CASSIDINES AS BIOCONTROL AGENTS

On the economically positive side of phytophagy, some cassidines serve as biological control agents for several weedy plants. *Cassida rubiginosa* (Müller) was acci-

dentally introduced into North America from Europe around 1901 (Barber, 1916). Fortunately, it became a valuable defoliator of creeping thistle, *Cirsium arvense* (L.) Scop., in Canada (Tipping, 1993; Ang et al., 1994; Ang and Kok, 1995; Bacher et al., 1999). *Cassida azurea* Fabricius (Julien and Griffiths, 1998) and *Cassida hemisphaerica* Herbst (Maw, 1976) are used to control bladder campion, *Silene cucubalus* Weibel (Caryophyllaceae), in North America. One southern African *Cassida* species was introduced to Australia to control *Chrysanthemoides monilifera* (L.) Norl. (Verbenaceae) (Kleinjan and Scott, 1996) but failed to become established (Julien and Griffiths, 1998). *Chelymormpha cassidea* (Fabricius) (Julien and Griffiths, 1998), *Chirida guttata* (Olivier) (Maw, 1984), and *Metriona bicolor* (Fabricius) (Maw, 1984) have all been used as controls of bindweeds, *Calystegia specium* (Linnaeus) and *Convolvulus arvensis* Linnaeus (Convolvulaceae) in Canada. Several members of *Anacassis* Spaeth have been used against weeds in the genus *Baccharis* (Asteraceae). *Stolas fuscata* (Klug) and *Stolas phaeopada* Buzzi were introduced from Brazil to control *Baccharis halimifolia* Linnaeus in Australia (McFayden, 1987) but failed to establish (Julien and Griffiths, 1998). *Stolas phaeopada* was introduced into the USA to control seepwillow, *Baccharis salicifolia* (R. and P.) (Boldt, 1989; Boldt et al., 1991). *Physonota* Boheman species have been used as a biocontrol of *Cordia* in the West Indies (Simmonds, 1949a, 1949b; Williams, 1951; Cock, 1985), and *Physonota alutacea* Boheman was introduced from Trinidad to control *Cordia macrostachya* (Jacquin) Roemer and Schultes in Mauritius (Williams, 1950). *Gratiana* species have been used in South Africa to control *Solanum sisymbriifolium* Lam. (Solanaceae), an invasive weed from South America (Siebert, 1975; Hill and Hulley, 1995, 1996; Julien and Griffiths, 1998). Members of the genus *Lantana* Linnaeus (Verbenaceae) have become a particular scourge worldwide, and 38 insect species have been introduced into 29 countries as possible controls of this weed (Broughton, 2001). Cassidine defoliators have proven to be the most successful control program of *Lantana* to date (Broughton, 2001). The Central American species *Octo-*

toma championi Baly was released in Australia, Fiji, Hawaii and South Africa (Wilson, 1979; Julien and Griffiths, 1998); the Mexican species *Octotoma scabripennis* Guérin-Ménéville was released into Australia, Cook Islands, Fiji, and Ghana (Staines, 1989; Harley, 1973, 1974; Swarbrick et al., 1995; Julien and Griffiths, 1998; Broughton, 1999); the Brazilian species *Uroplata girardi* Pic was introduced into 20 countries in Asia, Africa, and the Caribbean (Swarbrick et al., 1995; Julien and Griffiths, 1998; Broughton, 1999); and the Brazilian species, *Uroplata lantanae* Buzzi and Winder was released in Australia, Fiji, and South Africa (Winder et al., 1984; Julien and Griffiths, 1998). These all became established but failed to control the weed (C. Reid, personal commun.).

OTHER ECOLOGICAL ASPECTS

Ecological research has been done on several *Aspidimorpha* species (Thompson, 1964; Baltazar, 1970; Hawkeswood, 1982; Verma and Shrivatava, 1985), several *Cassida* species (Kosior, 1975; Steinhausen, 1950; Olmstead and Denno, 1993; Obermaier and Zwölfer, 1999; Ward and Pienkowski, 1978), two *Conchylotenia* Spaeth species (Olckers and Hulley, 1989; Heron, 1999), *Gratiana spadicea* Klug (Becker and Pires Friere, 1996), *Octuroplata* Uhmman species (Teixeira et al., 1999), *Plagiometriona flavescens* (Boheman) (Nogueira-de-Sá and Valverde de Macêdo, 1999), *Calyptocephala brevicornis* (Moura, 1984), and *Eurypedus nigrosignatus* (Gómez, 1997, 2004; Gómez et al., 1999).

Additional studies include Costa Rican hispines (Hespenheide and Dang, 1999), the *Stolas* complex on morning glories (Carroll, 1978), and biological control, for example, *Cassida viridis* Linnaeus (Engel, 1932, 1936), *Cassida hemisphaerica* (Maw, 1976), and *Gratiana* Spaeth species (Siebert, 1975; Olckers et al., 1999; Hill and Hulley, 1995, 1996; Hill, 1999). The hispine communities on *Heliconia latispatha* Benth. are well known due to the efforts of Donald Strong and collaborators (Strong, 1997a, 1997b; Strong and Wang, 1977; McCoy, 1984, 1985). With multiple species and generations occupying the same host plant, it is surprising that little

competition has actually been observed within these communities.

Exophagous feeding cassidines generally prefer host plants in sunny spots such as along road cuts, trails, borders, gaps, and tree falls. Some hosts are fast-growing weedy species common in disturbed tropical habitats (e.g., *Ipomoea* (Convolvulaceae) and *Mikania* Willd. (Asteraceae)). Cassidines appear to represent only a small proportion of chrysomelids living in tropical forest canopies (Basset and Samuelson, 1996; Farrell and Erwin, 1988; Wagner, 1999; Novotny et al., 1999) and Iberian forests (Baselga and Novoa, 2006). Malaise trap sampling around Costa Rica found that Cassidinae represented a small fraction of the chrysomelids (Flowers and Hanson, 2003).

These surveys involved canopy fogging or malaise traps and provide a picture of chrysomelid diversity skewed toward taxa collected by those techniques. A survey of other types of habitats or employing different collecting techniques (e.g., beating sheet) might reveal other patterns in diversity and community structure. The sedentary habits and ecological diversity of Cassidinae make them good models for exploring alpha and beta diversity and community structure.

TROPHIC PATTERNS

The best known cassidine life histories are those with larvae that mine or feed openly. Adult cassidines were considered to be exclusively open-leaf feeders; however, Gilbert et al. (2001) reported an unusual feeding pattern in adults of *Imatidium rufiventre* Boheman and *Imatidium thoracicum* Fabricius in Peru. Pairs of *Inga* leaves were found held together, with the lower leaf overlapping the upper leaf. Adults were inside, feeding only where the two leaves overlapped. Substances that would hold leaves together (e.g., saliva) are unclear.

The larval stages of Cassidinae are more diverse in their trophic patterns than are the adults. Leefmans (1918) first divided Hispinae s.str. into two groups: miners and those feeding between young palm leaves. Gressitt (1957) expanded the latter group to include taxa that feed on calyces, blossoms and petiolar bases. Kalshoven (1957) elaborated

on feeding types in Hispinae s.str. and recognized three feeding groups: larvae that feed between young unfolded leaves, larvae that mine stalks, and larvae that mine leaves. A fourth group, free-living external feeders, was later added (Monteith, 1970). Jolivet and Verma (2002) recognized these four groups. Mariau (2004) recognized only two feeding groups for Hispinae s.str., being those originally identified by Leefmans (1918). In contrast, Staines (2004) recognized four feeding groups in Cassidinae: open-leaf feeders, rolled-leaf feeders, leaf miners, and stem miners.

Although it has not been explicitly discussed, this classification of cassidine larval feeding evokes the guild concept (Root, 1967, 1973). Guilds are a useful term in analyzing and describing community ecology and diversity (Simberloff and Dayan, 1991). Individual cassidine researchers recognize different types and numbers of feeding groups (e.g., compare Staines, 2004 and Mariau, 2004). These feeding groups could be refined further. For example, "cryptic feeding" describes two very different behaviors: feeding within a constructed leaf shelter or feeding between unrolled layers of a young leaf. Additionally, some species often lumped with leaf-tube feeders actually live only in the water-filled bracts of *Heliconia* inflorescences, a microhabitat with a different regime of water, insolation and enemy pressure from that of the leaf-tube scrapers. I recognize six ecological guilds in Cassidinae larvae: leaf-shelter builders, stem miners, leaf miners, rolled-leaf strip miners, floral bract scrapers, and open-leaf feeders. I distinguish these groups on the basis of larval feeding modes and microhabitat. Biological information for each group is uneven; we know very little about leaf-shelter builders and stem borers but more information is available for leaf miners and open-leaf feeders. As far as we know, adult cassidines are external feeders; some adult Imatiidini appear to build cryptic leaf constructions (Gilbert et al., 2001). The guilds below may or may not reflect phylogenetic groups, and they may be found to overlap or could be more finely partitioned when we learn more about the biology of species.

1. *Leaf-shelter builders*. This behavior is recorded for larvae of Leptispini, an Old

World monogeneric tribe (67 species) (Froggatt, 1914; Fletcher, 1914; Maulik, 1919; Voronova and Zaitsev, 1982; Chen et al., 1986). Leaf-shelter building behavior in insects has been discussed in Frost (1942). Larvae of *Leptispa* Baly construct shelters by bending over leaves of their two very divergent hosts, rice and coconut palm (Froggatt, 1914; Maulik, 1919; Voronova and Zaitsev, 1982; Chen et al., 1986). It is unknown how the leaf is fastened together—with saliva, silk, or tight folds that dry in position. In *Leptispa pygmaea* Baly eggs are laid on the dorsal surface of leaves, and the larvae live within the half-folded leaves (Fletcher, 1914; Maulik, 1919). Feeding is probably by skeletonizing the leaf. Pupation occurs within this leaf fold. *Leptispa* individuals can withstand short periods of submersion under water (in a rice field), and their dense ventral pubescence may act as a plastron.

2. *Stem miners or borers*. Larvae in four genera and two tribes exhibit this behavior: *Gyllenhaleus* Weise and *Cryptonychus* Gyllenhal (Cryptonychini) (Maulik, 1932; Lepesme, 1947; Mariau, 2004), and *Estigmena chinensis* Hope (Maulik, 1919; Beeson, 1941) and *Anisodera* Chevrolat (Anisoderini) (Kalshoven, 1951, 1957; Koningsberger, 1915; Chen, 1985; C. Staines, personal commun.).

In *Gyllenhaleus*, larvae live initially in the terminal buds of *Costus* Linnaeus (Costaceae) and later bore into and mine stems. *Cryptonychus* larvae have labile choices in host plant family and host plant organ, using both stems of *Amomum* Roxb. (Zingiberaceae) and leaves of *Carex* Linnaeus (Cyperaceae) (Maulik, 1932). In *Estigmena chinensis*, one to four eggs are laid on young bamboo shoots. Early instars initially feed together around their natal site, then separate and bore into the bamboo stem where they tunnel up and down between the internodes. Pupation occurs within the stem (Maulik, 1919) and young adults emerge via exit holes when the first monsoon showers arrive (Beeson, 1941).

3. *Cryptic rolled-leaf feeders*. This behavior is recorded for some species in all four genera of Arescini (17 species) and in three of the nine genera of Cephaloleiini (311 species). Rolled-leaf hispines are so named because of

their occurrence within the partially opened leaves of their host plants. They should now be called rolled-leaf cassidines, in keeping with our updated view of relationships and nomenclature.

Champion and Bates first noted cassidines in *Heliconia* insect communities (Baly, 1885; Maulik, 1919). An interesting body of literature has grown on these cassidine species because of the sustained interests of several researchers (Maulik, 1937; Wang, 1977; Seifert and Seifert, 1979a, 1979b; Strong, 1977a, 1977b, 1981, 1982a, 1982b; Strong and Wang, 1977; Morrison and Strong, 1981; McCoy, 1984, 1985; Staines, 1996; Wilf et al., 2000; Johnson, 2004; McKenna and Farrell, 2005). The relationship between these cassidines and their host plants is thought to be very old, dating to the latest Cretaceous, 66.2 Ma ago (Wilf et al., 2000).

The unopened (immature) leaves of the host plants form tubes, with the leaf folds providing multiple layers. In the wet and dry forests of Central and South American where host plants occur, some water and debris can accumulate at the bottom of leaf tubes, creating a damp habitat. Adult rolled-leaf cassidines thus live within this tightly spaced, low-light, semiaquatic microhabitat. The immature stages of rolled-leaf cassidines are more varied than are adults in their microhabitat choices, spending most of their time either in the rolled leaf, or at the leaf base in the crescent-shaped cavity of the petiole, or in the case of some *Cephaloleia* on opened leaves under wet debris (D. McKenna, personal commun.). I follow Seifert and Seifert (1979a) and recognize some classical rolled-leaf cassidines as a distinct trophic type, the floral bracts scrapers (described next).

Larvae of Arescini and Cephaloleiini are flattened and extremely thin (only 2–3 mm thick) and are semitransparent, with some background leaf color showing through (Chaboo, personal obs.). This body form, resembling water-penny larvae (Coleoptera: Psephenidae) (Maulik, 1931), probably allows movement in tight spaces. Respiration is via ventrally positioned spiracles, in contrast to the laterally positioned spiracles in other cassidine immatures. Some larvae of rolled-leaf cassidine species have the venter densely

pubescent and the lateral margins with a setal fringe (Staines, 1996). This pubescence may aid in attachment, movement, respiration (as a plastron), or filter debris and keep mouthparts clean, but such potential functions do not explain why some *Cephaloleia* species lack hairs.

The two available life-history studies of *Chelobasis perplexa* Baly (Arescini; Wang, [1977]) and *Cephaloleia fenestrata* Weise (Cephaloleiini; Johnson [2004]) provide detailed models for understanding the biology in these two tribes. In *Chelobasis perplexa*, flat, oval eggs are laid within the leaf tube and hatch within 20 days of oviposition; many eggs are lost through desiccation and parasitism. *Chelobasis* has a remarkably long life cycle, with a prolonged period of immaturity (Wang, 1977; Strong and Wang, 1977). This life cycle is further extended through the addition of larval instars (eight instead of five) (table 5) and by slowed development (>200 days) (Wang, 1977; Strong and Wang, 1977). Host plant nutritional quality may be a key factor influencing this life-cycle extension (Strong and Wang, 1977). Wang (1977) found that leaf tubes of hosts appear to be edible for about 20 days, and then larvae migrated to new leaves and new plants. Pupae are cryptically colored and pupation occurs on the stalk of the host plant. Adults are iteroparous (reproducing throughout their lives), so multiple generations can be found in the same tube.

In *Cephaloleia fenestrata*, Johnson (2004) reported that eggs, the two larval instars, and pupae occupy the crescent-shaped petiolar concavity of unrolled leaves whereas adults live in the rolled leaf tubes. Oviposition is on the petiole; eggs are laid singly, in pairs, or occasionally in clusters up to eight, and they may be covered with frass. The first instar emerged in 10–14 days and lasted about 34 days. The second stadium lasted about 61 days. Pupation, lasting about 30 days, occurred both in the petiole and perhaps elsewhere on the plant. Although *Cephaloleia fenestrata* larvae have a relatively extended larval development, there are only two instars, a remarkable contrast with the six reported for *Chelobasis perplexa*.

Our biological understanding of rolled-leaf cassidines has significant gaps. Data are

TABLE 5
Variation in Numbers of Instars of Cassidinae

Taxon	Instars	Source
Alurnini		
<i>Alurnus humeralis</i> Rosenberg	9	Villacis Santos, 1968
<i>Alurnus humeralis</i>	8	Mariau, 2004
Arescini		Wang, 1977; Strong and Wang, 1977
<i>Chelobasis perplexa</i> Baly	8	
Cephaloleiini		
<i>Cephaloleia</i> Chevrolat	8	Staines, 1996
Chalepini		
<i>Odontota horni</i> Smith	3	Kogan and Kogan, 1979
Coelaenomenoderini		
<i>Coelaenomenodera elaeidis</i> Maulik	4	Coterell, 1925; Morin and Mariau, 1970
<i>Coelaenomenodera lameensis</i> Berti and Mariau	4	Mariau, 2004
Cryptonychini		
<i>Brontispa</i> Sharp	6	Jolivet and Hawkeswood, 1995
<i>Gestronella</i> Weise	6	Mariau, 2004
Hispini		
<i>Diclidispa</i> Gestro	5–6	Gressitt, 1950
<i>Diclidispa armigera</i> Olivier	4	Vadadia et al., 1988
Hispoleptini		
<i>Hispoleptis subfasciata</i> Pic	4	Mariau, 2004
Promecothechini		
<i>Promecothea cumingi</i> Baly	2	Maulik, 1919
<i>Promecothea reichei</i> Baly	3	Taylor, 1937
Uroplatini		
<i>Octotoma scabripennis</i> Guérin-Ménéville	3	Broughton, 1999
<i>Uroplata girardi</i> Pic	3	Broughton, 1999

lacking for five cephaloleine genera; *Stenispa* larvae are reported as leaf miners (Riley and Enns, 1979; Ford and Cavey, 1985). In the two other cephaloleine genera, some species have larvae that live only in floral bracts (described next). It is unclear how many different larval feeding types exist in these interesting tribes.

4. *Bract scrapers*. These are usually grouped with rolled-leaf cassidines; however Seifert and Seifert (1979a) distinguished them as distinct flower beetles, unlike strict rolled-leaf beetles. Larvae of species of two genera, *Xenarescus* Weise (Arescini) and *Cephaloleia* Chevrolat (Cephaloleiini), live both within the upright flower bracts of *Heliconia* and rolled leaves of *Heliconia* (Seifert and Seifert, 1976a, 1976b; Seifert, 1982). Our knowledge of flower-bract cassidines comes mainly from the significant works of Richard Seifert. He initiated research on this system for his

doctoral research (Seifert, 1974) and produced the fundamental papers on these insects (Seifert, 1975, 1982, 1984; Seifert and Seifert, 1976a, 1976b, 1979a, 1979b), but died at the age of 32.

Heliconia inflorescences can be pendulous or upright. The upturned open bracts of upright inflorescences catch water and debris thus providing miniature aquatic habitats for many insects. *Cephaloleia* larvae living in these pools are morphologically similar to *Cephaloleia* larvae living within closed leaves. They feed by grazing along the water line on the inner surface of the bract. The larval period can last for more than 32 days in *Cephaloleia neglecta* Weise and larvae migrate to younger apical bracts as bracts mature (Seifert and Seifert, 1979a).

I distinguish flower-bract cassidines and rolled-leaf cassidines on the basis of the different food choice and ecological regimes

of their habitats. Bract pools and leaf-tubes are similar as semiaquatic habitats, but leaf tubes constrain morphology and behavior (e.g., movements) of inhabitants considerably. The persistence, chemistry, sun exposure, temperature, and biotic interactions (competition, predation, and parasitism) of bract pools may vary widely and change rapidly with rainfall and debris; for example, flooding under heavy rains may flush the pool and threaten inhabitants.

Bract scrapers, petiolar strip miners and rolled-leaf strip miners are the three known feeding patterns discovered to date in the single genus *Cephaloleia*. It is still unclear how flexible or fixed are these feeding modes, whether larvae are capable of all types of feeding or switch under duress. The biological foundation established by Seifert and others, the careful generic revision of *Cephaloleia* by Staines (1996), and the phylogenetic hypothesis of McKenna and Farrell (2005) provide a firm basis for further work on this unusual genera.

5. *Leaf-mining cassidines*. Harris (1835) described the first mining larvae (and parasitoid) of *Hispa*. Twenty-two cassidine tribes with ca. 2500 species are presently considered to be miners. Notosacanthini was classically regarded as a tortoise beetle tribe (e.g., Borowiec, 1999) on the basis of adult morphology, but its mining larva was recently described (Medvedev and Eroshinka, 1988; Reid, 1995; Rane et al., 2000).

Needham et al.'s (1928) account of *Hispa*, *Chalepus*, *Baliosus* Weise, *Octotoma* Dejean, *Microrhopala* Chevrolat, *Stenopodius* Horn, and *Uroplata* Chevrolat is a good introduction to cassidine leaf-mining biology. Hering (1951) and Kalshoven (1957) added interesting information. Ford and Cavey (1985) also provided a valuable introduction to temperate cassidine miners. Hespeneheide and Dang's (1999) study is important because of its long duration and intensive examination of species in a single site in Costa Rica. Works on *Dicladisa armigera* (Sen and Chakravorty, 1970; Vadadia et al., 1988), *Microrhopala* Dejean (Hendrickson, 1930; Clark, 1983), *Octuroplata octopustulata* (Baly) (Teixeira et al., 1999), *Odontota horni* (Kogan and Kogan, 1979), *Oediopalpa* Baly (Bruch, 1906), *Pentispa* Chapuis (Boldt and Staines,

1993) and *Promecotheca* (Taylor, 1937) are also valuable.

The life history of the black locust leaf miner, *Chalepus dorsalis*, is typical of leaf-mining cassidines (Needham et al., 1928). *Chalepus* eggs are laid in groups of three to five and are covered with feces. The first larva to hatch chews a hole into the leaf that the others then use to enter into a common mine. In 2–4 days, they all leave the mine and separately seek new leaves to make solitary mines (which increases leaf damage). Altogether, the larval period is about 3 weeks. Pupation lasts 7–10 days and occurs within the mine (Needham et al., 1928). In *Odontota*, single eggs are laid under a cut flap of the leaf, and the larva mines outwards from this egg chamber (Kogan and Kogan, 1979). In *Oediopalpa guerini* the larval period lasts 15–20 days and pupation lasts about 14 days (Bruch, 1906).

Oviposition sites of mining cassidines may be on the dorsal or ventral surfaces of the leaf, within the leaf, or on the stem surface. Females of *Dicladisa* Gestro prepare a small excavation in the leaf before depositing a single egg (Vadadia et al., 1988). In *Uroplata* Boheman (Brèthes, 1902) and *Promecotheca* (Maulik, 1919; Taylor, 1937) eggs are deposited singly on the ventral surface of leaves. In *Hispellinus callicanthus* (Bates), a single egg is deposited at the leaf apex (Maulik, 1919). In *Notosacantha* Chevrolat, a single egg is inserted into a hole in the leaf or stem (Zaitsev and Medvedev, 1982) and covered with excreta (Monteith, 1991). In other genera, groups of eggs, or oothecae, may also be inserted into leaves, for example, *Coelaenomenodera* (Cotterell, 1925). Eggs may be naked, or they may be covered with chewed leaf fragments—for example, *Anisostena* Weise (Ford and Cavey, 1982), *Promecotheca* (Taylor, 1937), and *Coelaenomenodera* (Cotterell, 1925)—or with feces—for example, *Chalepus*, *Baliosus* (Chittenden, 1904) and *Microrhopala* (Hendrickson, 1930). Eggs hatch within 1 week and the young larvae tunnel into their natal leaf.

Cassidine miners appear to show some preference for host plants that are heavily or partly shaded (Ford and Cavey, 1985). In open habitats, leaves selected for mining are usually those on the lower shaded portion of

the plant. Insolation may inhibit larval development and survival. The shape of mines excavated by cassidines may be tubular, sinuous, or serpentine and may form blotches or blisters. Because several larvae may feed on a single leaf, the latter can become mined out as mines connect (Jones and Brisley, 1925). Hespeneide and Dang (1999) described a complex lobulate blotch mine in *Octhispa haematopyga* (Baly) where eggs are deposited in a chamber and larval feeding eventually produces radiating tunnels. Pupation occurred in the original, now central, chamber. They also observed larvae of some species emerge from their natal mines and make completely separate chambers for pupation. Some cassidine species have larvae that may occupy more than one leaf during their growth, for example, *Hispia testacea* Pic (Needham et al., 1928). Most mines have a single individual of one species but some mines can have individuals representing multiple species. Communal mines have been reported in *Microrhopala* (Hespeneide and Dang, 1999). Most mining cassidines appear to have five instars however some species have wide variation in instar number (table 5). This is a startling variation, uncommon within Insecta, and its significance is unclear.

Pupation may occur externally, with pupae affixed to the stem or leaf, or within mines, and adults emerge from exit holes. Pupation within mines may be within the natal leaf or in a new leaf. All cassidine miners may pupate solitarily; gregarious pupation is not known.

Leaf mining imposes such severe morphological constraints that mining insects tend to resemble each other (Frost, 1924, 1925; Needham et al., 1928). Cassidine leaf mining larvae superficially resemble other leaf mining chrysomelids in Galerucinae and Zeugophorinae. They tend to be flattened, having reduction and flattening in the head, the mouth in a prognathous position, and reduction or loss of legs and lateral projections. Larval legs are vestigial in *Octotoma* (Bruch, 1933), *Scoeloenopla* (Jolivet and Hawkeswood, 1995), and *Hispellinus* (Reid, 1995). The larval anus varies in its position, being ventral or posterior. The last abdominal segments may also vary; they may resemble

other abdominal segments in being naturally tapered posteriorly and with a simple apex, or the last one or two segments may be partially or completely fused and modified as a heavily sclerotized, shovel-shaped structure.

6. *Open leaf-feeders*. Many cassidine species have open foliar-feeding larvae and correspond roughly with the classical Cassidinae s.str. (tortoise beetles). Among plesiomorphic cassidines, *Aproidea* (Monteith, 1970) and *Oediopalpa* (Bruch, 1906) also have open feeding larvae. Given their conspicuousness, this feeding guild is better known than more cryptic cassidines. Life-history studies are available for many genera: *Aspidimorpha* Hope (Simon Thomas, 1964; Maulik, 1919; Balthazar, 1970), *Botanochara* Dejean (Habib and Vasconcellos-Neto, 1979), *Craspedonta* Chevrolat (= *Calopepla*; Garthwaite, 1939), *Cassida* Linnaeus (Maw, 1976; Müller and Hilker, 1999), *Chelymorpha* Chevrolat (Chittenden, 1924), *Dorynota* Chevrolat (Candèze, 1861; Buzzi, 1976b; Buzzi and Cruz, 1991), *Gratiana* Spaeth (Becker and Frierio-Costa, 1987, 1988), *Laccoptera* Boheman (Hoffman, 1933), *Metrioria* Weise (Yeung, 1934), *Stolas* Billberg (Buzzi, 1975b; Boldt et al., 1991), *Spaethiella* Barber and Bridwell, and *Hemisphaerota* Chevrolat (Chaboo and Nguyen, 2004, and citations therein).

Stolas fuscata (Klug) has a typical tortoise beetle life cycle (Paterson, 1931; Buzzi, 1975a, 1975b; Boldt, 1989; Boldt et al., 1991). Oothecae in this species include 8–55 eggs, and eggs hatch in 7–9 days. Hatching success is about 90%. Each of the five larval stages retains an exuvio-fecal shield, and the total larval period is about 3–4 weeks. Pupae are attached by the abdomen to the leaf apex and are capable of flexing their abdomens when disturbed. Boldt et al. (1991) reported a weight difference between male and female pupae. The pupal stage lasts about a week. Adult females can mate within 3–5 days after emergence and several times during their lives that can last 145 ± 42 days. Oviposition begins about 1 week after mating.

Open foliar cassidines deposit eggs singly or in groups. Single egg deposits have been reported for *Prioptera sinuata* (Olivier) (Schultze, 1908) and *Craspedonta leayana* (LeFroy, 1909). Small groups of 3–4 eggs

are deposited by *Aspidimorpha* (Schultze, 1908) whereas masses with more than 100 eggs are deposited in *Eugenysa coscaroni* Viana (Windsor and Choe, 1994). Egg mass sizes vary intraspecifically; for example, *Calochroma leayana* deposits masses of up to 100 eggs but average masses have about 60 eggs; laboratory-reared females may even lay single eggs when this is unknown in wild females (Garthwaite, 1939). In *Aspidimorpha miliaris* (Fabricius), the brood can range from 32 to 80 eggs, with one ootheca produced every 3–4 days. This species has been reported to produce 23 oothecae in 75 days (Maulik, 1919). Garthwaite (1939) recorded a laboratory-reared female of *Calopepla leayana* laying 23 oothecae over a 45-day period. Interspecific variation in egg mass sizes is also known; for example, *Lacoptera* (*Lacopteroidea*) *tredecimguttata* Wagener (= *Lacoptera philipensis*) deposits a single, naked egg (Schultze, 1908), whereas *Lacoptera chinensis* Fabricius deposits groups of up to four eggs and covers them with feces (Kershaw and Muir, 1907).

Oviposition sites of open foliar cassidines include apical leaves, as in *Aspidimorpha* (Nakamura and Abbas, 1989), or stems of host plants, for example, *Basipta stolidia* Boheman and *Eugenysa coscaroni* Viana (Windsor and Choe, 1994). Egg groups usually have each individual egg attached by its own stalk to the surface of apical leaves, but in *Acromis* the eggs are clumped (like grapes) and suspended by a single stalk (Chaboo, 2001).

Eggs may be naked or covered with glandular secretions or with both glandular and fecal coverings. Secretions may be shaped into a single, simple membrane (Paterson, 1931; Chaboo and Nguyen, 2004), or into elaborate constructions with multiple membranes that have been consequently called oothecae (Maulik, 1919; Garthwaite, 1939; Hinton, 1981; Hilker, 1994). The term “ootheca” has been used primarily in Orthoptera, Lepidoptera, Heteroptera, Diptera and Trichoptera (Nichols, 1989), and it clearly does not refer to homologous structures. Given this wide application of oothecae, as well as the historical use of oothecae in Cassidinae, the term is retained here for these ornately covered egg masses.

Within these oothecae, eggs are deposited in several longitudinal rows and covered with as many as 80 membranes. Marginal cells can contain unfertilized eggs or air pockets. Maulik (1919) reported that an *Aspidimorpha miliaris* female takes up to 1.5 hours to construct an ootheca. In addition to oothecal membranes, tortoise beetles may coat eggs with feces, regurgitated food, and colleterial secretions (which may also act as a glue), and they may even apply endosymbionts (Paterson, 1931; Engel, 1936; Barrows, 1979; Damman and Cappuccino, 1991; Becker, 1994; Hilker, 1994). Glandular cells in the tube-shaped accessory glands that open into the vagina in some Cassidinae (and Eumolpinae) (Hinton, 1981; Suzuki, 1988b) are responsible for secretions used in oothecal constructions (Hinton, 1981; Hilker, 1994). Chemical protection of eggs is known in Galerucinae and Chrysomelinae (Pasteels et al., 1982; Dalozze and Pasteels, 1979; Hilker, 1994), but this has not been investigated in Cassidinae.

Membranes can vary in number; for example, *Conchylotenia nigrovittata* (Boheman) has 3–4 membranes (Rane et al., 2001), while *Gratiana spadicea* (Klug) can have up to 77 membranes (Becker and Friero-Costa, 1987). Tropical species can have oothecae in the form of ribbons, nets and sacs (Muir and Sharp, 1904). Coverings may serve for concealment (Muir and Sharp, 1904), they many offer protection from desiccation and predators and parasitoids. Extra, empty peripheral cells in the oothecae of *Basipta* and *Aspidimorpha* (Maulik, 1919) may offer additional protection. These hypotheses on the role and effectiveness of egg coverings have been little investigated. Damman and Cappuccino (1991) found that fecal coverings in *Microrhopala vittata* Fabricius reduced egg mortality from predation, but eggs at the bottom of the mass were most vulnerable to parasitism. In *Acromis sparsa*, a species with maternal care, no eggs survived when mothers were removed (A. Trillo, personal commun.).

Eggs may hatch within days of oviposition. For example, egg hatch in *Cassida hemisphaerica* can be within 3 days or last up to 18 days depending on temperature (Muir and Sharp, 1904; Maw, 1976). In *Chelymophra*

cassidea the egg phase can last about 10 days, the larval period about 3 weeks, and the pupal period about 1 week. Larvae emerge from eggs by eating their way out at one end (Paterson, 1931). Remnants of the egg mass may remain on the plant for a long time; consumption of the entire eggshell has not been reported. Larvae start feeding on their natal leaf (Engel, 1936; Hawkeswood, 1982; Winder, 1987) or move to more apical leaves (Gómez et al., 1999).

Tortoise beetles usually have five active free-living instars. An inactive, sessile fifth larval instar, called a prepupa, has been reported in some *Cassida* species in Poland (Kosior, 1975), in *Calopepla leayana* in Myammar (Garthwaite, 1939), in *Eurypepla calochroma* in Florida (Chaboo, 2004), and in *Eurypedus* in Panama (N. Gómez, personal commun.). Generally, each larval stadium may last a week; in tropical areas, all instars from one brood can be observed within 3–4 months (Chaboo, personal obs.).

Open foliar cassidine larvae can have an ornate appearance, being elongate-oval, somewhat flattened, with numerous lateral projections on the thorax and abdomen. Lateral pleural (scoli) and caudal processes (urogomphi) can be quite long and even branched. Such projections may also occur in the pupae. These larvae usually retain their feces and exuviae into a shield that may weigh as much as the individual.

Pupation is always external, being attached to the ventral side of leaves (e.g., *Eurypepla*; Chaboo, 2004) or from stems (e.g., *Eugensya*; Chaboo, 2002a). Pupae are capable of making jerking movements (Maw, 1976; Chaboo, 2002a); McCauley (1938) recorded 20 such consecutive movements in *Microrhopala xerene* (Newman). Pupae may be solitary (e.g., *Eurypepla*; Chaboo, 2004), or grouped (e.g., Acromis; Chaboo, 2001). In species with maternal care, grouped pupae are also guarded (Chaboo, 2002a).

7. *Petalophagy*. Tortoise beetles are almost universally leaf feeders; however petalophagy (flower chewing) has been recorded in larvae of two species of *Echoma* Chevrolat (Windsor et al., 1995), in *Eurypepla calochroma* Boheman (Chaboo, 2004), and in *Cassida hemisphaerica* Herbst (Maw, 1976). Petalophagy appears to be obligate in *Echoma* but

flexible in *Eurypepla* and *Cassida*. It is known in other chrysomelids (Jolivet, 1988d; White, 1983; Schöller, 1999).

EXTENDED LIFE HISTORIES

Life cycles of most cassidines are commonly completed within 2–3 weeks in tropical habits or within 2–3 months in temperate species (Chaboo, personal obs.), and they may have five instars. A remarkable variation on this common pattern is a prolonged development in rolled-leaf species; for example, *Chelobasis perplexa* takes almost 1 year (Wang, 1977; Strong and Wang, 1977), and the palm-miner, *Alurnus humeralis*, is recorded as taking 428 days (Villacis Santos, 1968). Although this slowed development is not as spectacular as that displayed by the widely known 17-year cicada, it is still extraordinary by chrysomelid standards. Such metabolic stalling may be related to plant nutritional quality, antipredatory behavior, or to other factors.

Another remarkable variation from the common cassidine life history is the range in numbers of larval instars (table 5). The current record of nine species in eight tribes with unusual numbers of instar ranges has grown randomly. Further examination of life histories of more species may reveal a wider phenomenon within Cassidinae. The addition, insertion and deletion of instars may help prolong or accelerate the life history. The reasons for this modification of the life cycle are unclear.

MOVEMENT ON LEAVES

Leaf surface morphology is diverse, ranging from smooth to spiny to hairy, and it presents a special challenge for attachment and movement of phytophagous insects (Bernays, 1991). There have been few studies of cassidine leg morphology but they suggest that both larvae and adults have specialized tarsal features for attaching to and walking on leaves. Medeiros et al. (2004) studied larvae of six Brazilian cassidine species and found that the legs varied in lengths, and that the tarsungulus varied in morphology and in attachment to leaves. Tarsungulus morphology varied in width of the base and angle of

curvation of the apex (and therefore the relative size of the aperture between the apex and base). On glabrous surfaces, the tarsungulus is inserted into the epidermis and the animals appear to walk on the tarsungulus tips. On hairy surfaces the tarsungulus is attached to the leaf trichomes. An individual may use both modes of walking, depending on the surface. Longer legs can also pass between trichomes, so older larvae may walk on tarsungulus tips instead of attaching to trichomes as do younger instars.

Attachment to and movement on leaves has been studied in adults of a single cassidine species, *Hemisphaerota cyanea* (Attygalle et al., 2000; Eisner and Aneshansley, 2000; Eisner and Eisner, 2000; Eisner, 2003). Tarsomeres I–III are somewhat flattened and expanded, and they are packed ventrally with bristles with up to 10,000 bristles on each of the three tarsomeres (Eisner, 2003). Each bristle is bifid at the apex, thus multiplying the number of contact points with the leaf surface. These unique bifid setae secrete oil that provides an extremely strong adhesion to the leaf surface (Attygalle et al., 2000; Eisner and Aneshansley, 2000; Eisner and Eisner, 2000). This adhesion may also make it difficult to dislodge an individual once it is firmly attached to the substrate. Extending this line of research (Attygalle et al., 2000; Eisner and Aneshansley, 2000; Eisner and Eisner, 2000; Medeiros et al., 2004) to other cassidines will determine how widespread are these phenomena.

ENDOSYMBIONT TRANSMISSION

Coleopteran mycetomes (i.e., pouches that house intracellular symbionts such as bacteria) are known in Cassidinae, Donaciinae, Eumolpinae, Bostrychidae, and Silvanidae (Crowson, 1981) and in Spilopyrinae, Syntetinae, Sagrinae, and Cerambycidae (C. Reid, personal commun.). Cassidine mycetomes are located in outgrowths of the larval midgut and in the vaginal pouches of adult females. The vaginal pouches open into the common oviduct and bacteria are transferred to eggs (Stammer, 1936a, 1936b; Kasap and Crowson, 1980; Becker, 1994; Becker and Ferronato, 1990). The role of these endosymbionts in the egg or in larvae is unclear.

GREGARIOUSNESS

Larval gregariousness is common in many cassidines, starting from clustered eggs and lasting until the pupal stage in some species. The degree of gregariousness can vary; among instars of *Physonota* species and *Eurypedus nigrosignatus* larvae are initially gregarious but later instars are solitary (Caulfield, 1884, 1887; N. Gómez, personal commun.). In other species, larvae remain together through stadia and even pupate together (*Physonota*; unpubl. data). In species with maternal care, females stay with her offspring until young adults emerge. The mechanisms regulating group maintenance are unclear. Grégoire (1988) reviewed some of the advantages of chrysomelid clustering, citing parasitism, predation, cannibalism, efficiency of food use, and enhanced aposematism. There may be some relationship between gregariousness, larval cycloalexy (discussed next), and aposematism in Cassidinae (Olmstead and Chaboo, unpubl. data).

CYCLOALEXY

Cycloalexy (*kucklos* = ring, *alexo* = I protect) is a peculiar defensive behavior in gregarious larvae of some chrysomelid species in Cassidinae, Galerucinae s.l. and Chrysomelinae (Jolivet, 1988b; Vasconcellos-Neto, 1988b, 1990; Jolivet et al., 1990; Vasconcellos-Neto and Jolivet, 1988, 1989). At night, larvae converge into a tight circle. When disturbed during the day, cassidine larvae may quickly form a similar arrangement of tight circles with heads together directed inward and the abdomens directed outward, and they rapidly flex their abdomens in what appears to be coordinated waves of movement. Cycloalexy has been recorded in *Conchyloctenia punctata* (Fabricius) (Heron, 1999), *Aspidimorpha miliaris* (Verma, 1992), *Aspidimorpha puncticosta* (Heron 1992), *Chelymorpha infecta* Boheman (= *Chelymorpha informis* (Boheman)), *Echoma flava* Linnaeus (Vasconcellos-Neto, 1989), *Ogdoecosta biannularis* Boheman (Romero-Napoles, 1990), and *Eugenysa columbiana* (Boheman) (Chaboo, 2002). The group alarm and coordinated nature of cycloalexy suggests that some communications system is

operating among larvae. Vasconcellos-Neto and Jolivet (1989) suggested that the signaling device may be vibrational or pheromonal. These hypotheses are plausible in light of data from other insect groups; for example, Crocroft (1996) reported that when under attack by a predator, membracid nymphs produce vibrations to signal each other and also their guarding mother. In my observations of gregarious, maternally guarded larvae of *Eugenysa columbiana* in Costa Rica, *Acromis sparsa* in Panama and Peru, and *Acromis spinifex* in Trinidad, single larvae react rapidly to any contact with predators or parasitoids (or a pencil). All larvae will group within seconds, even those that had no contact, and the mother becomes very active, moving rapidly over her brood and moving toward the predator. This sequence of behavior resembles that described for the treehopper, *Umbonia crassicornis* (Homoptera: Membracidae), and examination of gregarious cassidine larvae and of maternal care species using the model of Crocroft (1996) may unveil the existence and nature of a signaling system.

FECAL USE IN CASSIDINAE

One of the most interesting behaviors of tortoise beetles is the recycling of feces and exuviae to construct a shield that is carried over the dorsum by larvae and is retained in some pupae (figs. 19, 20). Fecal recycling is not unique to cassidines; fecal coating on eggs and fecal lining of pupal chambers are known in various chrysomelids (Jolivet and Petitpierre, 1981). Constructions made of feces appear within five chrysomelid subfamilies. Criocerine larvae retain a wet viscous unstructured fecal mass on their dorsum (Sailsbury, 1943; Chapuis and Candèze, 1855; Schmitt, 1985, 1988; Morton and Vencl, 1998; Müller and Hilker, 2003). The galerucine genera *Blepharida* Chevrolat (Furth, 1982, 1985, 2004; Morton and Vencl, 1998; Vencl and Morton, 1998, 1999; Vencl et al., 1999; Evans et al., 2000) and *Diamphidia* Gerstaecker (Chaboo et al., 2007) have larvae that retain fecal coats or fecal strands; these larvae may use their neuromuscular system to move feces from the posterior to the anterior to maintain this shield cover. Members of the

chrysomelid subfamily Cryptocephalinae share a complex morphological synapomorphy associated with an elaborate fecal case carried by immature stages (Chapuis and Candèze, 1855; Chapuis, 1875; Briggs, 1905; Jacoby, 1908; Böving and Craighead, 1931; Chen, 1940; Gressitt, 1942; Fiori, 1950; Monrós, 1954, 1959; Wallace, 1970; Karren, 1972; Otto and Svenson, 1980; Seeno and Wilcox, 1982; Root and Messina, 1983; Erber, 1988; Reid, 1995; 2000; Chaboo et al., in press). Females have a rectal apparatus (“kotpresse”) to press feces as construction material for a fecal case (“scatoshell”) around the egg, and the terminal abdominal segment has a medioventral excavation (“egg dimple”) where the egg is stabilized while the female constructs the case around it. This case is retained, expanded, and maintained throughout the entire larval phase as a large turret-like dome, and then it is sealed to provide a pupation chamber. The larval abdomen is inflated and bent under and this helps to anchor the case. A flattened head blocks the entrance of the case, and elongate legs extend well beyond the case for walking (Erber, 1988). Sagrinae also makes a fecal pupation cocoon (Crowson, 1948). Cassidine shields have been called larval clothing, fecal appendage (= “kontanlag”), fecal mask, fecal shield, fecal pad, fecal annex, exuvio-fecal annex, dorsal shield, feci-fork, stercoral packet, and parasol. Chaboo and Nguyen (2004) selected “shield” as the most neutral term.

The few synthetic accounts of cassidine shields include Muir and Sharp (1904) for 4 species, Fiebrig (1910) for 21 Paraguayan species, Maulik (1919) for 6 Indian species, Steinhausen (1969) for 15 *Cassida* species, and Takizawa (1982) for an additional 29 Indian species. Chaboo and Nguyen (2004) discussed the basket-like or bird’s nest-type shields in the Neotropical tribe Hemisphaerotini. Świątojańska (2005b) compared shields within *Cassida* but overlooked the earlier Steinhausen (1969) paper. *Oediopalpa negligens* has long been classified within the traditional Hispininae s.str., but its larvae retain an exuvial shield (Bruch, 1906; Monrós and Viana, 1947).

Cassidine shields have diverse architectures (figs. 19, 20), with variations in size

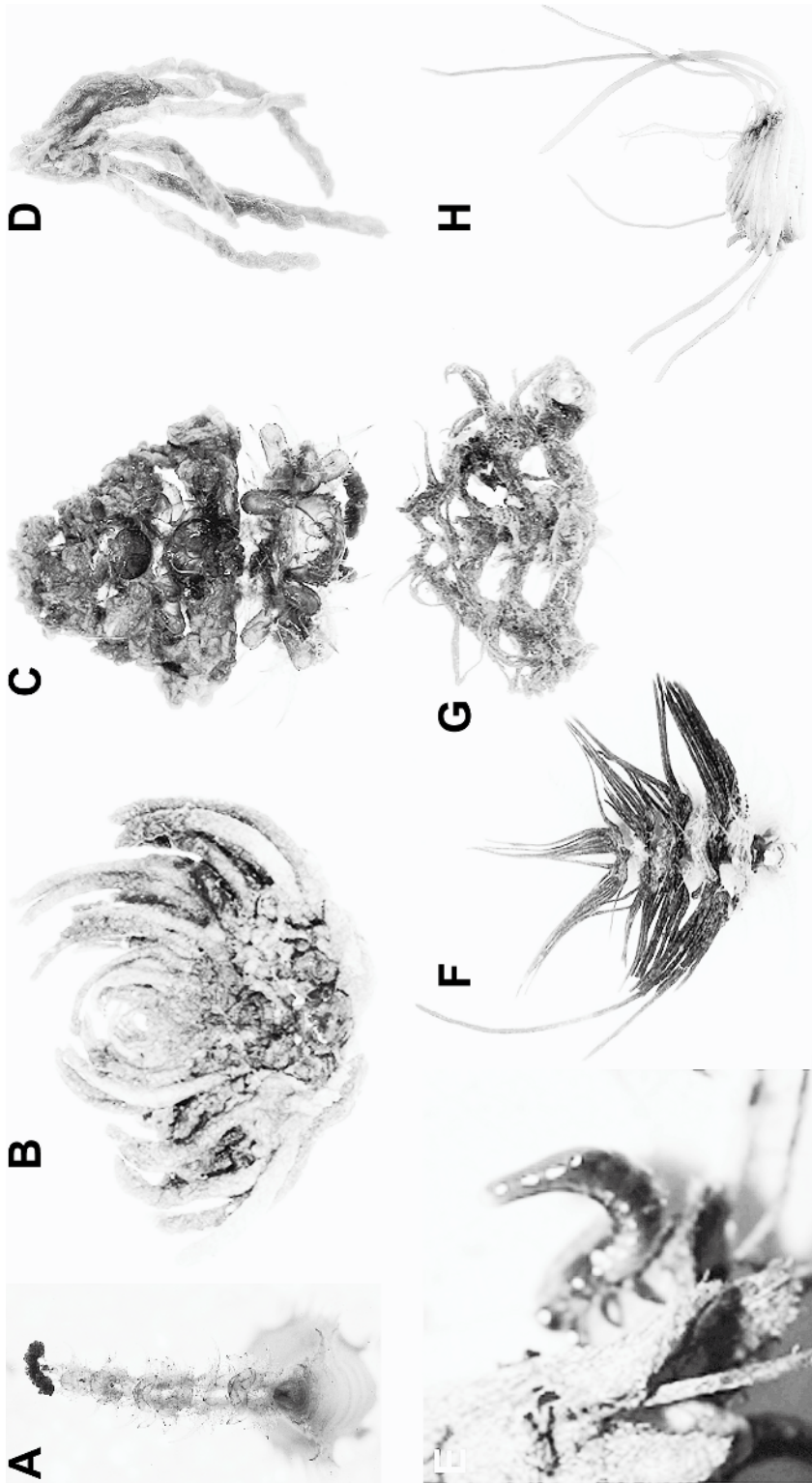


Fig. 20. Shields of larval Cassidinae. **A.** *Agroiconota bivittata*, posterior view. **B.** *Basiprionota cerata*, anterior view. **C.** *Chelymorphia cribaria*, posterior view. **D.** *Craspedonta moulouti*, dorsal view. **E.** *Eurypepla calochroma*, wet fecal coat. **F.** Unidentified species, Panama, posterior view. **G.** Unidentified species, Trinidad, posterior view. **H.** *Spathiella circumdata*, lateral view.

(and presumably weight), shape and arrangement, moisture content, and exuvial presence and compaction. They can comprise feces (e.g., fig. 20E), exuviae (e.g., fig. 20A) or both feces and exuviae (e.g., fig. 20B–D, F–G) and they appear to fall into four basic architectures: exuvial stacks (e.g., fig. 20A), exuvial stacks with fecal filaments (e.g., fig. 20C, F–G), wet fecal coat (e.g., fig. 20E), and basket-like or bird's nest arrangement (e.g., fig. 20H). Shields are built by larvae only but may be retained by pupae in some species, for example, *Acrocassis* (fig. 19) and hemisphaerotines (Chaboo and Nguyen, 2004).

Shield-retaining larvae have morphological modifications associated with shield construction, maintenance, and retention. The flexible telescoped anus, comprised of abdominal segment X and an elongation of the anus, permits construction and rebuilding if the shield is damaged. Caudal processes (urogomphi) of abdominal tergum IX hold the shield on the body and provide mobility.

Shield architecture can vary within a life cycle, minimally between larvae except in getting larger by addition of materials but more pronounced between a larvae and pupae, with many pupae lacking shields or retaining only the fifth larval exoskeleton. Species of *Cassida* and *Aspidimorpha* can have either exuvio-fecal shields or exuviae-only shields.

It is unknown what effect host plants may have on shield architecture (as opposed to chemistry). *Spaethiella tristis* appears to retain the same conservative basket-type shield architecture on two very different hosts, palms and cocoa (Chaboo and Nguyen, 2004). Thus far, soil and plant fragments have not been identified in cassidine shields, in contrast to such inclusions into some cryptocephaline cases (Chaboo et al., in press).

Olmstead (1994) argued that because exuviae and feces are waste products, they are cheap and reliable construction materials. Feces may additionally be impregnated with plant chemicals that may enhance their defensive properties (Gómez, 1997; Gómez et al., 1999; Morton and Vencl, 1998; Vencl and Morton, 1998, 1999). Chapuis and Candèze (1855) were the first to propose that chrysomelid fecal retention may protect

against temperature changes, sun or enemies. Additional hypotheses include mimicry of bird droppings, protection against desiccation and rain, and a physical barrier or a club against attackers (Barrows, 1979; Root and Messina, 1983; Eisner and Eisner, 2000; Olmstead, 1994; Müller and Hilker, 2003, 2004). Defensive functions of the shield have been indicated in several studies of predation of tortoise beetles (Eisner et al., 1967; Olmstead and Denno, 1992; Olmstead, 1994; Gómez, 1997; Gómez et al., 1999; Eisner and Eisner, 2000; Nogueira-de-Sá and Trigo, 2002, 2005; Eisner, 2003). Alternatively, odors from waste products can increase conspicuousness of larvae to predators and parasitoids, and Müller and Hilker (1999) indeed found contradictory data where shields of *Cassida* species appear to act as a secondary signal to ant predators.

PUPAE

Cox's (1996a) review of chrysomelid pupae revealed the diversity of pupal morphology and pupation sites. He reported that individual accounts of pupae were known for 235 species in 85 genera belonging to 27 tribes of Cassidinae. Tribal generalizations proposed by Cox (1996a) suggest that the pupae may offer phylogenetically informative characters.

Pupation occurs within leaf mines, hidden in leaf bases, on the venter of leaves (Cox, 1996a), or pupae may be cryptically colored and fixed to host plant stems (Wang, 1977). Examples of solitary and gregarious pupae and maternally guarded pupae are given above. They may also be naked (e.g., most mining forms) or retain the fifth larval exuviae (e.g., *Aspidimorpha miliaris*; Schultze, 1908) or the shield of the fifth larva (e.g., *Charidotella (C.) sexpunctata*; Olmstead, 1994). They may have the terminal segment undifferentiated or modified with caudal processes as in the larvae (Chaboo and Nguyen, 2004). The available data are not precise enough to indicate whether only shield-retaining pupae have these processes.

Contrary to the general perception that insect pupae are an immobile stage, some cassidine pupae can be mobile (Harris, 1835; Hendrickson, 1930; Ford and Cavey, 1985;

Chaboo, 2002). *Anisostena* pupae can move quite rapidly within their mines, up to 10 cm in 2 seconds (Ford and Cavey, 1985). In *Microrhopala vittata*, pupae are able to wriggle around in their pupation chambers (Hendrickson, 1930). Pupae of *Eugenysa columbiana* are affixed externally to plant stems, and individuals respond to touching by quick jerky abdominal flexion both in the field and laboratory (Chaboo, 2002). These movements may ward off enemies.

ANNUAL CYCLE

Rates of development in cassidines have been correlated to abiotic factors such as environmental humidity (Kosior, 1975) and temperature (Nogueira-de-Sá and Vasconcellos-Neto, 1988), and to biotic factors such as host plant choice (Baltazar, 1970) and plant quality (Obermaier and Zwölfer, 1999). Survivorship is discussed below under predators and parasites.

Northern temperate species are generally univoltine (Kosior and Klein, 1970) whereas more southern species can be multivoltine (Paterson, 1931). Adults may overwinter and emerge in spring. Tropical species can have more than three generations per year (Boldt, 1989; Boldt et al., 1991). The argus tortoise beetle, *Chelymorpha cassidea*, is univoltine in northern North America and bivoltine in the South (Chittenden, 1924). Adults survive 1–2 years over one or more breeding seasons. In his careful following of individuals in the wild during a 5-year period, Kosior (1975) found adults surviving over an impressive 4 years.

COURTSHIP

Chrysomelid sexual behavior has been briefly discussed (Jolivet, 1999). Rodriguez (1993, 1994a, 1995) described male courtship in *Chelymorpha cribaria* (Fabricius) (= *Chelymorpha alternans* Boheman), a *Charidotella* sp. near *sexpunctata*, *Omaspides convexicollis* Spaeth, and *Omaspides bistrata* Boheman. Mating can last more than 24 hours, depending on environmental conditions (Kosior, 1975). Post-copulatory attendance has also been reported in *Chelymorpha*, *Charidotella* Weise, *Omaspides* Chevrolat (Rodriguez,

1993, 1994a, 1995), *Odontota* (Kirkendall, 1984), and *Eugenysa* (Chaboo, 2002). It was unclear in *Eugenysa columbiana* (Boheman) if male attendance was due to mate guarding or parental care since both males and females were found with groups of larvae (Chaboo, 2002).

In cassidines the lengths of the male flagellum and of the female spermathecal duct can vary from short to very long, up to three times body length, and they are correlated (Rodriguez, 1993, 1994a, 1995; Rodriguez et al., 2004). This pattern may be related to female choice and male paternity.

SEXUAL DIMORPHISM

Generally it is difficult to distinguish cassidine males and females externally, but females may be 10–20% longer than males (Jolivet, 1999), as is typical of many insects. In *Chelymorpha cribaria* Fabricius (= *Chelymorpha alternans*) the largest males approach the size of the smallest females (Windsor et al., 1992). Other reported sex-related variations include color in *Rabdotohispa* Maulik (Würmli, 1975), stridulating organs in *Spilisa* Chapuis (Gahan, 1900), terminal indentations in males of Callispini Weise (Würmli, 1975), metasternal protuberances in males of *Botryonopa grandis* Baly (Würmli, 1975), the last abdominal sternum of females with a semicircular impression (sometimes with hairs) in Botryonopini Weise (Maulik, 1919; Würmli, 1975), longer coronal carina in *Xiphisa* Chapuis and *Aulostryx* Maulik (Würmli, 1975), and in distances between elytral striae in *Estigmaena* Hope (Maulik, 1919).

Acromis is rare among cassidines in having an extreme sexual dimorphism wherein males have the anterolateral elytral corners projected. Males often have holes in the elytral margins, gained during male-male combats for females (Windsor, 1987; A. Trillo, personal obs.). A second male form lacking the elytral spine was described in *Acromis sparsa* (Chaboo, 2001); these cryptic males may be using a sneaker male or minor male mating strategy (e.g., Eberhard, 1980; Emlen, 1997). Males of *Xenarescus monoceras* also joust for females by using the frontal head projection (Beaman, 1980).

MATERNAL CARE

Maternal care is an intriguing behavior for insects since the vast majority of females abandon their eggs. Only a few groups within Coleoptera exhibit guarding of their young (Crowson, 1981). For example, among the 40,000 species of Chrysomelidae, only 28 species from Cassidinae and Chrysomelinae exhibit this phenomenon (Chaboo, 2002; Frieiro-Costa, 2005). Within Cassidinae maternal care has been reported for only 17 species in nine genera in two closely related tribes, Eugenysini and Stolaini (table 6). The two best known systems are of *Omaspides* (*Omaspides*) *tricolorata* Boheman (Frieiro-Costa and Vasconcellos-Neto, 2000, 2003) and *Acromis sparsa* (Windsor, 1987; Upton, 1996; Chaboo, 2002; F. Vencl, unpubl. data; A. Trillo, unpubl. data). Females guard their eggs, all larval stages, and pupae until the young adults emerge (e.g., fig. 21). Mothers will attack threatening predators such as ants or reduviids (Chaboo, personal obs.) or use their carapaces to deter advances on larvae (Upton, 1996). In the face of continued threats, females guide their larvae to new leaves by prodding and pushing them. If females survive, they will continue guarding pupae until the young adults emerge. The possible existence of a signaling system between gregarious larvae and guarding females is discussed under "Gregariousness" above. Frieiro-Costa and Vasconcellos-Neto (2003) found that the entire immature period of *Omaspides* lasted up to two times longer than in other nonmaternal care cassidine species in the area, and that mothers will guard their young more than 2 months. Pupation in *O. (O.) tricolorata* occurs on host plant branches close to the ground (Frieiro-Costa and Vasconcellos-Neto, 2003). In *Acromis*, pupation occurs on the uppermost branches, and in *Eugenysa*, it is on the upper part of host stems (Chaboo, pers. obs.).

Based on two distantly related hosts recorded (*Ipomoea* and *Mikania*) and egg arrangement (stalked eggs suspended from the underside of leaves and arrangements circling stems), Windsor and Choe (1994) hypothesized that maternal care originated twice in Cassidinae. Comparative details of each species are needed to delineate this

complex behavior in refined phylogenetically meaningful characters.

FLIGHTLESSNESS

Cassidines are reluctant flyers and when threatened adults exhibit an escape response called thanatosis where they fall (onto vegetation or the ground) and feign death (Bleich, 1928; Nichols, 1989). Jolivet and Hawkeswood (1995) listed *Delocrania* Guérin and *Elytrogona* Chevrolat as apterous, and *Stoiba* Spaeth, *Fornicassis* Spaeth, *Cassida* (*Pilemostoma*) Desbrochers and *Cassida* (*Mionycha*) Weise as micrapterous. Jolivet (1954) illustrated the brachypterous hindwings of the latter three genera. *Elytrogona* species range from micrapterous to apterous (Chaboo, 2000), *Stoiba* species range from having fully developed wings to microptery (Chaboo, unpubl. data) and all *Delocrania* species have fully developed hindwings (Chaboo, unpubl. data). In the Aprozini, two species are flightless and one actively flies (*C. Reid*, personal commun.). My examination of specimens of these cassidines indicates that hindwing development may be accompanied by modifications of the body profile (more convex), metasternum (distortion), flight muscles (degenerate), pteronotum (reduced sclerotization), and elytra (shape, sutural fusion). It is possible that some cassidines may have fully developed hindwings but are flightless due to degenerate flight musculature. Flightlessness in cassidines could be associated with high altitude and island habitats, a pattern common in flightless insects (Roff, 1990, 1994; Wagner and Liebherr, 1992).

COLOR

Maulik's (1919) description of cassidines as "living jewels" is most apt. Adult coloration spans the full spectrum from black to orange and matte to metallic, as well as iridescent and golden. Some cassidines exhibit shades of green that match the background leaf, whereas others are transparent, lacking color, and blend against their background. A single color or multiple colors can appear in combinations of stripe and/or dots. Structural metallic colors occur as in Omo-

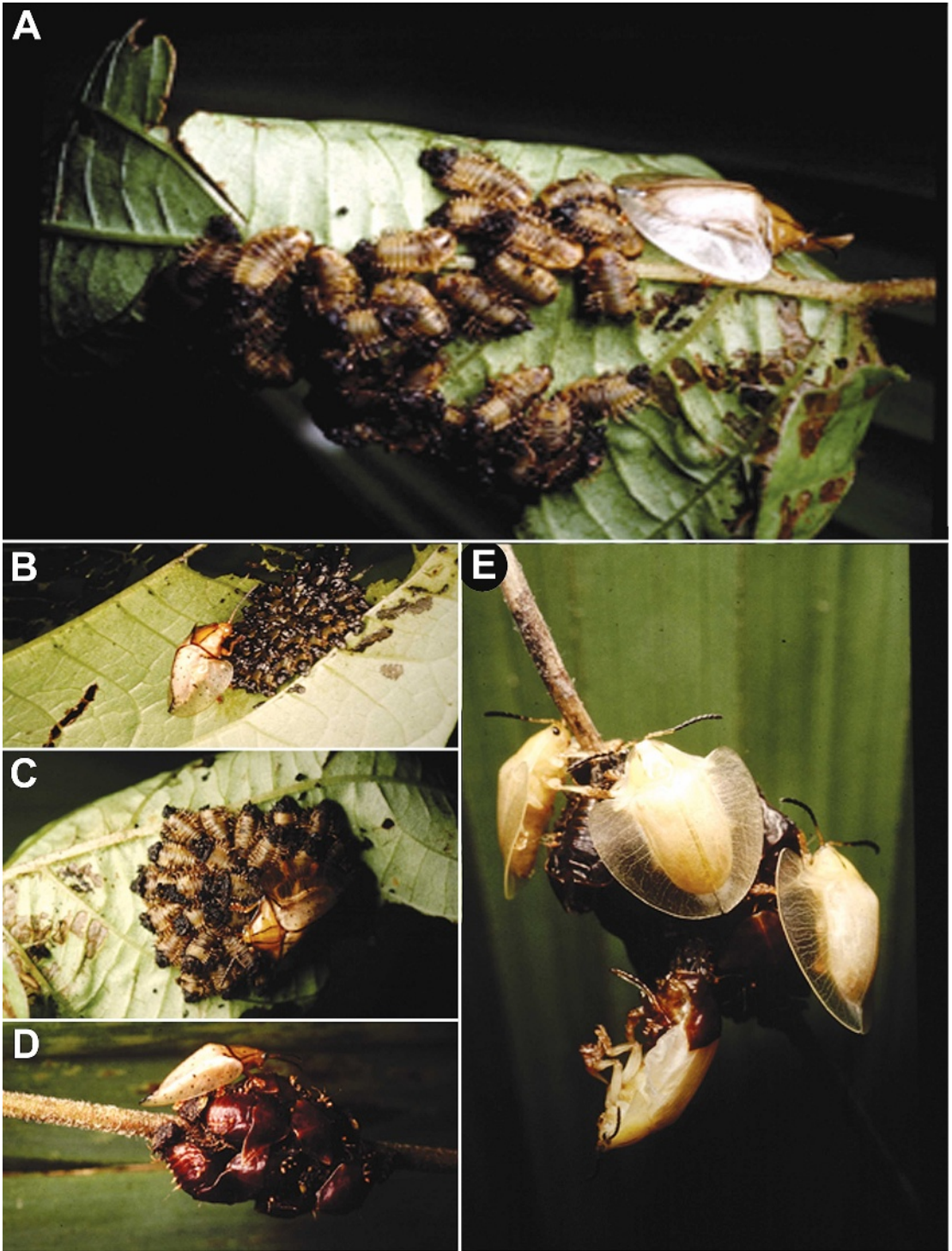


Fig. 21. Maternal care in *Acromis sparsa* (Panama). **A.** Larvae scattered over leaf. **B.** Mother herding larvae. **C.** Larvae in cycloalectic ring, guarded by mother. **D.** Mother on pupal brood. **E.** Young adults emerge. (Photographs courtesy Nick Upton.)

TABLE 6
Maternal Care in Cassidinae

Species	Host plant	Source
<i>Acromis sparsa</i> (Boheman)	<i>Merremia umbellata</i> (L.) Hallier f. (Convolvulaceae)	Windsor, 1987; Preston-Mafham, 1993; Chadwick, 1998; Upton, 1996; Maes, 2003
<i>Acromis spinifex</i> (Linnaeus)	<i>Ipomoea</i> spp. (Convolvulaceae)	Fiebrig, 1910; Buzzi, 1980; Preston- Mafham, 1993
<i>Cyrtanota thalassina</i> (Boheman)	<i>Ipomoea batatas</i> (L.) Lam. (Costa Lima 1936)	Ohaus, 1899, 1900; von Lengerken, 1939
<i>Eugenysa columbiana</i> (Boheman)	<i>Mikania</i> sp. (Asteraceae)	Chaboo, 2002
<i>Eugenysa coscaroni</i> Viana	<i>Mikania guaco</i> H. and B.	Windsor and Choe, 1994
<i>Omaspides (Omaspides) bistrata</i> Boheman	<i>Ipomoea philomega</i> H.	Windsor and Choe, 1994
<i>Omaspides (O.) convexicollis</i> Spaeth	<i>I. philomega</i>	Rodriguez, 1994a
<i>Omaspides (O.) nigrolineata</i> (Boheman)	<i>I. batatas</i>	Monte, 1932; Buzzi, 1988
<i>Omaspides (O.) pallidipennis</i> (Boheman)	<i>Passiflora</i> sp. Passifloraceae) (von Lengerken, 1939); <i>Ipomoea alba</i> L. (Buzzi 1994)	Ohaus, 1899, 1900; Costa Lima, 1914, 1955; von Lengerken, 1939
<i>Omaspides (O.) tricolorata</i> (Boheman)	<i>I. alba</i> (Buzzi 1994)	Friero-Costa and Vasconcellos-Neto, 2000, 2003
<i>Omaspides (Paromaspides) sobrina</i> (Boheman)	Unknown	Jolivet, 1988
<i>Omaspides</i> sp.	Unknown	O'Toole and Preston-Mafham, 1985; O'Toole, 1995
<i>Omaspides</i> sp.	<i>Ipomoea</i> sp.	Yanega, unpubl. data
<i>Paraselenis (Spaethiechoma) flava</i> Linnaeus	<i>Convolvulus</i> sp. (Convolvulaceae)	Weyenberg, 1874
<i>Paraselenis (S.) dichroa</i> (Germar)	<i>I. batatas</i>	Monte, 1932; Buzzi, 1988
<i>Paraselenis (S.) solieri</i> (Boheman)	<i>I. batatas</i>	Monte, 1932; Buzzi, 1988
<i>Paraselenis (S.) tersa</i> (Boheman)	<i>Ipomoea tiliacea</i> (Willd.)	Windsor and Choe, 1994

cerini. Gold and silver colors in some members of Cassidini and Charidotini are produced from the interaction of elytral hydration and light diffraction (Neville, 1977) and may be reversible in life and lost in death. Drying of elytral water may explain the loss of metallic gold and silver colors in dead cassidines (Hinton, 1976); museum specimens of these particular species provide little hint of the lovely coloration of live individuals. Minute surface sculpturing or multilayer reflectors (Parker et al., 1998) may also contribute to color diversity.

Cassidine eggs tend to be cream-colored, being obscured by tan oothecal membranes or dark feces. Larval and pupal colors range from white to jet-black, with many combinations of yellow or red with black suggesting aposematic coloration (Olmstead, unpubl. data).

Adults are also capable of color changes. Adult colors change during the teneral phase

of *Mecistomela marginata* (Thunberg) (Grenha et al., 2004). *Metriona bicolor* and *Cassida murraea* Linnaeus are capable of reversible color changes during copulation or when disturbed (Knab, 1909; Méquignon, 1941; Jolivet, 1994; Hinton, 1976; Mason, 1929; Hinton, 1976; Neville, 1977; Barrows, 1979; Crowson, 1981; Fuzeau-Braesch, 1985; Vasconcellos-Neto, 1987; Jolivet, 1994). This phenomenon resembles transient color changes of acridids, which has been explained as pigment movements (Mason, 1929).

Species-level color polymorphisms are known in *Aspidimorpha* (Simon Thomas, 1964; Verma and Kalaicheven, 2004), *Chelymorpha* (Vasconcellos-Neto, 1987, 1988a), *Botanochara*, *Lacoptera*, *Ogdoescosta*, and *Stolas* (Borowiec and Świętojańska, 2005), *Cassida* (Borowiec, 1999; Verma and Kalaicheven, 2004), *Conchylotenia* (Heron, 1999), *Eurypedus* Gistel (N. Gómez, personal com-



Fig. 22. Adult polymorphism in *Xenarescus monoceras*. Individuals vary in color patterns, development of the apical margin of the elytra, anterior projection of the elytral disc, carina interval of the elytral disc, and the interantennal projection.

mun.), *Eurypepla* (Chaboo, 2004), *Mecistomela* (Grenha et al., 2004), *Microctenochira* (Vasconcellos-Neto, 1987, 1988; Windsor et al., 1992), *Physonota* (Kirk, 1971; Caulfield, 1887; Sanderson, 1948; Kirk, 1971; Britten et

al., 2003), *Spaethiella* (Chaboo and Nguyen, 2004), and *Xenarescus monoceras* Olivier (fig. 22). Many of these color morphs can be viewed on the Internet (Borowiec and Świętojańska, 2005).

Chelymorpha in particular has many species with various color forms, in addition to male and female color dimorphism. Vasconcelos-Neto (1987, 1988a) diagnosed eight genetically based color morphs in *Chelymorpha cassidea* in Brazil. Color polymorphism in *Physonota helianthi* Boheman was correlated with host plant variation (Kirk, 1971) and timing of emergence (Caulfield, 1887; Sanderson, 1948; Kirk, 1971; Britten et al., 2003). In *Physonota unipuncta* Say, timing of emergence also produced different color morphs (Caulfield, 1884). Sex-related color dimorphism has been described in *Rabdotohispa* (Würmli, 1975).

Some color patterns have been explained as mimicry of bird droppings, flowers, lacewings (Jones, 1994), and leaves (Crowson, 1981). Maulik (1919) listed six mimicry relationships between Hispinae s.str., other chrysomelids, Cerambycidae, and Curculionidae. Spectacular mimicry complexes involving the cassidine genera *Cephaloleia*, *Chalepus*, *Dactylispa*, *Estigmena*, *Gonophora* Chevrolat, *Hispa*, *Lasiochila* Weise, *Odonotota*, and *Sceloenopla*, and other Coleoptera (cantharids, cerambycids, clerids, curculionids, alticine and criocerine chrysomelids, oedomerids, tenebrionids) and Heteropteran mirids have been observed (Gahan, 1891, 1913; Shelford, 1902, 1916; Maulik, 1959; Mawdsley, 1992; Lane, 1951; Linsley, 1959; Hespenheide, 1996; Menier, 1985; Balsbaugh, 1988; Staines, 1999). Mawdsley (1992) described one mimicry complex involving the cassidine *Odontota scapularis* (Olivier), as well as multiple species of Buprestidae, Cerambycidae, Cleridae, Elateridae, Lampyridae, Lycidae, Oedemeridae, Pediliidae, and Ptilodactylidae. Hespenheide (1991) also described a complex that may involve up to 50 cassidine species. It is unclear which taxa are models and mimics or what might be the level of distastefulness or toxicity in each species.

GENETICS

Cytogenetic analyses of cassidines have focussed historically on chromosomal patterns (Petitpierre, 1977, 1985, 1988, 1989; Alegre and Petitpierre, 1984, 1990; Brum and Postiglioni, 1988; Saha, 1973; Yadav and Pillai, 1975; Virrki et al., 1992) and more

recently have focussed on evolutionary genomics (Hsiao and Windsor 1995; McKenna and Farrell, 2005). Chromosomal analyses have revealed that cassidines have $2n = 18$ chromosomes and a Xy_p sex determination system (Petitpierre, 1977, 1985, 1988, 1989; Alegre and Petitpierre, 1984, 1990; Brum and Postiglioni, 1988; Virrki et al., 1992). Within the tribe Stolaini, Vaio and Postiglioni (1974) found a second type of sex determination system, X_p neo X neo Y_p . Pericentric inversions have been suggested as a process in cassidine chromosomal evolution (Yadav and Pillai, 1975). In at least one species, *Hispa armigera*, races appear to be based on diploid and triploid chromosome numbers (Saha, 1973). Phenotypic color polymorphism in *Chelymorpha cribaria*, *Botanochara decempustulata* (Boheman), and *Stolas discoidea* Linnaeus appear to have a genetic basis (Zolessi, 1968; Vaio et al., 1975; Vasconcelos-Neto, 1987, 1988).

Evolutionary genomics in Cassidinae is just beginning with a few studies exploring sequence data. Presently on GenBank (<http://www.ncbi.nih.gov/Genbank>) the main studies have used about 500 base pairs (bp) of 12S small subunit ribosomal RNA gene (Hsiao and Windsor, 1999); about 450 bp of 28S ribosomal RNA (Cuignet et al., submitted); and about 1000–2000 bp of cytochrome oxidase I (McKenna and Farrell, 2005). As the field develops, the diversity and lengths (base pairs) of sequences will expand, and we can anticipate phylogenetic analyses that compare the information and level of application of different parts of the genome.

AESTIVATION AND DORMANCY

In tropical areas with a distinct dry season, cassidines can have a summer and winter diapause with peak activity in mid-January through March and mid-June through November (Bhattacharya and Verma, 1982). Some cassidines may pass extreme weather conditions in a state of dormancy, gathering in the dampest microclimate they can find. Diapausing aggregations involving multiple species have been observed during the Neotropical dry season (Flowers, 1991) and in the cooler months in elevated conditions (500–8,000ft) (Garthwaite, 1939). These aggrega-

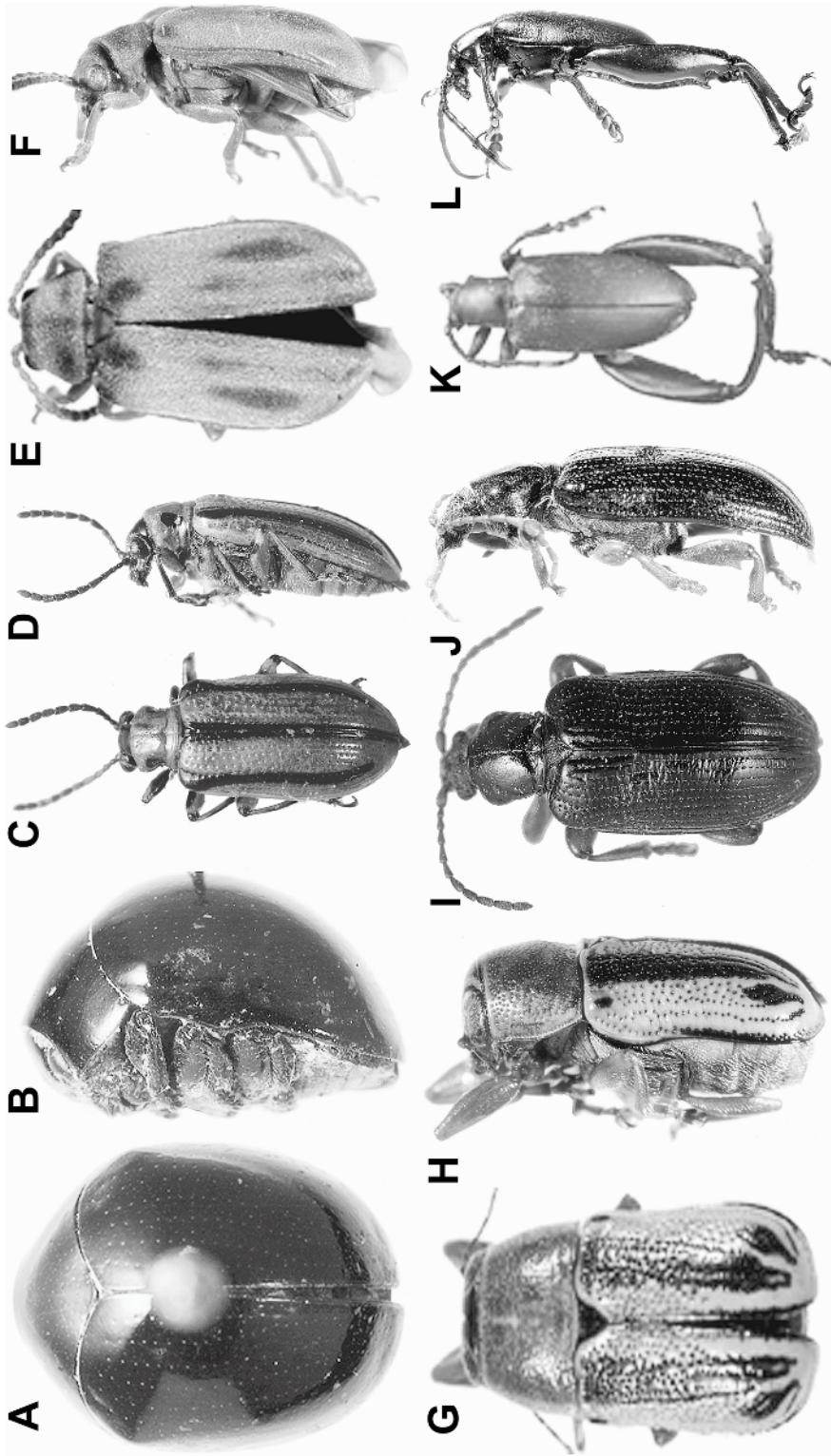


Fig. 23. Outgroups sampled, adults. A. *Lamprosoma* sp. 1, dorsal view. B. Lateral view. C. *Lemna trivittata*, dorsal view. D. Lateral view. E. *Ophraella* sp. 1, dorsal view. F. Lateral view. G. *Pachybrachis circumcincta*, dorsal view. H. Lateral view. I. *Platammaris rufa*, dorsal view. J. Lateral view. K. *Sagra* sp. 1, dorsal view. L. Lateral view.

tions can be spectacular; for example more than 10,000 cassidine beetles were observed under bark of one felled tree in northern Myanmar (Garthwaite, 1939). Aggregations occur under bark, in cracks and hollows of trees (standing or felled) and grass stems (e.g., bamboo), in thick low vegetation, in thatched roofs and in loose, dry leaf litter (Beeson, 1941). Where the dry season is not so distinct, the beetles may be active throughout the year. In temperate climates, adults overwinter under bark, in leaf litter at the base of the host plant, or in soil (Chittenden, 1924; Hendrickson, 1930; Paterson 1931; McCauley, 1938; Labeyrie, 1959; Kosior, 1975; Boldt and Staines, 1993; Müller and Hilker, 1984; Ford and Cavey, 1985).

MASS MIGRATIONS

Diurnal and seasonal movements of cassidines may be correlated with temperature, rainfall, wind, and biotic disturbances. Diurnal movements of adults and larvae occur with weather changes. During periods of heavy wind or rain, cassidines hide under leaves, or retreat to leaf bases and even into soil (Kosior, 1975). Strong and Wang (1977) suspected that cryptically feeding cassidines sought out new host leaves and plants at night, thus minimizing enemy detection.

Mass seasonal migrations of thousands of individuals have been reported in *Coelaenomenodera elaeidis* Maulik (Cotterell, 1925) and some temperate *Cassida* species (Engel, 1932; Palij and Klepikova, 1957; Palij, 1959; Kosior and Klein, 1970). In *Coelaenomenodera* Blanchard, migrations began early in the morning and reached a peak in the early afternoon, covering a distance of over 16 miles to new sites. Kosior and Klein (1970) found that *Cassida* species migrated seasonally, feeding in meadows from spring to fall and overwintering as adults in leaf-litter of nearby warmer, south-facing forests. In spring, they returned to the meadows.

DEFENSIVE MECHANISMS

The large array of defensive capabilities of Chrysomelidae has been one hypothesis explaining their evolutionary success (Blum, 1994). Every life stage of Cassidinae appears

to have several defensive features. Eggs in groups, with oothecal membranes, leaf fragment coverings, fecal coatings, and maternal care are discussed above. Mining or cryptic feeding habits may reduce the impact of predation of those cassidine larvae. In species with exposed larvae and pupae, spiny lateral projections may deter attackers and may also extend the field of detection around the animal (Eisner et al., 1967). Aposematic colors (Olmstead, unpubl. data), and behavioral mechanisms such as gregariousness, cycloaexy, shield retention, host plant chemistry, and shield chemistry may also enhance survival. Adults exhibit a range of potentially defensive mechanisms, including stridulation, thanatosis, mimicry, and maternal guarding. Adult body armament in the form of dorsal spines, including antennal spines, may reduce grasping by predators. Their explanate margins are uniquely shaped for settling flat against surfaces, making it difficult to lift or turn the animal over (e.g., ants cannot find purchase along the periphery of a cassidine in this position; Chaboo, pers. obs.).

In addition to protection of explanate elytral margins, cassidines have leg characters that enhance their protection. Some adults (e.g., *Hemisphaerota* species) have excavations on the legs for compacting the whole limb, as well as spaces under the elytra where legs are retracted. When under attack, these cassidines can present a compact armor-like exterior. *Hemisphaerota cyanea* legs have another feature that helps in protection. Tarsomeres I–III are somewhat flattened and expanded, and they are packed ventrally with bristles, up to 10,000 on each of the three tarsomeres (Eisner, 2003). Each bristle is bifid at the apex, thus multiplying the number of contact points (ca. 60,000) with the leaf surface. These unique bifid setae secrete tarsal oils that provide an extremely strong adhesion to the leaf surface (Attygalle et al., 2000; Eisner and Aneshansley, 2000; Eisner and Eisner, 2000). This enhances the difficulty of dislodging an individual once it is secured to the substrate, with legs contracted and body pressed to the surface.

Chrysomelids show a considerable defensive chemistry repertoire (Blum et al., 1972; Blum, 1965, 1994, 1999; Deroe and Pasteels, 1982; Pasteels et al., 1988; Pasteels and

Rowell-Rahier, 1989). Chemical analyses of cassidines have focused thus far on the shields carried by exophagous larvae, with examinations having been made of seven species—Stolaini: *Chelymorpha alternans*, *Acromis sparsa*, *Stolas plagiata* Boheman; Cassidini: *Cassida denticollis* Suffrian, *Cassida sanguinosa* Suffrian, and *Cassida stimatica* Suffrian (Müller and Hilker, 1999, 2002, 2003); and Physonotini: *Eurypedus nigrosignatus*. These analyses all together reveal that both exuvio-fecal and skin-only shields can have plant-derived chemicals (but absent in *Cassida sanguinosa*) that may act as ant deterrents or attractants. Sequestered chemicals have been identified so far as mono- and sesquiterpenes (Gómez et al., 1999).

STRIDULATION

Within Chrysomelidae, stridulatory files have been found on abdominal tergum VIII in Criocerinae (Réaumar, 1737; Schmitt, 1991), the head of some Cassidinae (Gahan, 1900; Dudich, 1920; Schmitt, 1989, 1991), the mesonotum and pronotum in Megalopodiinae (Lacordaire, 1830; Crowson, 1966), the mesoscutum in Zeugophorinae (Crowson, 1955; Schmitt, 1991), and on the pronotum in Cryptocephaline Clytrini (Darwin, 1871; Gahan, 1900; Jolivet and Petipierre, 1981; Schmitt, 1991). In some Bruchinae, metepisternal striae are rubbed against spines on the metafemur (Kingsolver et al., 1993).

Cassidine stridulatory organs consist of transverse striae (= pars stridens) (Dudich, 1920; Schmitt, 1994) on the vertex (of the adult head) that are rubbed along the inner anterior pronotal rim that acts as a plectrum (scraper). When adults of *Eurypepla calochroma* are picked up, the head is rapidly rubbed back and forth against the pronotal margin, producing an audible sound (Chaboo, personal obs.). Gahan (1900) reviewed Coleopteran stridulating organs and indicated their occurrence in the cassidines *Anisodera scutellata* Baly, *Estigmaena chinensis* Hope, *Hispopria foveicollis* Baly, and *Spilispa imperialis* Baly. In *Spilispa* only males have these organs (Gahan, 1900). Files have since been found in *Wallacea* Baly, *Botryonopa* Blanchard, *Oxycephala* Guérin-Ménéville, *Cephalodonta* Chevrolat, *Prosopodonta* Baly,

and *Hispa* (Maulik, 1919), in *Di cladispa testacea* Linnaeus, *Hispa atra*, and *Leptispa filiformis* Germar (Dudich, 1920), and in *Drepanocassis profana* (Boheman) (Buzzi, 1988), *Odontota dorsalis* (Schmitt, 1989), *Physonota caudata* Boheman (Schmitt, 1989, 1992), and *Cassida viridis* Linnaeus (Schmitt, 1994). They are reportedly absent in *Aspidimorpha sanctaecrucis* (Fabricius) and *Stolas chalybaea* (Germar) (Buzzi and Winder, 1986; Schmitt, 1994).

Stridulation may attract mates or startle and therefore deter predators. Variation in the striae arrangement may modulate frequency, pitch, and tone of sound. In *Hispopria foveicollis*, the striae are arranged in three groups separated by two smooth intervals suggesting some ability to modulate sound (Jolivet and Hawkeswood, 1995). Schmitt (1991) hypothesized that the presence of the file is a basal condition and is secondarily lost convergently. Recordings and experimental tests of cassidine stridulation await study.

NATURAL ENEMIES

The literature on parasites and predators of Cassidinae has been reviewed (Cox, 1996b; Olmstead, 1996; Nogueira-de-Sá and Vasconcellos-Neto, 2003a; Gómez, 2004). All stages face persistent attack by diverse parasite, parasitoid, and predator enemies including Protozoa, Fungi, Hymenoptera, Heteroptera, Diptera, spiders, and birds. Cassidinae suffers from the highest levels of parasitoidism among all chrysomelid subfamilies, and this has been attributed to their sedentary lifestyle (Cox, 1996). Attacks and losses are frequent and severe; for example, *Eocanthecona furcellata* (Wolff) (Heteroptera: Nabidae) was shown to destroy 80% of the larvae of *Craspedonta leayana* (Garthwaite, 1939).

The most frequent predators appear to be bugs (Heteroptera: Pentatomidae, Reduviidae), spiders (Araneae), wasps (Hymenoptera: Vespidae), and ground beetles (Coleoptera: Carabidae) (Olmstead, 1996; Eisner and Eisner, 2000). Eggs are preyed upon by bugs and ants (Carroll, 1978; Cox, 1996), and are mostly parasitized by Hymenoptera (Carroll, 1978; Cox, 1994b) and Protozoa (Nogueira-de-Sá and Vasconcellos-Neto, 2003a).

Eggs with membranous and/or fecal coverings are more vulnerable to Hymenopteran parasitoids (Boldt et al., 1991; Cox, 1994b; Damman and Cappuccino, 1991) than to predation.

Larvae and pupae are most affected by Dipteran and Hymenopteran parasitoids (Cox, 1994b). Cox (1996) reported that leaf-mining cassidines are most threatened by parasitoids, whereas external foliar cassidines were most vulnerable to predatory insects. Leaf-mining larvae can be preyed upon by reduviids, lebiine carabids and formicids. Bugs (Nabidae, Reduviidae, and Pentatomidae), aculeate wasps, coccinellid beetles, and ants eat exophagous cassidine larvae and pupae (Chaboo, personal obs.). According to Cox (1996), 72% of cassidine predation reports involve Heteroptera and larval Neuroptera. Wasps, hemipteran bugs, and carabids turn over shielded tortoise beetles and attack the soft underbellies; bugs retain the larvae on their proboscis and walk away (Chaboo, personal obs.). Carabid beetles turn over shield-bearing larvae and eat the entire animal except the caudal process and shield (Eisner, 2003). Heteropteran pentatomids and ants will eat adult cassidines. Parasitoids of adults include Diptera, Nematoda (Nogueira-de-Sá and Vasconcelos-Neto, 2003a), and Fungi (Olmstead, 1996). A novel advance in the study of cassidine parasitoids will be that of Caignet et al. (submitted) on the possible co-evolution between Cassidinae and eulophid egg parasitoids.

Carroll (1978) reported *Emersonella niveipes* (Eulophidae), *Brachymeria* spp., and *Spilochalcis* spp. (Chalcidae) as parasitoids, and pentatomids as predators of *Stolas* species. Wasps sit on adult females and as they oviposit, the wasps start ovipositing their own eggs onto the beetles' egg mass. It is unclear how the wasps identify the sex of beetles since most species are not obviously sexually dimorphic.

Mites are common on cassidine adults but their impact is unknown (Maulik, 1919). A curious relationship exists between the mite family Canestriniidae (Acari) and Cassidinae. Most of the 76 species of canestriniid mites known from the Neotropical region are ectoparasites of cassidines. Haitlinger (1989,

1992, 1994) documented this relationship and described many new genera and species of the mites (whose impact and specificity are unclear).

CONSERVATION

Although no endangered or declining cassidine populations are known, it is obvious that global climate changes and anthropogenic habitat fragmentation and destruction will alter cassidine communities, along with all other species. Fine-scaled distributional maps of cassidine species will be important tools in determining rare and common species and in tracking changes in species ranges and assemblages.

MATERIALS AND METHODS

The present study is based on the examination of more than 5000 specimens of Cassidinae in 39 of the 43 recognized cassidine tribes. Detailed examinations were done of 146 species and character states were coded for species in 94 genera (appendix 1). Four tribes (Callohispidini Uhmman, Hispoptini Uhmman, Hybospispini Weise, and Oncocephalini Weise) were not sampled due to lack of material.

TAXON SAMPLING AND PREPARATION OF SPECIMENS

Taxa examined are given in appendices 1 and 2. Specimens were assembled through my field collections, from loans from museums and private collections, and by gifts from individual collectors. Additional information on immature stages was taken from published sources, which are listed in appendix 2. Repositories of all specimens examined are listed in appendix 3.

Taxon sampling was guided by two goals: 1) to maximize taxonomic and biogeographic diversity, and 2) to score characters for individual taxa. Seeno and Wilcox's (1982) classification of Cassidinae s.str. and Hispidinae s.str., with 43 tribes, guided taxon selection. Subsequent synonymies of Riley (1986), Borowiec (1999) and Staines (2002b) could also be tested under this strategy. Of the three approaches to taxon sampling (i.e.,

intuitive, exemplar or exhaustive; Yeates, 1995; Bininda-Emonds et al., 1998), I chose the exemplar approach using species as terminals to score characters. Time and availability of specimens did not permit an exhaustive sampling of all 320 cassidine genera.

Characters of immature stages were scored based on examination of material and from data in published literature. Because immatures are unknown for many of the species sampled here, character scoring in some cases was based on pooling information from several species and treating the terminal as a composite (this was not done with adult characters). Further discussion of this chimerical taxon coding is presented under the discussion of immature morphology.

Outgroups. The ideal outgroup must be monophyletic with the ingroup and be located outside the ingroup, near the root of the ingroup (Gaffney, 1979). My selection of outgroups was therefore guided by recent cladistic analyses of higher-level relationships of Cassidinae, including Lee (1993), Hsiao (1994a, 1994b), Reid (1995, 2000), and Farrell (1998), which help narrow the range of chrysomelid outgroups. These studies suggest several different subfamilies as the sister clade of Cassidinae (table 2). I utilized single species exemplars to represent the following outgroups: Criocerinae, Cryptocephalinae, Donaciinae, Galerucinae s.l., Lamprosomatinae, and Sagrinae. These represent all the major clades of Chrysomelidae and help narrow the range of possible sister clades.

Schmitt (1985c) summarized the four probable autapomorphies of Criocerinae as: adult seventh abdominal tergite with elytra-abdominal stridulatory apparatus, larval labrum with three pairs of labral setae (Steinhausen, 1966), larval anus dorsal, and larval segments 1–8 with ambulatory warts (Böving and Craighead, 1930; Hennig, 1938). Autapomorphies of Sagrinae are the prosternal process broad and prominent, and larval construction of stem galls (Schmitt, 1985). An autapomorphy of Donaciinae is the eighth abdominal spiracle of larvae projecting and spur-like (Böving and Craighead, 1930; Schmitt, 1985). Cryptocephalinae and Lamprosomatinae have been historically allied as a distinct clade within Chrysome-

lidae, the “Camptosomata” (Chapuis, 1874; Briggs, 1905; Jacoby, 1908; Böving and Craighead, 1931; Chen, 1940; Gressitt, 1942; Monrós, 1952, 1959; Wallace, 1970; Otto and Svenson, 1980; Seeno and Wilcox, 1982; Root and Messina, 1983; Erber, 1988), supported by a suite of characters associated with maternal fecal case production, larval case retention, expansion and repairs, and pupal case retention (Erber, 1968; Chaboo et al., in press).

Böving (1910) allied Donaciinae and Criocerinae on the basis of criocerine fifth instar larvae entering the ground and making a cocoon of sand and saliva glued together. Donaciinae larvae also make a cocoon with mouth and gut secretions, but it is unclear if this cocoon was spun from silk (Böving found no silk glands). The position of Donaciinae was thought to be somewhere between sagrines and criocerines (Lucas, 1873; Böving, 1927). Schmitt (1985) hypothesized a relationship ((Criocerinae+Sagrinae) + Donaciinae), the “Crioceriformes”, supported by the development of the tegminal manubria as a vertical plate. Crowson (1994) hypothesized that Cassidinae s.str. + Hispinae s.str. arose from a Donaciinae (aquatic) ancestor.

Ingroup Taxa. Selection was based on specimen availability, on whether a series (collected on the same date in the same locality) was available, and whether the series was large enough to permit multiple genitalic dissections and at least a single complete disarticulation. Multiple dissections reduced the problem of interspecific variation. Twelve tribes (Aproidini, Arescini, Asterizini, Basipini, Botryonopini, Epistictini, Eurispini, Exothispini, Gonophorini, Leptispini, Promecothecini, and Prosopodontini) were sampled by a single species. *Cyperispa* and *Pharangispa* represented Colaenomenoderini but *Pharangispa* was ultimately omitted because of missing data. The final analysis could not test the monophyly of 13 tribes. *Basipta* was removed in the final analysis because of levels of missing data. Delocraniini is diagnosed by several autapomorphies, and only one species was scored in the matrix because tribal monophyly was confirmed by examining all species before analysis. Several unique features circumscribe Notosacanthini,

so its monophyly was not tested here. The large tribes, Stolaini and Cassidini, were represented by multiple genera to obtain maximal morphological diversity. Adult specimens of species from 39 of the 43 cassidine tribes were selected, dissected and examined.

Specimen Identification. In the case of adults, identifications were secured by type examinations, keys to species where available, identified material in collections and through the website of Borowiec and Świętojańska (2005). Specimens of immature stages were identified by rearing for adult associations and by using identified museum material. A few taxa remain unidentified to species.

Dissection Techniques. Dissections involved 1–10 specimens, depending on availability. Complete disarticulation of single individuals selected from series (same locality and same date of collection) was done where feasible (with permission of curators and with personal specimens). At least one adult specimen was completely disarticulated and at least one male and one female were dissected for genitalic examinations. Where a specimen series was large enough, several dissections were done.

The dissection protocol followed Kingsolver (1970). Specimens were relaxed in boiling water or in a humidity chamber overnight. The head and abdomen were removed and cleared at room temperature overnight in cold 10% potassium hydroxide (KOH), then washed in 70% alcohol, dissected and separated in cold water. Hindwing preparations involved relaxing specimens in a humidity chamber, raising the left elytron, and removing the left hindwing (the right hindwing is pierced in pinned specimens). Hindwings were flattened in water, between a slide and coverslip for examination. Complete disarticulations of genitalia, wings, and mouthparts were stored in plastic genitalia microvials with glycerol, and maintained on original pins with original data labels.

Structures were first examined in glycerol in porcelain spot trays to assess three-dimensional structure, and then mounted temporarily in glycerol on glass microscope slides with coverslips for drawing and photography. Clearing of specimens in potassium hydroxide (KOH) is a very useful and

standard entomological technique. Unfortunately membranous portions of the reproductive system (e.g., spermathecal muscles, accessory glands) are quickly destroyed. In my study of *Eugenysa columbiana*, I found that the natural coiling of the ejaculatory duct was destroyed once specimens were in contact with KOH (Chaboo, 2002). In that study, dissection of fresh or recently killed alcohol-preserved specimens (adults and tenerals) in water was critical to assessing variation in the natural size of the appendix, the position of muscles, and the natural coiling of duct.

Equipment. Examinations and illustrations were done with several microscopes: Wild M5A stereomicroscope with Wild Type 256576 camera lucida attachment; Zeiss compound microscope with Type 256576 camera lucida attachment; Nikon Eclipse E600 compound microscope with camera lucida attachment; Leitz Wetzlar Dialux 20 phase contrast microscope with camera lucida attachment. Wings were illustrated with a Ken-a-Vision projector. Measurements were taken with a Lasico digital ocular micrometer.

Photography. Specimens and structures were photographed using a Nikon D1 digital camera, Infinity K2 lenses, and Microoptics ML1000 fiber optic flash unit at the American Museum of Natural History. Mouthpart and genitalia photography used the same camera and lighting system attached to a Nikon compound microscope.

Scanning Electron Microscopy (SEM). This was utilized to explore the antennae, pronotal setae, elytron, and tarsal pads. Coated and uncoated specimens were viewed. For coated material, samples were first cleaned in soapy water in an ultrasonic cleaner, dehydrated in a graded alcohol series, and critical point dried with a Bal-Tec critical point dryer 030. They were then mounted on standard aluminum Scanning Electron Microscopy stubs (diameter of 12 mm, height of 7 mm; Electron Microscopy Sciences) and sputter coated with gold/palladium in a Denton Vacuum Desktop II model. Specimens were examined with a Hitachi S4700 field emission scanning electron microscope at the American Museum of Natural History.

Plate Preparation. Illustrations were scanned, digitized, and minimally edited in MS-Paint 2000. Digital photographic images were minimally edited (background removed, some contrast manipulation) in Adobe Photoshop 6.0. Plates were prepared with Adobe Photoshop 6.0, CorelDraw 9 and Microsoft PowerPoint 2000.

TERMINOLOGY AND CHARACTER ANALYSIS

Specific terms and literature are reviewed under character discussions. Terminology generally follows Snodgrass (1935). McHugh et al. (1997) provided a useful model for Coleoptera, and Ashe (2000) served for mouthparts. Konstantinov and Vandenberg's (1996) illustrated morphology of the chrysolimid *Altica oleracea* was helpful, as was Chamorro-Lacayo and Konstantinov's (2004) study of the prothorax in Cryptocephalinae. Morphology and character hypotheses discussed in Askevold (1990a, 1990b, 1991) were also considered. Terminology that appears in the chrysolimid literature was assessed on the basis of homology criteria, consistency with terms used in other chrysolimid subfamilies, and generally with those in Coleoptera. For example, hindwing terminology applied to Chrysolimidae in the past varies between the systems of Forbes (1926), Comstock and Needham (1898) and Snodgrass (1935), and of individual chrysolimid specialists. In Coleoptera, a combination of terms and concepts was applied by Kukolová-Peck and Lawrence (1993) and their terminology is applied here with these vein abbreviations: HP, humeral plate; laxe, first axillary sclerite; 2axe, second axillary sclerite; Sc, SubCosta; R, radius; r3, radial cross-vein 3; RA, Radius Anterior; rc, radial cell; r4, Radial cross vein 4; RP, Radius Posterior; AA, Anal Anterior; CuA, Cubitus Anterior. Group-specific terms for criocerine and donaciine morphology were taken from Schmitt (1985a, 1985b, 1985c) and Askevold (1990a) respectively. In general, my preferred terminology is based on my own homology assessments and in accordance with those used in the modern literature.

The change in the position of the mouth, the fusion of the clypeus with the frons, and the general transformation of the ancestral

prognathous chrysolimid head to the hypognathous condition in Cassidinae make circumscription of some landmarks such as the gena and clypeus difficult. I refer to these areas in their geographic sense (i.e., position), but these may be better defined in the future in the morphological sense. On the abdomen, I refer to segments in their morphological sense, and the first visible sternum is sternum III. Certain cassidine-specific terminology (e.g., caudal process, shields) are only be briefly addressed here as they have been discussed in Chaboo and Nguyen (2004). The terms "flange", "carina", "spine", "tooth", "denticle", "serration", and "crenulation" are used as defined in Nichols (1989). The term "parascutellary stria" (Will, 2002) is used instead of "scutellary striole" (Würmli, 1975). The cassidine-specific term "caudal process" is used instead of the more general "urogomphi" (reviewed in Chaboo and Nguyen, 2004).

Character Analysis (appendix 4): Adult Morphology. Few character systems and characters have been utilized in the systematics of Cassidinae. Given this paucity of adult morphological characters, I extensively explored adult morphology to review characters previously applied in Cassidinae, to examine homology and terminology issues, and to propose new character hypotheses.

Diagnoses and keys to tribes of Cassidinae s.str. (Hincks, 1952) and of Hispinae s.str. (Würmli, 1975) provided a starting point for searching for characters. Genitalia and wings have been dismissed as uninformative. Apart from mouth position, mouthpart morphology has also been ignored. Michalski (1995) examined adult external morphology of *Stolaini* and proposed some characters that are used here. Borowiec's (1995) analysis of Cassidinae included 19 characters, derived primarily from Hincks (1952). A detailed study of all life-history stages of Cassidinae is needed to establish a common, homology-based nomenclature and to generate new morphological character hypotheses.

One hundred ninety-nine adult morphological characters (appendix 4) are defined and scored. Characters derived from the literature, or novel for Cassidinae, are indicated under the character discussion. Characters from other life stages and ecology are

developed from personal examination and the primary literature. For this study, the adult morphology of *Hemisphaerota palmarum* is detailed as a basis for defining terms, structures, and characters. A comparative general description of adult morphology across Cassidinae follows this account.

Character Analysis: Characters of Immatures. Descriptions of cassidine immature stages are available for about 350 cassidine species in 170 genera, but a synthesis of their morphology is not yet available (appendix 2). It is not always possible to compare characters across taxa and states since descriptions in the primary literature can be lacking, incomplete or inaccurate. From the egg stage, one character was defined and scored. Ten characters for larval morphology were coded on the basis of my personal examination of specimens and the literature. In some cases (indicated under the relevant character discussion), I use terminals as composite genera, coding states on the basis of available species descriptions. Clearly this approach creates room for error where states are unknown for all species in that genus, so I have conducted separate analyses of matrices with composite terminals (incorporating data of several species) and with only taxa I have examined. The morphological and ecological diversities of the immature stages of Cassidinae are great and the process of incorporating this rich dataset into arguments of Cassidine systematics must begin somewhere.

Character Analysis: Ecological and Behavioral Characters. Cassidines exhibit distinct life histories that may provide powerful characters. Ten characters were defined and scored here.

MORPHOLOGY OF CASSIDINAE IMMATURE STAGES (figs. 15–20, 24–26)

A detailed comparative morphology of immature stages of Cassidinae is not available and is beyond the scope of the present research. In general, collections of immature cassidines are poorly developed, as in most insects. This gap severely restricts development of general ideas about Cassidinae. Morphological and behavioral character hypotheses for immatures (proposed below) were scored from published data, examina-

tion of specimens, and information provided by colleagues. The taxa and sources are listed in appendix 2.

Publications of J.L. Gressitt were particularly useful and impressive—for the number and diversity of immatures described (based on his personal collections and rearing) including biological information, illustrations, and keys to species. Some results of my ongoing research with morphology and behavior of immature stages are published (Chaboo, 2001, 2002, 2004; Chaboo and Nguyen, 2004).

In coding states for immature stages, information for one or more species was combined, and terminals represent composites. The wide variation in cassidine life histories has played a fundamental role in recognizing the classical Cassidinae s.str. and Hispinae s.str. Morphological modifications under these life-history regimes are expected to provide powerful information for resolving phylogeny. Specimens examined here indicated great morphological diversity in immature stages of Cassidinae. To achieve the most informative dataset and most reliable phylogenetic hypothesis, this information must be included in the form of characters. Undoubtedly, immatures will provide far more information in the future, but it will take some time before sufficient specimens are available (through rearing, examination of unidentified and unsorted wet materials in museums, and species identifications).

Information from literature sources has some problems. Illustrated descriptions can be particularly useful because structures that were not considered by authors, or were described in a limited way, can still be compared. Problems do arise, however, in the completeness and accuracy of both descriptions and illustrations; for example, Chaboo and Nguyen (2004) pointed out several inaccuracies in descriptions and illustrations available for hemisphaerotine species.

In my analysis, terminals represent chimeric taxa for immature characters. The use of composite generic characters (i.e., combining information from multiple species) is not the best approach in a phylogenetic analysis for a variety of reasons. Published information may be incorrect, as already mentioned. The

genus may not be monophyletic, and an assumption of universality may be incorrect. States may apply to some or all species, and this introduces some uncertainty in the dataset. Given these concerns, I have nonetheless proceeded with composite coding because I think that the information is reliable for this level of characters and that omitting the significant ecological, behavioral, and morphological information already available would exclude a great deal of information about Cassidinae.

MORPHOLOGY OF EGGS (fig. 15)

Egg biology has been discussed for ecological guilds of Cassidinae. In general, egg descriptions are available for fewer taxa than for larvae. Oviposition sites may be on the surface or in maternal excavations of stems and leaves, and eggs may be deposited singly, in small groups (20–40 eggs), or in large groups of more than 100 eggs. Eggs may be naked or they may have coverings of colleterial secretions, fecal deposits, or chewed leaf fragments prepared by the mother. Suspended masses of eggs are known so far only in *Acromis* and *Omaspides* (Chaboo, 2001). These features can be developed as phylogenetic hypotheses; however, I only include two egg characters here because information is lacking for many taxa.

In species where maternal guarding has been recorded (table 6, fig. 21), females guard all immature stages. Maternal guarding may be a stereotypical behavior, but it is quite complex. As we know more about maternal care and care-providing species, variation in the behavior may be partitioned into multiple characters. Instead of treating maternal care as several characters to represent each stage that is guarded, I used maternal care as a single character for adults. We presently lack detailed comparative information on how guarding might vary from one immature stage to another, or how species and genera vary.

MORPHOLOGY OF LARVAE (figs. 16, 18, 20, 24–26)

Larval sizes range from 1 to 2 mm up to 6 cm and their color ranges vary from creamy

white to black, with some aposematically colored yellow and black forms. First-instar larvae can differ from later instars in color (usually darker), asperities (usually more), spines (more), setation (more), and in possessing egg bursters. Egg bursters occur in many first-instar larvae throughout Insecta and help the larva escape from its eggshell (van Emden, 1946). In taxa lacking egg bursters, larvae presumably exit the egg by chewing their way out (Cox, 1988). In Chrysomeloidea, egg bursters may be found dorsad of spiracles on the thoracic and/or abdominal segments IX (Cox, 1988). Askevold's (1990a) character 25 treated the presence/absence of egg bursters. Reid's (1995) characters 61 and 62 refined the states as presence/absence on specific segments, on the meso- and meta-thoracic segments only, or on abdominal segment I only, or on additional abdominal segments, up to segment VIII.

These previous state definitions do not take into account that egg bursters vary in segment position (on the head, thorax, or abdomen, or in some other combination) and can comprise spines, setae, or tubercles. Egg burster per se refers to structures that are not homologous among insects (indeed, snakes also emerge with the aid of egg bursters), and the structures covered by the term need to be reviewed and brought into line with phylogenetic concepts. I have used egg bursters on the abdomen according to Reid (1995), but including or excluding this character from the present analysis does not affect the topology.

Generally, cassidine larvae tend to be dorsoventrally flattened, with the extreme condition being found in the platyform "water-penny"-like immatures of rolled-leaf cassidines (Maulik, 1932, 1933). Variations in head exposure and mouth position relative to the antennal bases appear to parallel the condition on the adult head. The antennomeres vary in number from two to three (Maulik, 1919; Paterson, 1931b). The lateral margins of thoracic and abdominal segments can be expanded and bordered with spinules and hairs, and the prothoracic segment can be explanate frontally, covering the head dorsally. Mining insects appear to show reductions in head, mouthparts, lateral projections, and legs (Frost, 1924; Maulik, 1933; Ford and Cavey, 1985). Variation and

function of larval stemmata have not been widely studied (Gilbert, 1994) but could be diverse across Cassidinae.

Mouthparts. Sanderson (1900) and Paterson (1931) briefly discussed differences of larval mouthparts at the subfamily level and pointed out some unusual features of Donaciinae. Paterson (1931) found resemblances between *Lema* (Criocerinae) and Cassidinae in setal arrangements. From my preliminary examinations, mouthparts do vary greatly. Triangular unidentate mandibles in hemisphaerotines (Chaboo and Nguyen, 2004) and palmate four-dentate mandibles in *Acromis* (Chaboo, 2002) suggest a wide variation in mandible morphology. Preliminary examinations of mouth morphology and observations of nearly stereotypical feeding patterns suggest great variation in mouth morphology and feeding mechanics to deal with the diversity of host plants (from grasses to morning glories) and diversity of feeding modes (boring, mining, skeletonizing, scraping, and chewing).

Thorax. Thoracic segments frequently have scoli (pleural lateral projections) that vary in their number, arrangement, branching, and setation (Gressitt, 1963; Maulik, 1931; Zaitsev and Medvedev, 1982). Additionally, the margins of all thoracic segments may be explanate laterally (e.g., Coelaenomenodera; Maulik, 1931), paralleling the pattern in adults. Anterior extensions of the prothorax may also cover the head, as in many adults. Thoracic spiracles, especially the prothoracic spiracle, vary in proportions.

Legs. Exophagous Cassidinae always have three-segmented legs but mining forms appear to be more labile in leg development (Roberts, 1930; Maulik, 1926, 1931; Jolivet and Hawkeswood, 1995). Miners can have legs soft with reduced sclerotization or vestigial and clawless, for example, *Craspedonispa saccharina* Maulik (Callan, 1954) and *Sceloenopla* (Jolivet and Hawkeswood, 1995). Entire segments may be lost, for example, *Wallacea dactylifera* has two segments (Maulik, 1919). Some mining larval cassidines lack legs altogether, for example, *Octotoma* and *Odontota* (Needham et al., 1928; Ford and Cavey, 1985).

Abdomen. The number of larval abdominal segments varies with 8, 9, and 10 segments

known. In nonshield-retaining cassidines, there is much confusion and disagreement about the terminal segment and the urogomphi. Mining larvae have been reported as having 8, 9, 10, and 11 segments (Chen et al., 1986); Coleoptera larvae can have up to 10 abdominal segments but never 11 segments (Lawrence, 1982, 1991; Lawrence and Britton, 1994). This information is ambiguous even for other chrysomelid subfamilies; for example, data for *Donacia* larvae (Donaciinae) are similarly conflicting with eight segments being commonly reported, but nine segments (Schmidt-Schwedt, 1887) and a rudimentary segment X (Sanderson, 1900) are also reported.

The last two abdominal segments of many mining forms are commonly fused, with the suture distinct or reduced. The terminal segment can therefore appear to be one segment or to comprise two segments (fig. 24A, C, F and H). It is frequently heavily sclerotized, sometimes with bladelike (razor sharp in some species) or blunt edges, and/or it has a large dorsal concavity. Maulik (1931) termed this peculiar posterior a "shovel" and suggested that the dorsal concavity may provide a pocket of air for respiration, may be used for slicing within the leaf mine, or it may help keep the mine clear of excreta and debris. It is also possible that these "shovels", termed here as urogomphal plates, may act as blocking device within a mine.

The fusion and loss of abdominal segments in Cassidinae poses special problems in discussing homologies of posterior structures. Urogomphi are projections of the tergum of segment IX and they appear in unrelated immatures throughout Coleoptera (Crowson, 1981). Urogomphus may be an umbrella term for a variety of structures found on the terminal abdominal segment. Within Chrysomelidae, Cassidinae appears to be the only group with hind-end projections. More remarkably, Cassidinae exhibits two types, the urogomphal plate ("tail shovels") and caudal processes. Chaboo and Nguyen (2004) provided an illustrated discussion of the various terminology, morphology, and homology of caudal processes. Tail shovels are not homologous with caudal processes as the former involve one or more segments and form a single functional unit. A case could be

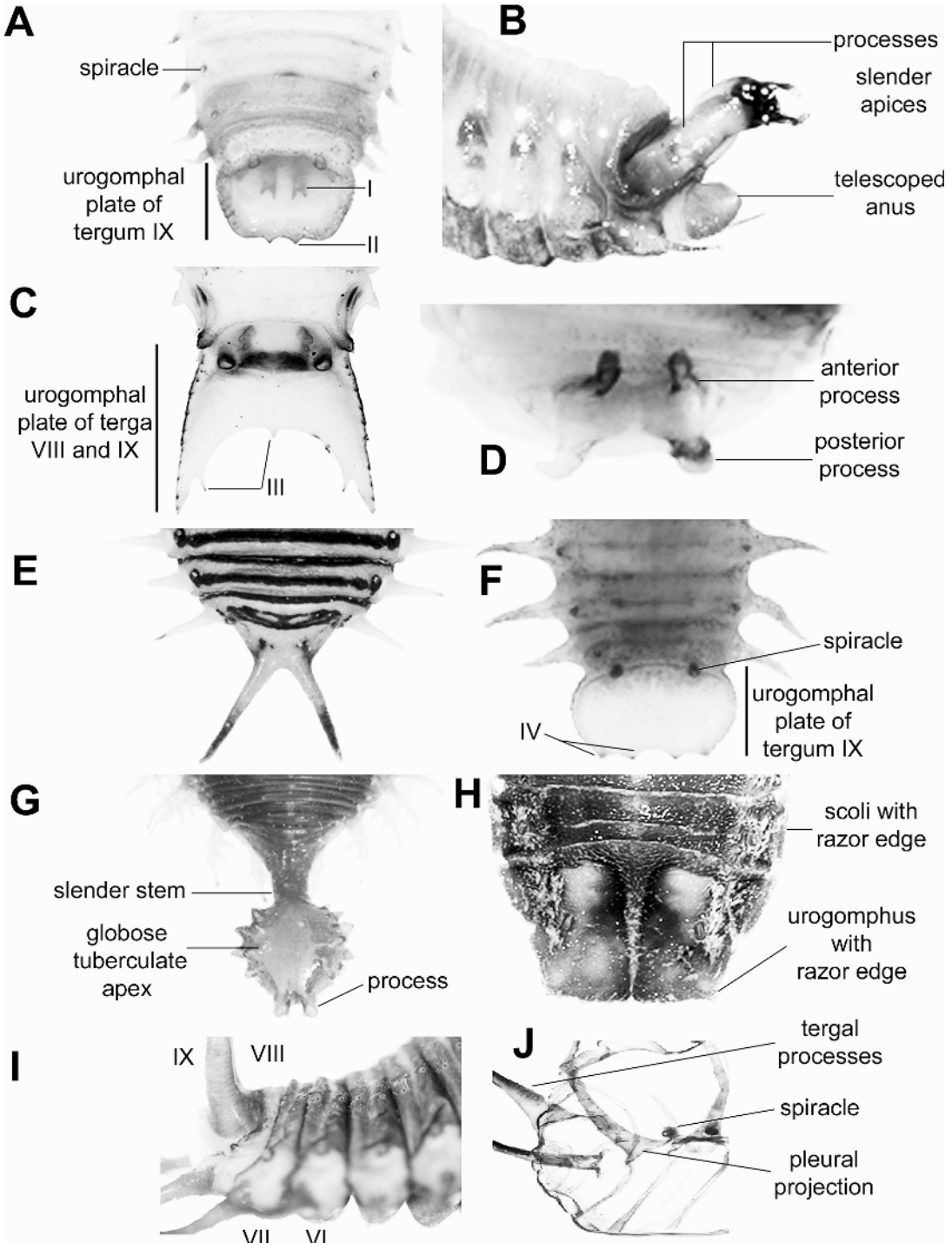


Fig. 24. Larvae of Cassidinae, hind end, dorsal view. A. *Anisodera* sp. B. *Basiprionota* sp. C. *Botryonopa* sp. D. *Hemisphaerota palmarum*. E. *Physonota* sp. 1. F. *Prosopodonta corallina*. G. *Coptocyclus* sp. H. Undetermined mining species. I. *Eugenysa columbiana*, lateral view. J. Cleared abdomen, lateral view of sagittal section.

made for homologizing spines, small marginal lobes, elongate lobes, or other secondary projections on tail shovels (figs. 24A, C, F, 26B) with caudal processes, but this idea needs more detailed morphological examination. Illustrations of *Leptispa* by Chen et al. (Chen, 1973; Medvedev, 1982; Chen et al., 1986) show larvae with a single elongate bifid process, which, however, appears on an abdominal segment IX in their illustration. Caudal processes range from one to four, are not articulated, and may be bifid. In addition to numbers, processes vary in length, position, orientation, morphology and setation (Chaboo and Nguyen, 2004).

Scoli. Larval abdominal segments can be similar to paired thoracic pleural projections in having scoli. These may be present or absent across Cassidinae. When present, their lengths are highly variable from tubercle-like to long. Scoli may be simple or branched and smooth or with sharp barb-like setation. Świątojańska et al. (2005) discussed scoli number as a phylogenetic character, with 13 representing the most plesiomorphic condition in "true cassids", then 14 as the next evolutionary step, and 16 as the most derived. However, scoli number varies within genera (e.g., *Chlamydocassis* Spaeth; Świątojańska et al., 2005), so any hypothesized transformation series should consider variation at all hierarchic levels.

Spiracles. These vary in number and position. The thoracic spiracles can be positioned laterally or ventrally. Laterally directed prothoracic spiracles were first described in *Oediopalpa* larvae (Maulik, 1933). Hemisphaerotines also have similar prothoracic spiracles that are elongate tubes directed laterad and extend slightly beyond the lateral margins of the exuvio-fecal shield (Chaboo and Nguyen, 2004). The fifth abdominal spiracle is long and conical in *Dactylispa* (Maulik 1929, 1931), unlike the short ones in most other cassidine larvae. The terminal pair of abdominal spiracles may be well developed or vestigial, functional or not, lateral or dorsal, and may be biforous or annular (Böving and Craighead, 1931; Jolivet and Hawkeswood, 1995; Chu, 1949; Peterson 1960). Abdominal spiracles, especially the terminal pair, can be laterally or dorsally positioned. Spiracles associated with uro-

gomphal plates may be present and well developed (fig. 24A, E), reduced or absent. When present, they may be positioned on the suture between segments VIII and IX, or laterally like other abdominal spiracles.

Anus. This varies greatly in shape and position across Cassidinae (fig. 26). In shield-retaining cassidines, the anus complex comprises the anal pore, which is at the end of an elongate rectum that is telescoped with segment X. These two sections are narrowed relative to preceding segments (fig. 26A). *Eurypepla* is unique among shield-retaining cassidine larvae in having segment X and the rectal extension resembling the preceding abdominal segments (Chaboo, 2004; fig. 25). In many nonshield-retaining forms the anus is a narrow transverse ventral slit (fig. 26B) or an apical pore (fig. 26C). The functional significance of the telescoped anus appears to be for shield construction and repairs, but the significance of this wide variation in anal position is unclear. Shrivastava and Verma (1983) briefly examined rectal morphology, and this is worth pursuing to understand how rectal morphology and physiology influence fecal production and shield construction.

Chaetotaxy could be an important tool in the taxonomy of immatures (Paterson, 1931). Borowiec and Świątojańska (2003) developed a chaetotaxonomy for cassidine immatures but their terminology is different from that utilized for other chrysomelids (e.g., Cox, 1996) and in Coleoptera. Their study provides a starting point for anatomical study and homology determination.

Modifications for Semiaquatic Living. The larvae of rolled-leaf and bract cassidines are not only extremely dorsoventrally flattened, but they also tend to have the venter and margins densely pubescent (Maulik, 1937). *Cephaloleia* species vary in having glabrous or pubescent larvae. Larvae of the Old World genus *Leptispa* also have fine ventral hairs and live in rice paddy fields where they can withstand periodic submersion (Maulik, 1919; Chaboo and Prathapan, unpubl. data). The significance of these hairs (whether locomotion or plastron) is unclear.

Behavior. Gregariousness, cycloalexia, and exuvio-fecal shield retention occur in cassidine larvae and pupae and are complex

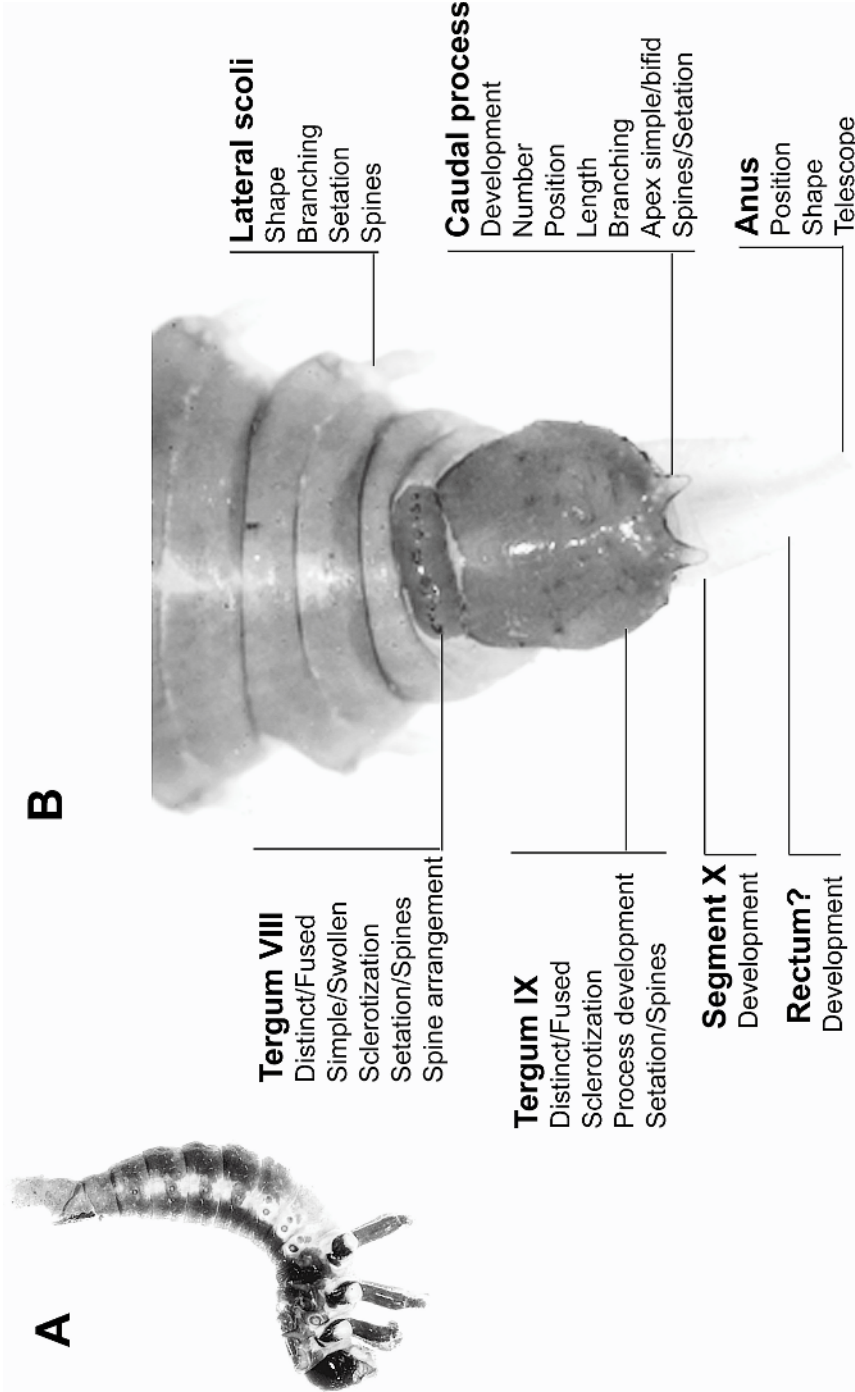


Fig. 25. The hind end of larval Cassidinae as a character system. **A**, **B**. *Eurypepla calochroma*, instar V. **A**. Lateral view. **B**. Dorsal view.

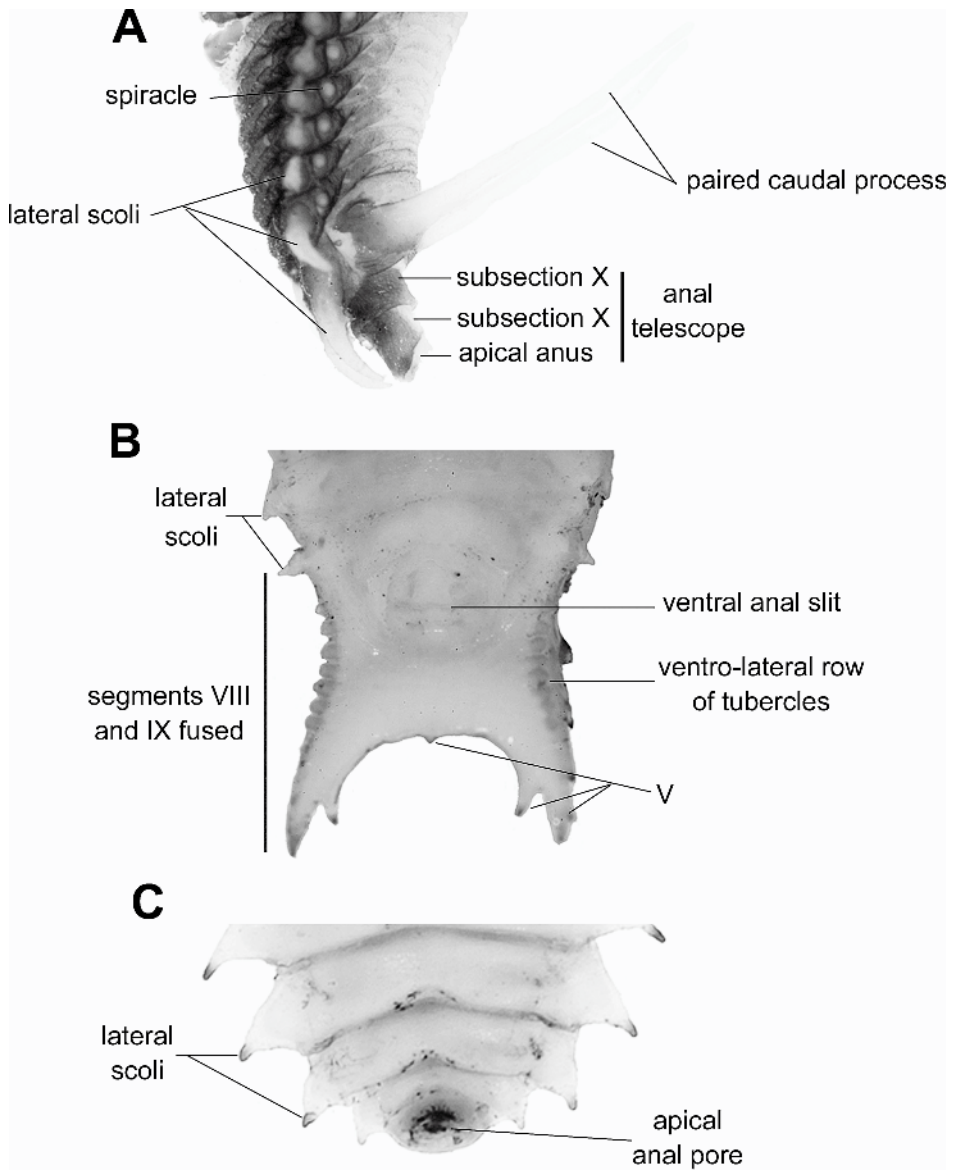


Fig. 26. Anus of mature larval Cassidinae. **A.** *Acrocassis gibbipennis*, lateral view. **B.** *Brontispa* sp. 1, ventral view. **C.** *Chalepus ater*, ventral view.

character systems. Shields (fig. 20) are a particularly interesting aspect of immature stages and are actively being studied by many researchers. Shield retention can vary among larval instars and in pupae and thus very precise observational data are needed for exact scoring as character states. Steinhausen (1969) was the first to define shield-related characters in larvae and pupae of *Cassida*

species; his characters 14 and 28 concerned shield presence or absence and composition of exuviae or feces.

Fecal recycling occurs in five clades of Chrysomelidae: Cassidinae, Cryptocephalinae, Criocerinae, Galerucinae, and Lamprosomatinae (Chaboo et al., 2007). The diverse fecal cases and shields, the life-history stages involved, and the elaborate morphology

associated with constructions (anal and rectal modifications) and retention (setation and caudal processes) promise rich ground for developing novel character hypotheses.

MORPHOLOGY OF PUPA (figs. 17, 19).

Cassidine pupae parallel larvae in their morphology, with a tendency to dorsoventral flattening and with lateral scoli of various sizes. Many morphological characters of larvae can be compared in the pupal stage. Pupation patterns (singles or groups, sites) are also of interest. As far as is known, all exophagous cassidines pupate externally. Cassidines with mining larvae have pupation sites within the mine or externally. Pupae may be naked or they may retain the exuvio-fecal shield of the fifth larvae or only the fifth larval exuviae on its abdomen. *Stenispia* appears to be unique in having pupation occur within the last larval exuviae (Ford and Cavey, 1985); this genus is also unusual because it has an external feeding larvae, but it is currently classified in the tribe Cephaloleiini, whose members are otherwise cryptic closed leaf feeders.

From my examination of specimens, it appears that the development of caudal processes and shield retention in the pupa cannot be predicted from the larval condition. Pupae may be naked (fig. 17E), may retain the last larval exuviae (fig. 17F), or may retain the shield of the last larva (fig. 19). Shield retention requires caudal process development, but retention of the last larval exuviae does not. When caudal processes are developed, their morphology can be very different from the corresponding larval processes. For example, hemisphaerotine larvae have four caudal processes, but pupae have two (Chaboo and Nguyen, 2004).

Only two characters are proposed for pupae. Available descriptions of pupae are fewer than those for larvae, and these suffer from the same problems in adequacy and accuracy as in larval descriptions.

MORPHOLOGY OF CASSIDINE ADULTS

In the following discussion, I first describe the morphology of a focus taxon, *Hemisphaerota palmarum* (Boheman), to introduce adult morphology and terminology of Cassi-

dinae. I then compare structures among the cassidine taxa sampled in this study. Without background knowledge about the most basal cassidine, I selected *H. palmarum* for several reasons including the availability of a long series of specimens obtained through personal collecting and the tribe's "intermediate" morphological qualities between Hispinae s.str. and Cassidinae s.str.

Chaboo and Nguyen (2004) described the biology and immature stages of *H. palmarum*. Individuals live solitarily on palm hosts. Hemisphaerotine immatures retain a basket-type shield that completely covers the body dorsally and laterally. Adult specimens are fairly common in United States collections, especially *Hemisphaerota cyanea* (Say) that occurs in the Gulf of Mexico states. Hemisphaerotines are usually found in high population densities on their palm hosts, and some are regarded as pests. The following description of *H. palmarum* adults will supplement the existing knowledge of Hemisphaerotini and will serve as a model for Cassidinae.

MORPHOLOGY OF ADULT *HEMISPHAEROTA PALMARUM* (BOHEMAN) (figs. 27–40)

Adults ($N = 10$) are 5.54–6.98 mm long and 4.27–5.06 mm wide. The body is compact and cheloniform, and being broadly oval in dorsal view (fig. 27) with a continuous lateral line. It is hemispherical in profile and the dorsal and ventral surfaces are not parallel. The dorsal surface is curved and the ventral surface is straight (fig. 28B). The pronotal base and elytral humerus are angled anterad. Body color is red, with punctures that are black centrally. The eyes and the venter are generally black, and the abdominal segments are mostly black with reddish posterior margins. The dorsum is coarsely punctate with punctures varying in width, depth, and distributions; generally, elytral punctures are wider and deeper than pronotal punctures. Pubescence is generally sparse.

The head (figs. 29–30) is small and exposed dorsally, not being covered by the pronotum. It is also exposed ventrally, not being covered by the prosternum. The head is hypognathous, with the mouth medially positioned on the venter. The mouthparts are

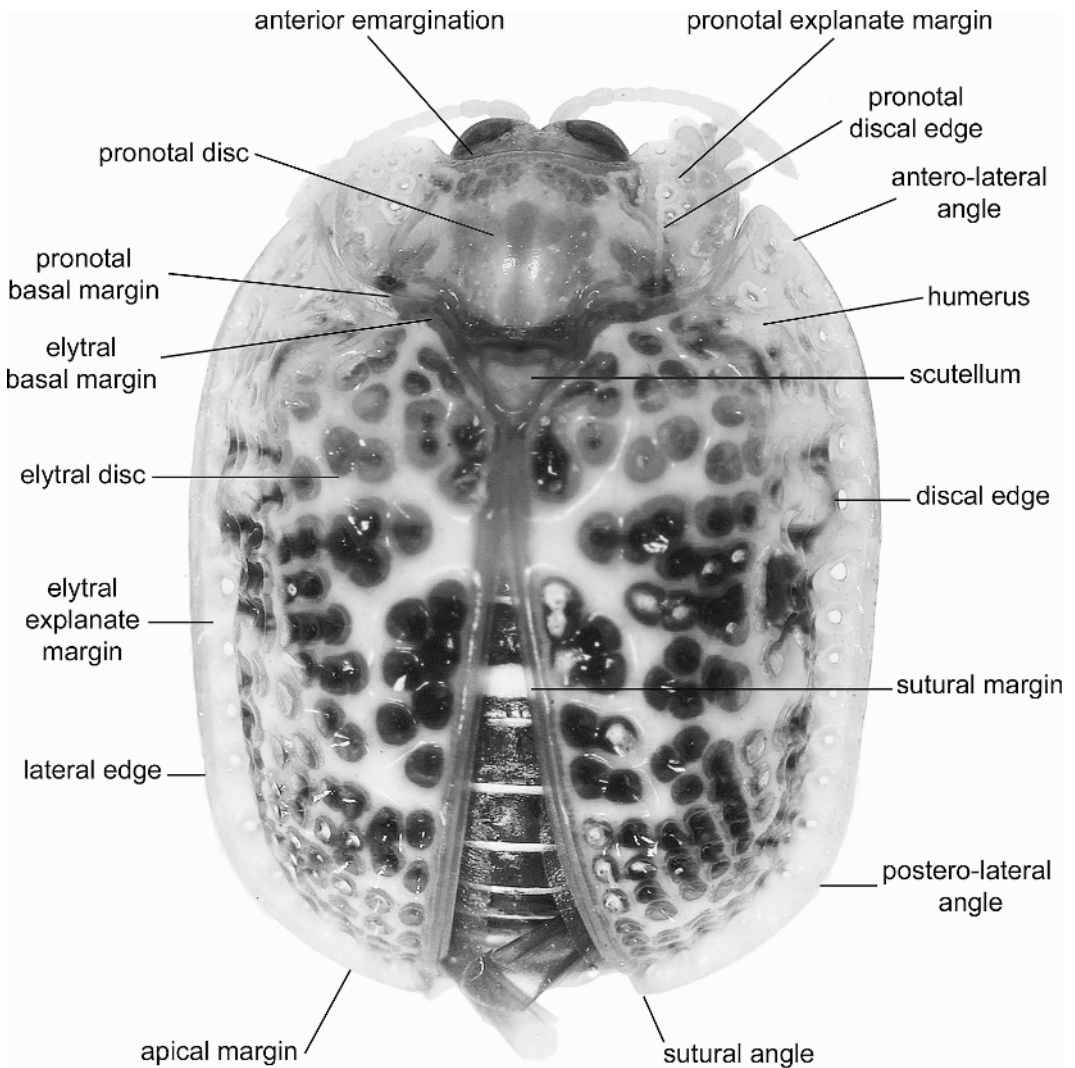
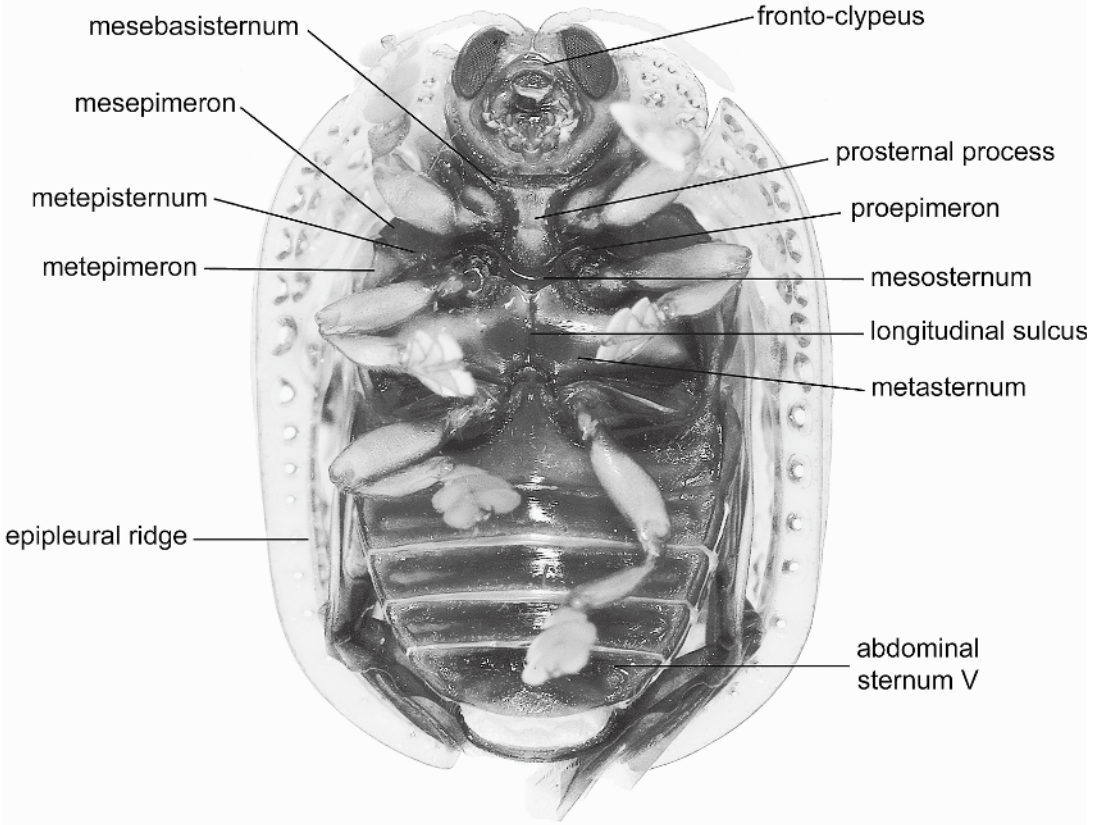


Fig. 27. *Hemisphaerota palmarum*, adult, dorsal habitus.

fully developed, free, and enclosed laterally by an anterior extension of the explanate margin of pronotum. The head is quadriform in dorsal view, slightly wider than long, and very slightly narrowed behind the eyes. The vertex is smooth, lacking any striae of a stridulatory file. The occipital opening is round. In lateral view, the clypeus and frons form a somewhat flattened plane that is angled diagonally to the antennal bases. The eyes are oriented ventrally and occupy less than one fourth of the lateral head length in dorsal view. The facets are small, round, and

flat, and the eye margins are continuous, straight, and not margined. Dorsally, the eyes are rectangular-shaped, wider than long, with dorsomedial and dorsoposterior margins forming a 90° angle. The dorsomedial and posterior margins have a row of small round punctures. The eyes appear elongate oval in the lateral aspect and triangular in the ventral aspect. The ventromesal margin is long, with a row of sharply curving setae. The lateral margin is short; the ventromesal and lateral margins form a rounded 45° angle near the subgenal brace.

A



B

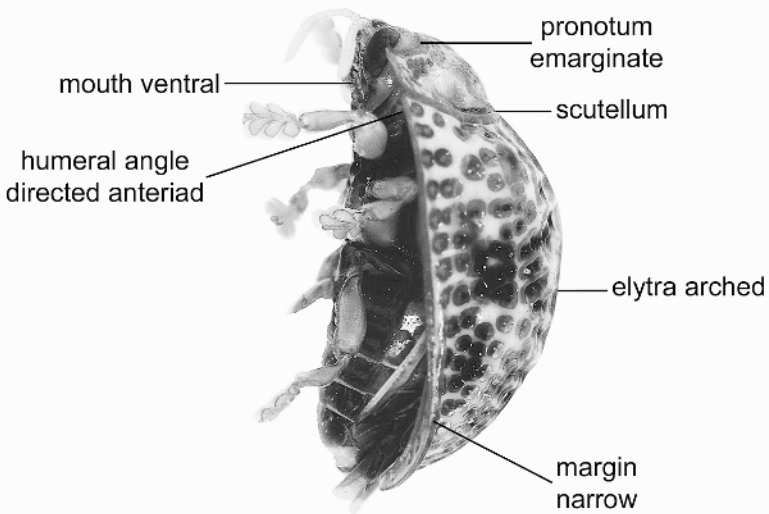


Fig. 28. *Hemisphaerota palmarum*, adult. **A.** Ventral view. **B.** Lateral view.

The corona appears as two flattened plates being medially dissected by the longitudinal coronal sulcus. It has a slight transverse furrow posteriorly. The transverse furrow is angled alongside the mesal eye margin. A supraorbital puncture is absent.

The frons is depressed and fused with the clypeus. Its mesal border has a row of four setae. The clypeus is triangular to hemispherical in shape; an anterior protuberance obscures the epistomal suture. The clypeal surface is smooth, impunctate, and asetose; the lateral corners are confluent with the secondary anterior articulation of the mandible. The gena is punctate with punctures small, shallow, and randomly scattered. The genal brace is thickened at the primary mandibular articulation. The gular sutures terminate before the mouth margin, curve weakly posteriorly, then sharply so anteriorly, converging but not meeting medially. The gula is wide posteriorly, about one third the ventral head width, but the pregula is short. The posterior tentorial pits are not recognizable externally but occur at a sharp angle in the gular suture.

Head Appendages. The antennae (fig. 29D) are 11-segmented, filiform and short; they reach just posterior of the pronotal margin. The antennal sockets are positioned mesally between the eyes on the corona and are almost contiguous, separated only by the coronal sulcus. The antennomeres are discrete and shallowly telescoped. Their shape is cylindrical, being wider apically than basally with the mesal and external margins of each antennomere proportional; no sections appear swollen. Antennomeres I–VII are longer than wide and antennomeres IX–XI are wider than long. The scape is the longest, the pedicel is longer than antennomere III, and antennomeres III and IV are roughly equal in length. Setation is sparse basally but increases between antennomeres VI and VII, and the apical antennomeres are densely pubescent. The antennae lack grooves or depressions.

Mouthparts. The labrum (fig. 31A–D) is deeply inserted into the head. Its exposed portion is trapezoidal-shaped, being longer than wide; distally it is transversely thickened and protuberant with the protuberance obscuring the base of the labrum frontally. The

dorsal surface has sparse medium-long setation. The apex is flattened (fig. 31C) and punctate and the sub-apical margin has a row of bristles. The epipharyngeal membrane is thick, extending to the anterior margin of the mandibles, and the ventral surface has a medial tract of hairs. The mandible (fig. 31E–F) has a trigonal shape with a broad base, large fossa, and the distal portion dorsoventrally flattened, tapering to a sharp cutting edge. The anterior margin is transverse and the posterior margin is short and continuous with the mesal margin. The mesal margin is rounded basally and has molar cusps and a single apical incisor. The mola is densely asperate. The right mandible is slightly longer than the left one. The maxilla (fig. 32A–B) has the cardo narrowed medially and deflected into the head, with only the rectangular anterior portion exposed frontally; its basal margins are arcuate, with a lobate basolateral extension and the apical portion is heavily sclerotized and protuberant from the stipes. Dorsally, the cardo has clusters of bristles on the sublateral and mesoanterior surfaces. The stipes and cardo meet broadly; the stipes lacks bristles or pores. The rectangular palpifer has a single apical seta. The maxillary palp and galea have long setae whereas the lacinia has short dense setae. The four-segmented palpus has the basal palpomere shortest and narrowest, palpomeres II and III subequal, and palpomere IV longest. Palpomeres II and III have their external margins slightly longer and curved than the mesal margins. Palpomere I is asetose, palpomeres II and III have sparse apical setae, and palpomere IV has scattered sparse setae. The two-segmented galea has the basigalea with a straight apex; the shorter distigalea has a rounded apex. The lacinia is rounded and with dense short pubescence distally. The labium (fig. 32C) has a cup-shaped mentum, with the anterior portion being wider than the basal portion. The basal margin is straight, broadly articulating with submentum. The anterior margin is slightly wider than the base of the prementum, and the anterolateral areas have a small field of long setae. The prementum is wider apically than basally and the surface is sparsely setose. The palpigerae are mediolaterally positioned. The junction between the pre-

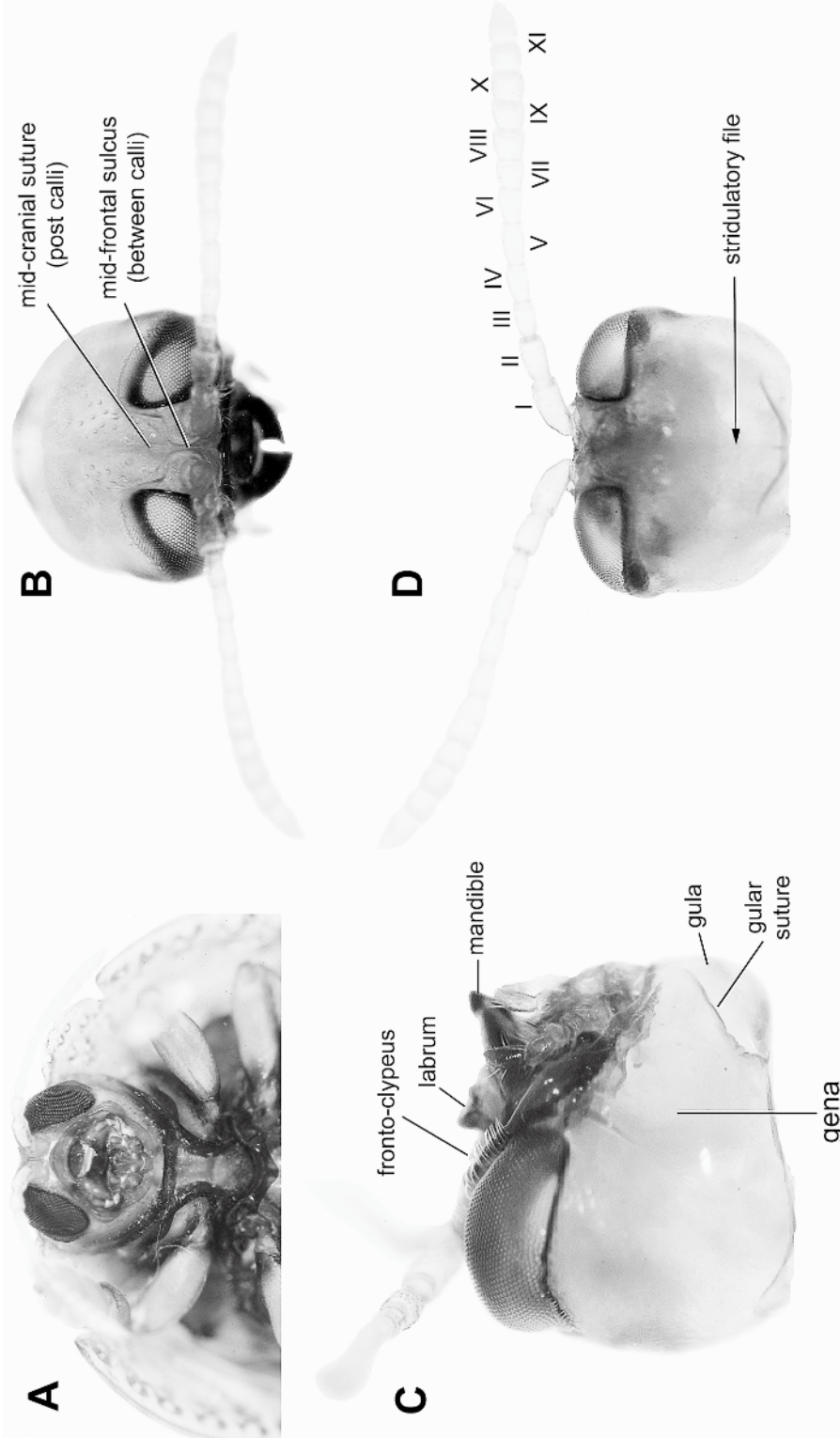


Fig. 29. *Hemisphaerota palmarum*, head. A. Ventral view, in situ. B. Anterior view. C. Lateral view. D. Dorsal view.

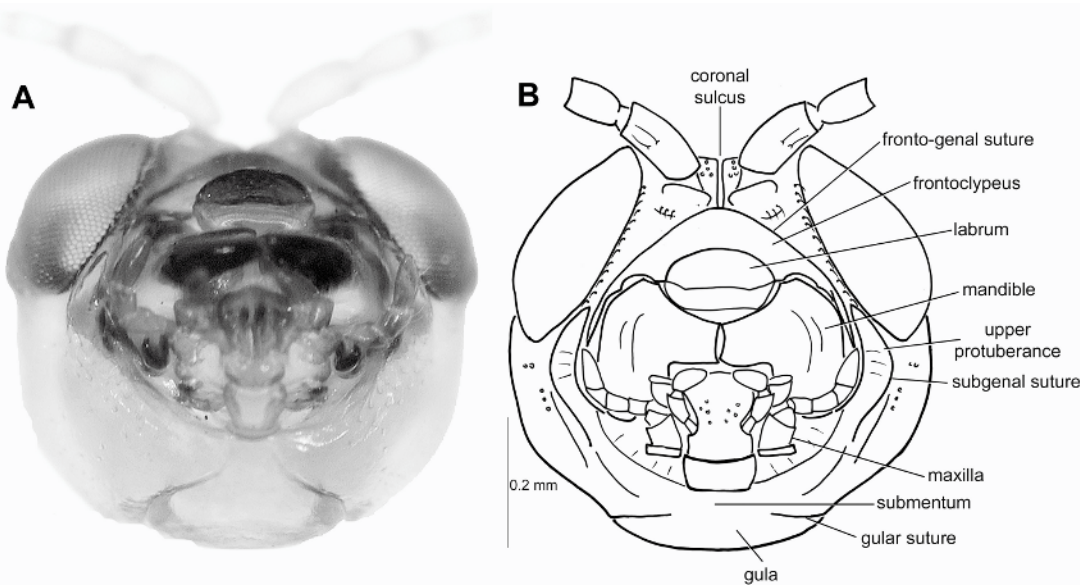


Fig. 30. *Hemisphaerota palmarum*, head, ventral view. **A.** Photograph. **B.** Illustration.

mentum and ligula is indistinct, and the ligular margin is continuous and slightly expanded medially. The three-segmented labial palpus is comprised of cylindrical, sparsely setose palpomeres. Palpomere I is shortest, and palpomeres II and III are subequal, almost twice as long as palpomere I. Palpomere II is wider apically than basally and palpomere III is wider basally than apically.

Thorax. The prothorax (fig. 33) has the pronotum wider than long, with well-developed explanate margins. These margins are expanded anteriorly and enclose the head laterally. The lateral profile is arched with the basal margin highest. The anterior margin is deeply emarginated, with the head partially exposed. The basal margin is truncate at the scutellum, being evenly curved laterad and anterad. The well-defined complete discal edge separates the discal and marginal areas. The pronotal edges are smooth, lacking setation or dentation. The dorsum is irregularly punctate, having discal punctures smaller and concentrated anteriorly and basally; the marginal punctures are larger and deeper, and some have a single setae of variable length. The mesal angle of the anterior edge has a single pore with three long bristles. The posterior trichobothrium is absent. The

pronotum is strongly deflexed ventrally, forming the hypomeron. The hypomeron provides the vertical wall of the prothorax, and its surface has fine irregular ridges. The procoxal cavity is set in a basolateral position. The tergo-sternal suture separates the hypomeron and prosternum anterad of the procoxal cavity. The suture is evanescent anteriorly. The long, narrow hypomeral lobes close the procoxae behind. The prosternum is narrow anteriorly, and the apical margin is simple, not expanded, and lacks serration. The width of the prosternal process (fig. 33D) equals one third the prosternal width. The process is broadly rectangular, having thickened lateral edges and a depressed sparsely punctate central area. The apical margin is angular, with two posterolateral lobes and two sub-apical lobes. The posterolateral lobes are narrowed and elongate and the apex is rounded, overlapping the hypomeral lobes. The sub-apical lobes are short.

The mesothorax (figs. 34–37) has the mesotergum (fig. 34A) mostly hidden under the pronotum, and the mesoscutellum (fig. 34A) is medially depressed and trapezoid-shaped with a smooth shiny surface. Its anterior margin is gently emarginated and overlapping the posterior pronotal angle, its

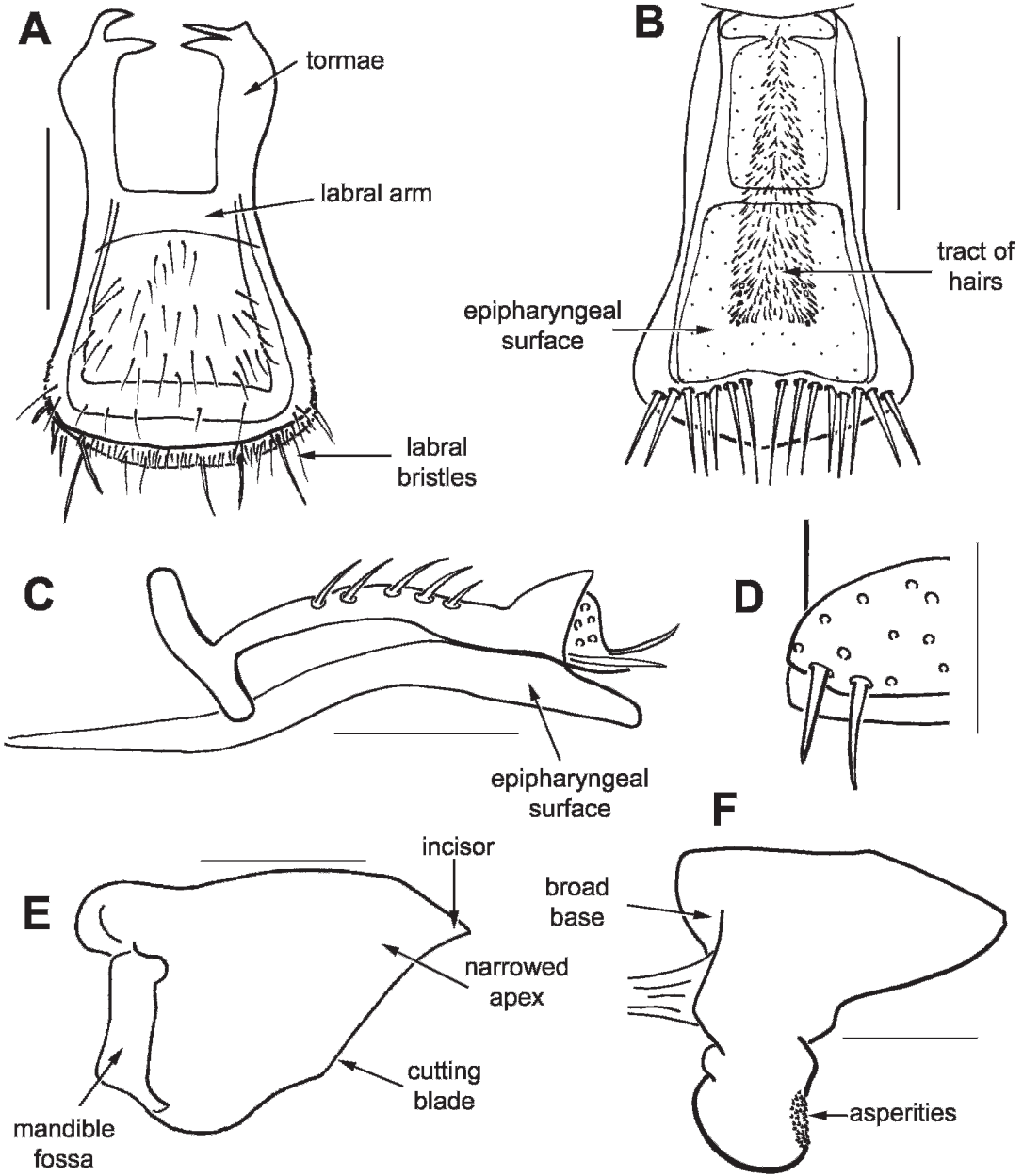


Fig. 31. *Hemisphaerota palmarum*, mouthparts. A. Labrum, anterior view. B. Labrum, posterior view. C. Labrum, lateral view. D. Labrum, ventral view. E. Mandible, ventral (external) view. F. Mandible, dorsal (internal) view. Scale bars = 0.25 mm.

posterior margin is straight, and its lateral and posterior edges are beveled, overlapping the elytra laterally and posteriorly. The mesepisternum (figs. 35A, 36A) is comprised of three areas (in lateral view): one is angled

anteriorly, abutting with the prohypomeron; another is angled laterally and hidden under the elytra; and the third is angled ventrally, forming a triangle that is bordered anteriorly by the mesosternal groove, posteriorly by the

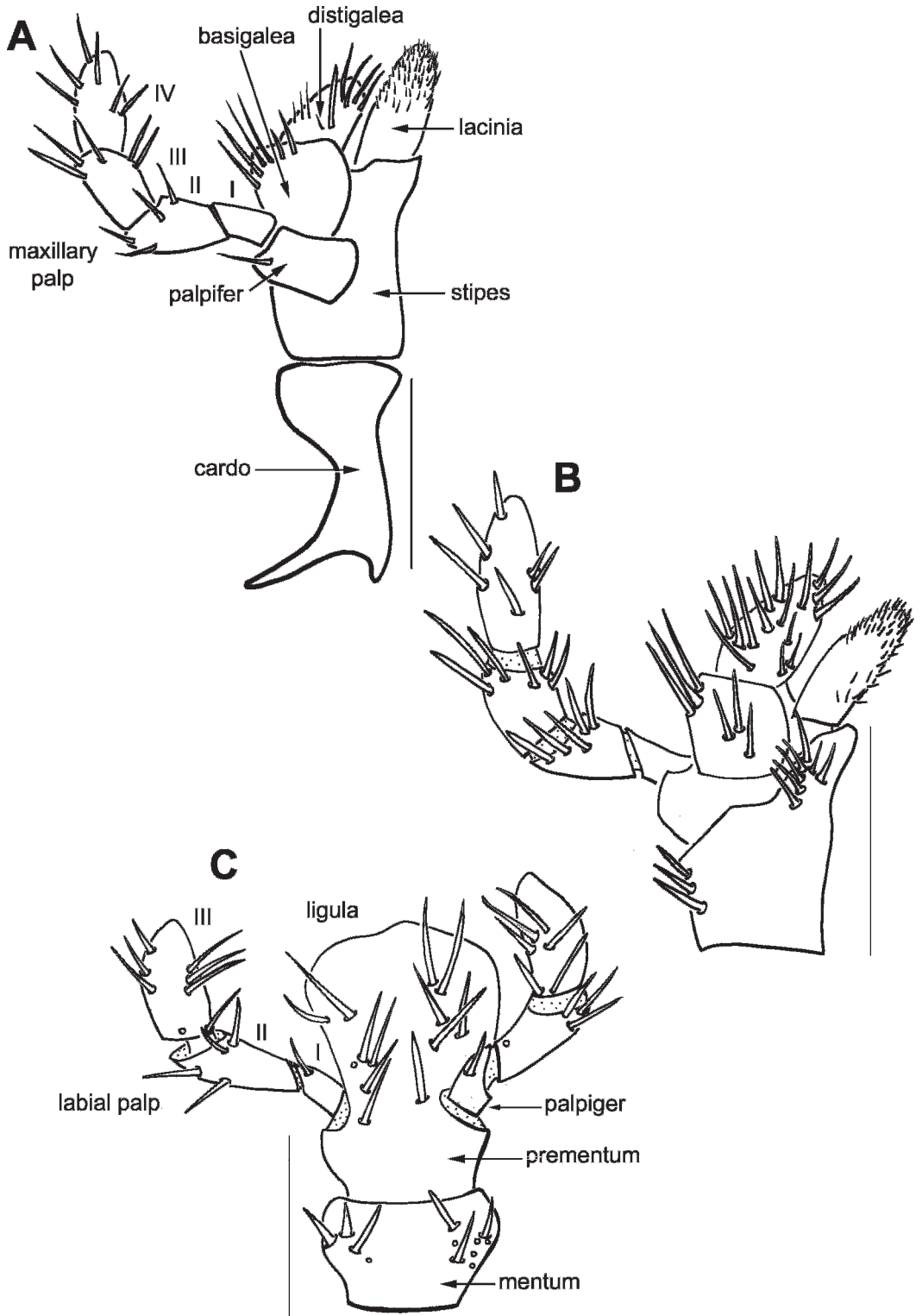


Fig. 32. *Hemisphaerota palmarum*, mouthparts. **A.** Maxilla, ventral (external) view. **B.** Maxilla, dorsal (internal) view, cardo not shown. **C.** Labium, ventral (external) view. Scale bars = 0.25 mm.

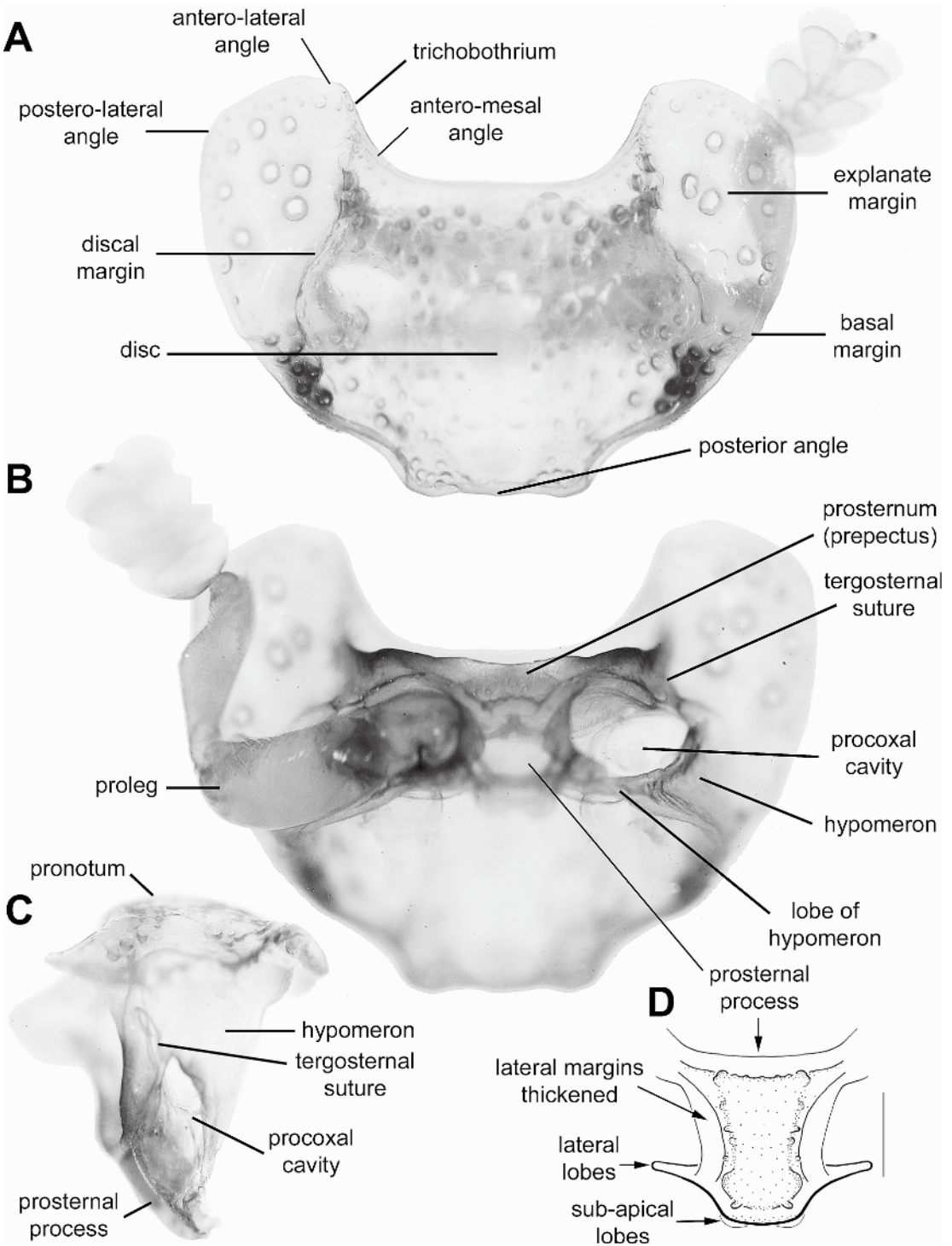


Fig. 33. *Hemisphaerota palmarum*, pronotum. A. Dorsal view. B. Ventral view. C. Lateral view. D. Prosternal process, ventral view, scale bar = 0.5 mm.

mesepimeron, and ventrally by the lateral lobe of the mesosternum. The mesepisternal ridge is punctate along the posterior side. The mesopleural suture is sinuous and curves anterad. The mesepimeron (fig. 36B) has two broad parts (in lateral view), with an anterolateral portion forming a broad plate hidden under the elytra and a ventral portion forming a triangle bordered anteriorly by the mesepisternum, posteriorly by the metepimeron, and medially by the mesocoxa and metasternum. The mesosternum (fig. 35B) is short and broad, forming two lateral lobes anteriorly of the mesocoxae. The mesosternal process has the posterior margin thick and protuberant, forming an angular notch that receives the prosternal process.

The metathorax has the metanotum (fig. 35A) membranous and the metapostnotum has straight margins. The metapleuron (fig. 35B) is comprised of the metepisternum and the metepimeron. The metepisternum is heavily sclerotized, with three triangular surfaces: an elongate ventral section, a broad smooth anterior section, and a narrow punctate posterior section. The metepleuron has a small smooth anterior surface and an elongate dorsal surface that is broader anteriorly and terminates in the metapleural wing process. The metepimeron is sclerotized anteriorly and membranous posteriorly. The metasternum (fig. 35B) is transverse, with the posterior margin being wider than the anterior margin. It is protuberant in the posterolateral area and has a complete medial longitudinal groove. The metendosternite (fig. 36C) has an internal anterobasal longitudinal flange off the metasternum. Two anterior metafurcal arms arise laterally off the metafurcal lamina. Two metafurcal tendons arise medially from the anterior margin of the metafurcal lamina.

Wings. The elytron (fig. 37) is convex and its sub-scutellar area is indented. The sutural margin is generally evenly curved in lateral profile, having a slight protuberance posteriorly of the sub-scutellar area. The lateral margin is explanate, and its width is much narrower than the width of the disc. The basal, lateral and posterior edges are smooth. The lateral margins are sub-parallel, with evenly curved anterior and posterolateral angles. The humeral angle is not protuberant

or expanded. The anterior angle is projected slightly anterad. The elytral surface is deeply punctate, with punctures varying in size and depth and not in any discernible rows; some punctures are confluent. The venter of the elytron (fig. 37B–C) has a keel extending off the epipleural ridge in the anterior half. This keel curves posteriorly and runs parallel to the ridge.

The fully developed hindwing (fig. 34B) has veins Cu, Sc, RA, RP, MP1+2, MP4, CuA, AA and AP3+4 present. Veins RP1 and RP2 are obsolete. The radial cell is also developed and closed. Cubitoanal cells 1 and 2 are both developed and closed. The wing coloration is uneven, with the distal region being dusky.

Legs. The legs (fig. 38) are short, compact, and of similar lengths and appearance. The procoxal cavity is laterally positioned, while the meso- and metacoxal cavities are ventrally positioned. The procoxa is pear-shaped, not protuberant, and its surface is finely pitted, sparsely punctate and sparsely setose. The mesocoxa is rounded, being sparsely punctate anteriorly and with sparse bristles laterally. The pro- and mesocoxae are moderately separated by the sternal processes, whereas the metacoxae are separated by a small abdominal intercoxal notch. The elongate transverse metacoxa has a small medial lobe, and its surface is finely ridged and sparsely punctate. The trochanter is generally smooth, with a few scattered punctures and short setae basally. The mediolateral surface of the distal margin has three to four long setae. The femur is short, slightly longer than the tibia, and its dorsal surface has short horizontal ridges mediolaterally and a smooth central area. The tibia is notched apically and receives the tarsus; tibial pubescence increases distally. The tibial notch is approximately $\frac{1}{2}$ the tibial length and its surface is finely ridged, setose and impunctate. The tarsus has tarsomeres I, II, III, and V present, but tarsomere IV absent. Tarsomeres I–III are expanded laterally, flattened dorsally and ventrally, and densely setose ventrally. Tarsomere I is one-half the width of tarsomere II. Its apical margin is straight and the lateral expansions are slightly asymmetrical. The external margin is wider than the mesal margin. Tar-

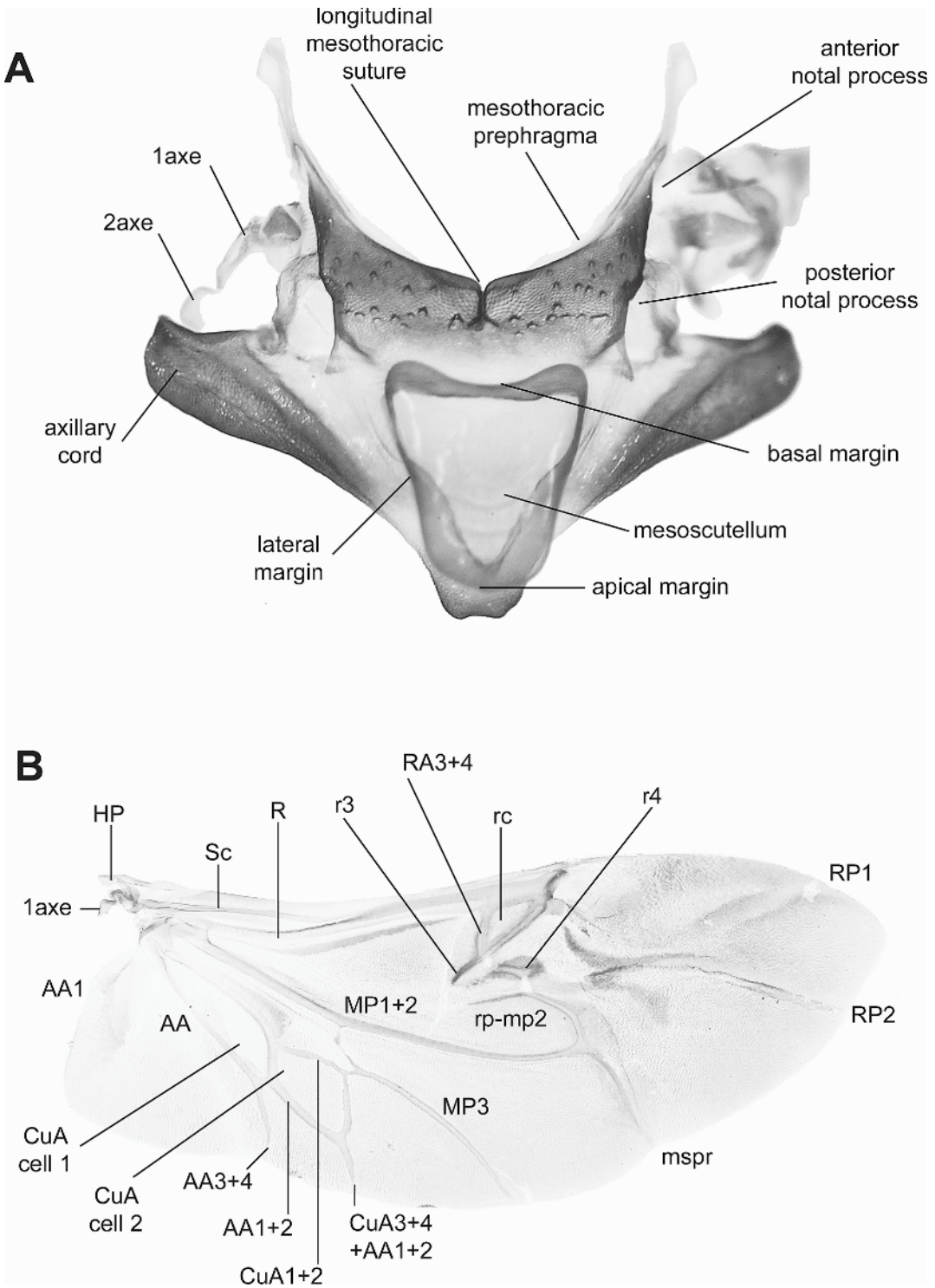


Fig. 34. *Hemisphaerota palmarum*, thorax. **A.** Mesonotum. **B.** Hindwing.

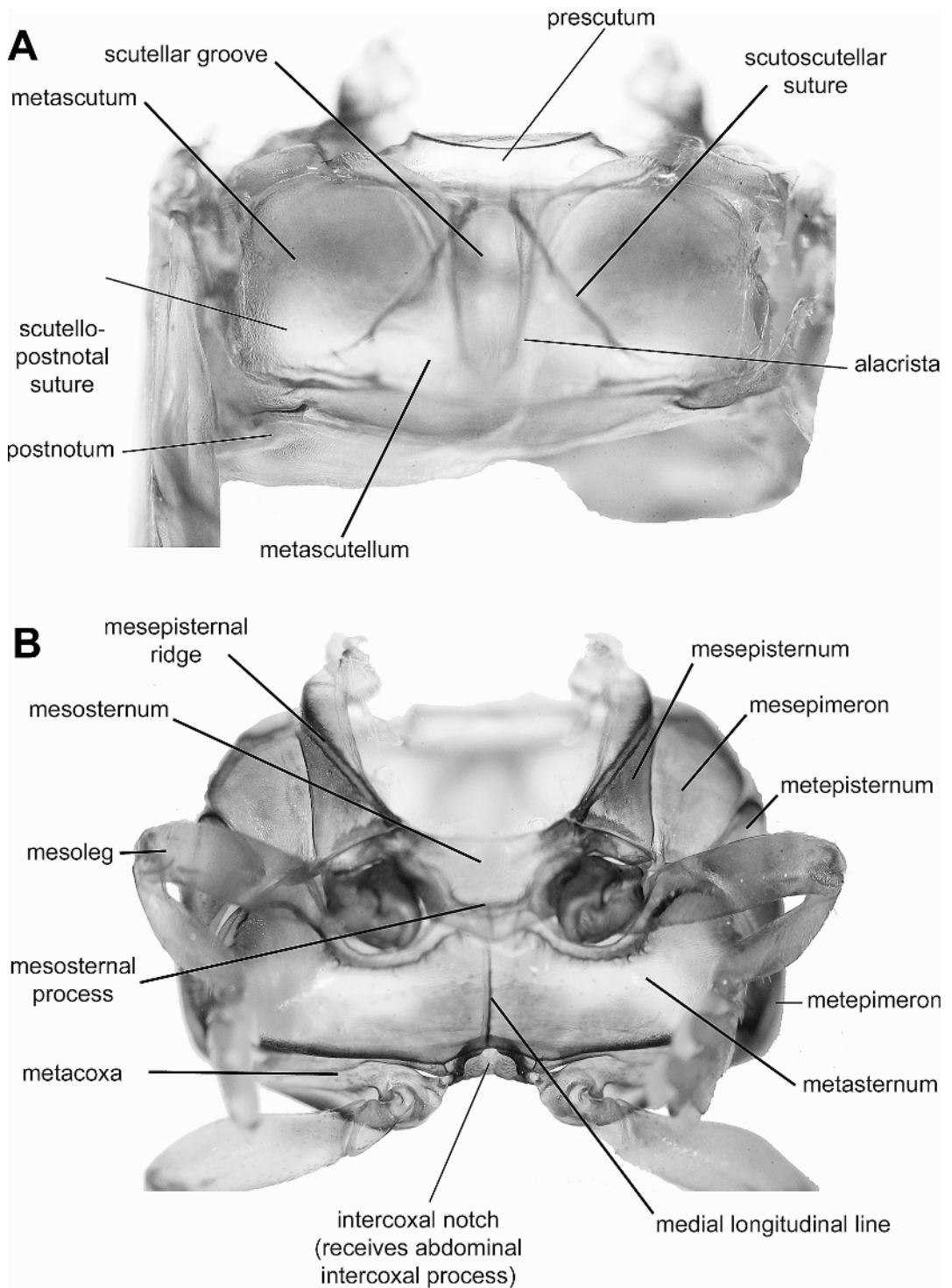


Fig. 35. *Hemisphaerota palmarum*, thorax. **A.** Dorsal view. **B.** Ventral view.

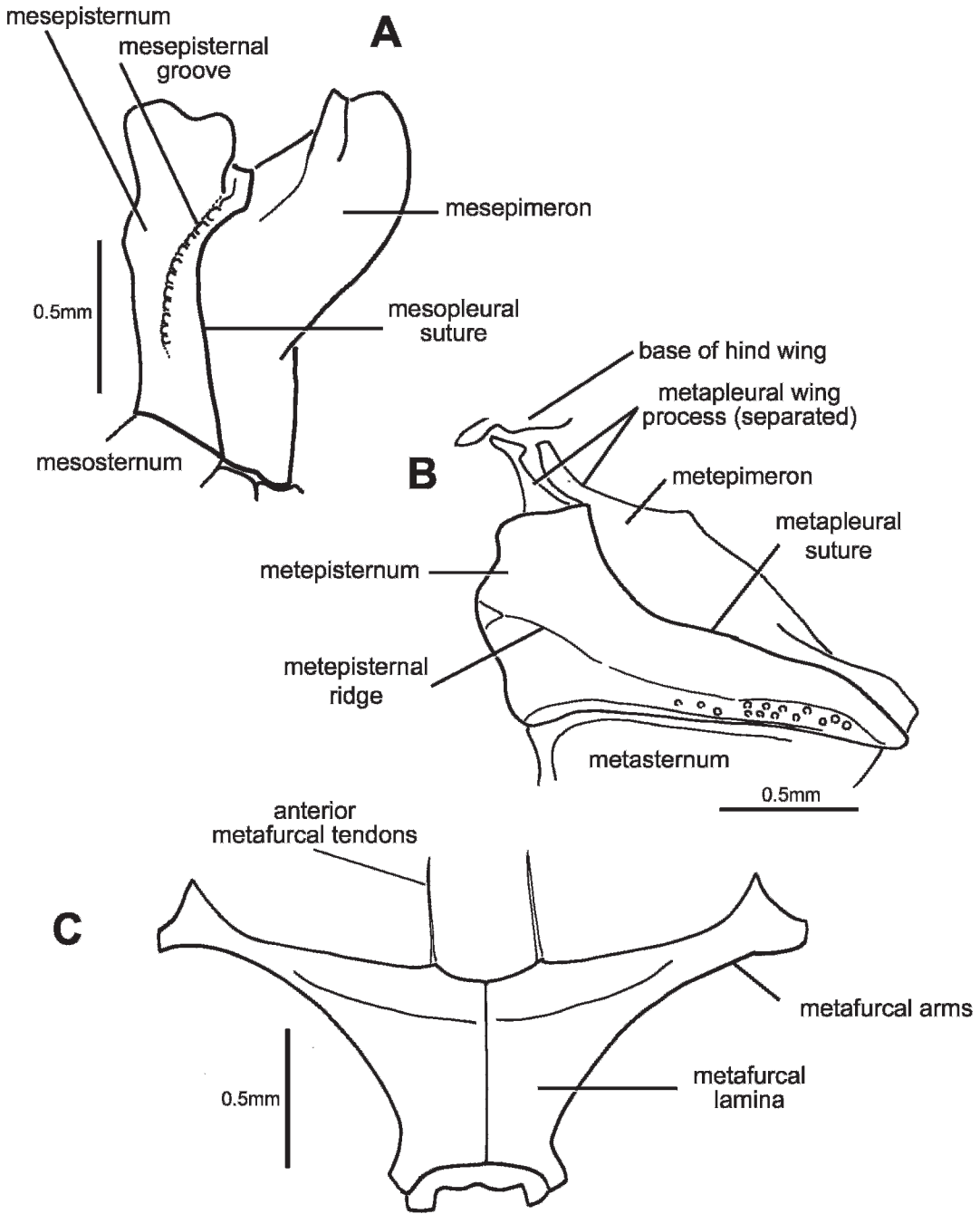


Fig. 36. *Hemisphaerota palmarum*, thorax. A. Mesopleuron, lateral view. B. Metapleuron, lateral view. C. Metendosternite.

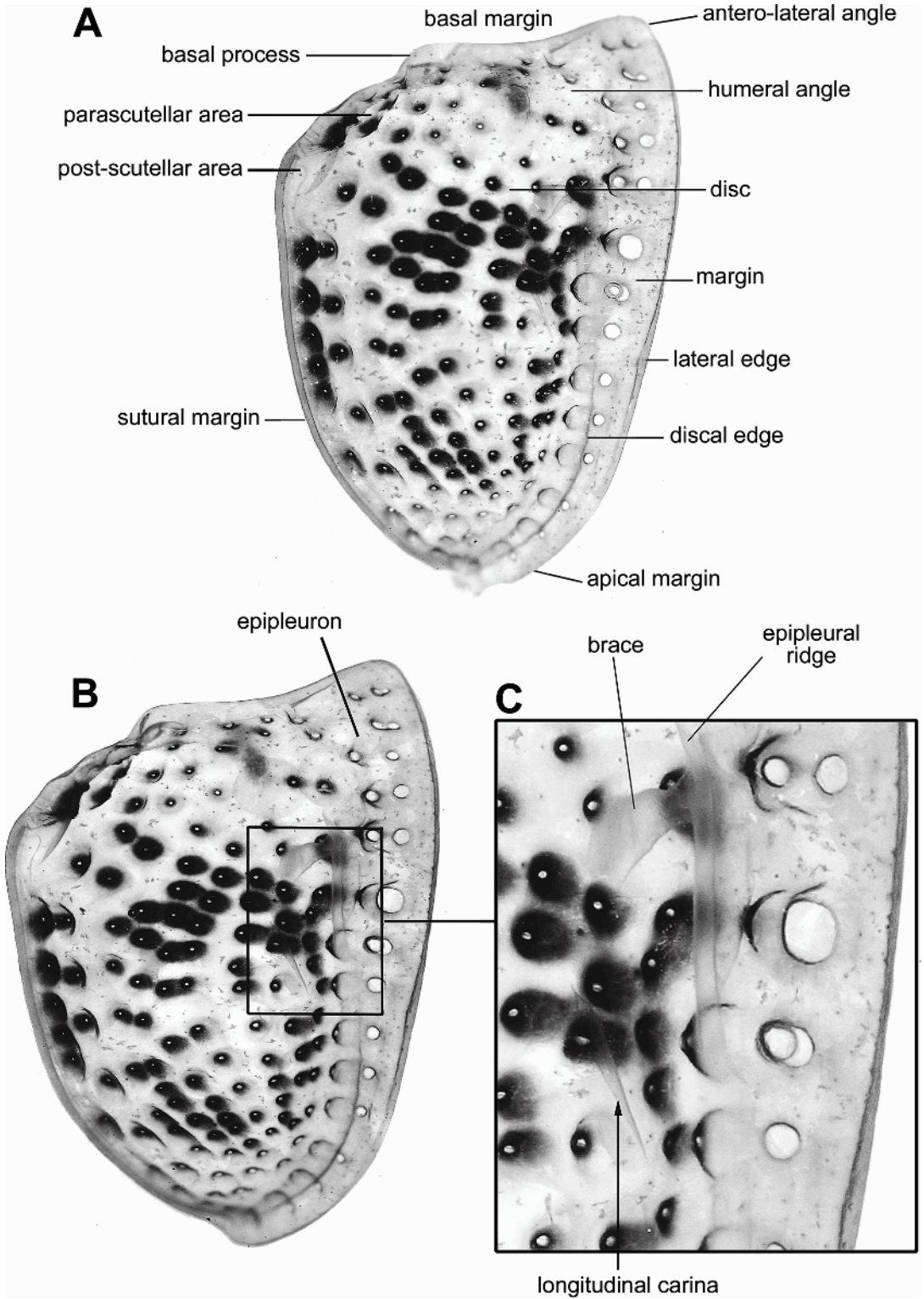


Fig. 37. *Hemisphaerota palmarum*, elytra. A. Dorsal view. B. Ventral view. C. Epipleural pocket.

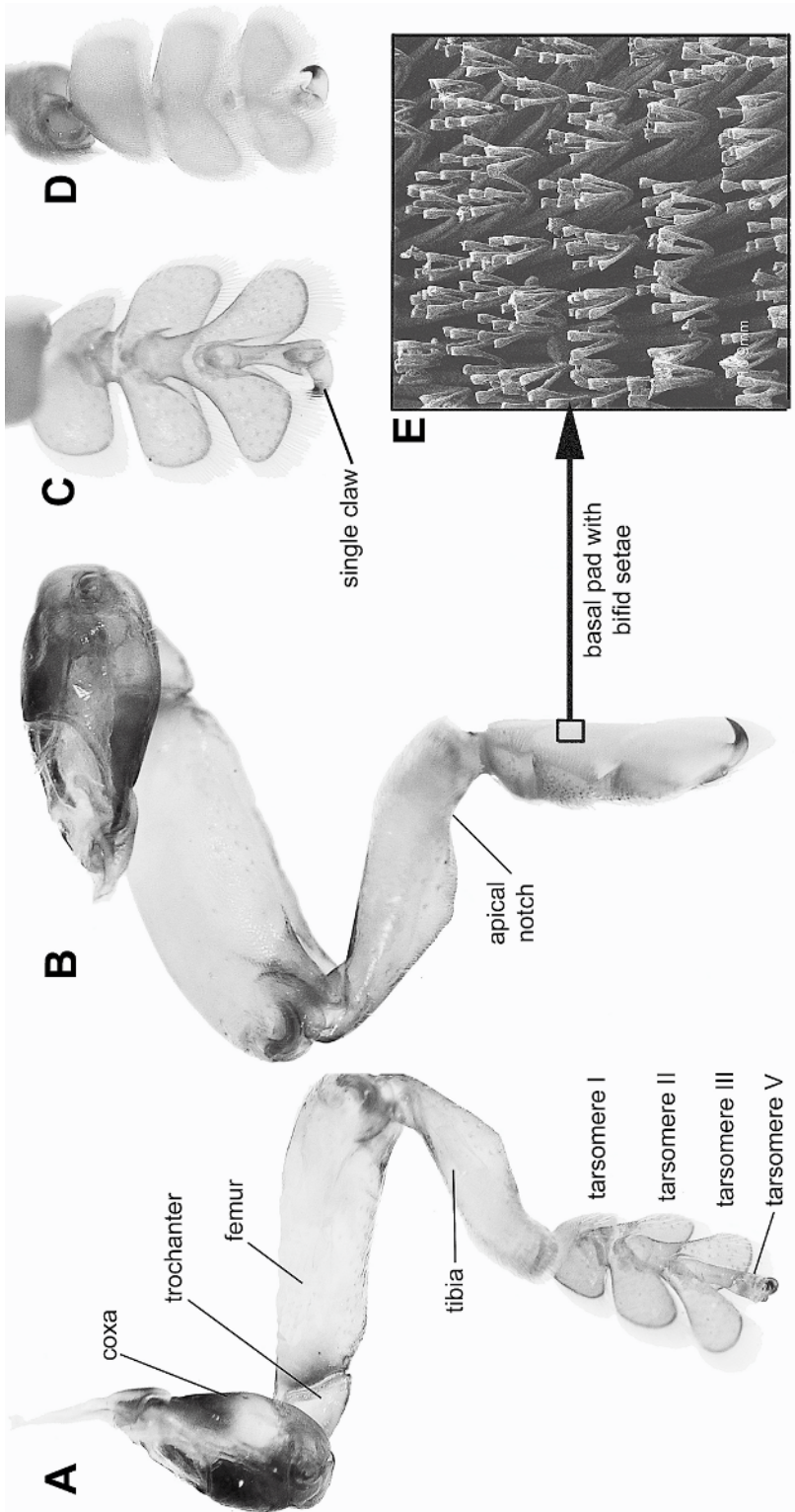


Fig. 38. *Hemisphaerota palmarum*, proleg. A. Anterior view. B. Lateral view. C. Tarsus, ventral view. D. Tarsus, dorsal view. E. *Basipta* sp., bifid hairs on tarsal pad.

somere II is shallowly bilobed, and its apical margin is moderately indented and has symmetrical lobes. Tarsomere III is deeply bilobed, with a deeply indented apical margin and long symmetrical lobes that enclose tarsomere V laterally. Tarsomere V is extended slightly beyond the apical margin of tarsomere III. Its shape is cylindrical, being slightly swollen basally and slender distally. Its apical margin is straight. A single claw is present and oriented ventrad. Its surface is smooth and the base is thick and exposed. The claw has the apex curving sharply ventrad, and its ventral surface is simple, rounded, and without distinct margins or basal pectens.

Abdomen. The abdomen (fig. 39) is five-segmented with apparent segments I and II connate; their suture is discrete and complete. *Genitalia.* For the female genitalia (figs. 39B–C, 40B, C) the spiculum is a single, moderately sclerotized, elongate process with a slightly expanded apex and slightly emarginate apical margin. The coxites, tergum IV, and sternum VIII are membranous. The coxites are short with sparse distal setation. The reproductive tract (fig. 39B) is tan and enclosed in a coarse membrane; the oviduct is whitish, short, and has a single round protuberance. The bursa copulatrix is rounded and protuberant. The spermatheca (fig. 39C, D) is well sclerotized, and has a single rounded receptacle with a broadly attached pump. The pump is tapered, deflexed, and about three times longer than the receptacle. A flattened apical appendix is present with spermathecal muscles attaching to it, the venter of the receptacle and the inner margin of receptacle. A receptacle appendix is absent. The spermathecal duct and spermathecal gland are present and are attached basolaterally to the receptacle. They enter the receptacle via a single entry. The spermathecal gland is ribbon-shaped, long, flattened, and membranous. The spermathecal duct is long and entirely coiled, with coils of regular diameter and spacing. This duct inserts at the apical margin of the bursa copulatrix.

Male genitalia (fig. 40A) are comprised of the elongate sclerotized median lobe that forms a 90° angle with the base. The tegmen is incomplete around the base of the median lobe, with muscles completing the connection

around the base. The manubrium (= basal piece) is as long as the lateral lobes. The lateral plates are slightly projected from the rim of the apical foramen. The long ejaculatory duct has a few large irregular folds but no coiling.

COMPARATIVE MORPHOLOGY OF ADULTS

Cassidine adults are difficult to characterize due to a remarkable diversity in size, body form, surface texture, and structural details. Body sizes range from 2–3 mm long, as in some *Oxylepus* and *Spaethiella*, more than 4 cm long, as in *Alurnus*. Body shapes (figs. 5–12) tend to two basic forms: elongate with parallel or sub-parallel lateral margins (e.g., fig. 5H) or rounded to circular (e.g., fig. 5A); however, there is a great range between these two forms. The head may be long or short, and it may be prominently exposed or hidden by the pronotum in dorsal aspect. Bodies are generally flattened ventrally (char. 24), but the profile in lateral aspect can be flattened, rounded, or arcuate (figs. 12G–K, 11, 12). Some arcuate species have a post-scutellar protuberance that can reach an extreme as a spine (e.g., fig. 12I; char. 151). The widest point of the body can be the pronotum or the base, midpoint or apex of the elytra. Body pubescence (char. 25) is generally scarce; however, *Trichispa* has dense dorsal pubescence and *Dorcathispa* has sparse but regularly arranged short, thick setae with swollen apices.

HEAD (figs. 29–32, 41–54; chars. 26–83)

The cassidine head differs from that of other chrysomelids in some fundamental ways, and their structural diversity is exceptional. Because the cassidine head tends to be deeply inserted into the prothorax, complete disarticulation is required for a detailed examination. For this study, head disarticulation was possible for only a subset of the taxa studied. This body region accounts for most of the missing data in the character matrix. Cassidine head and mouthparts are compared briefly below, and a more comprehensive account will be given elsewhere (Chaboo, unpubl. data).

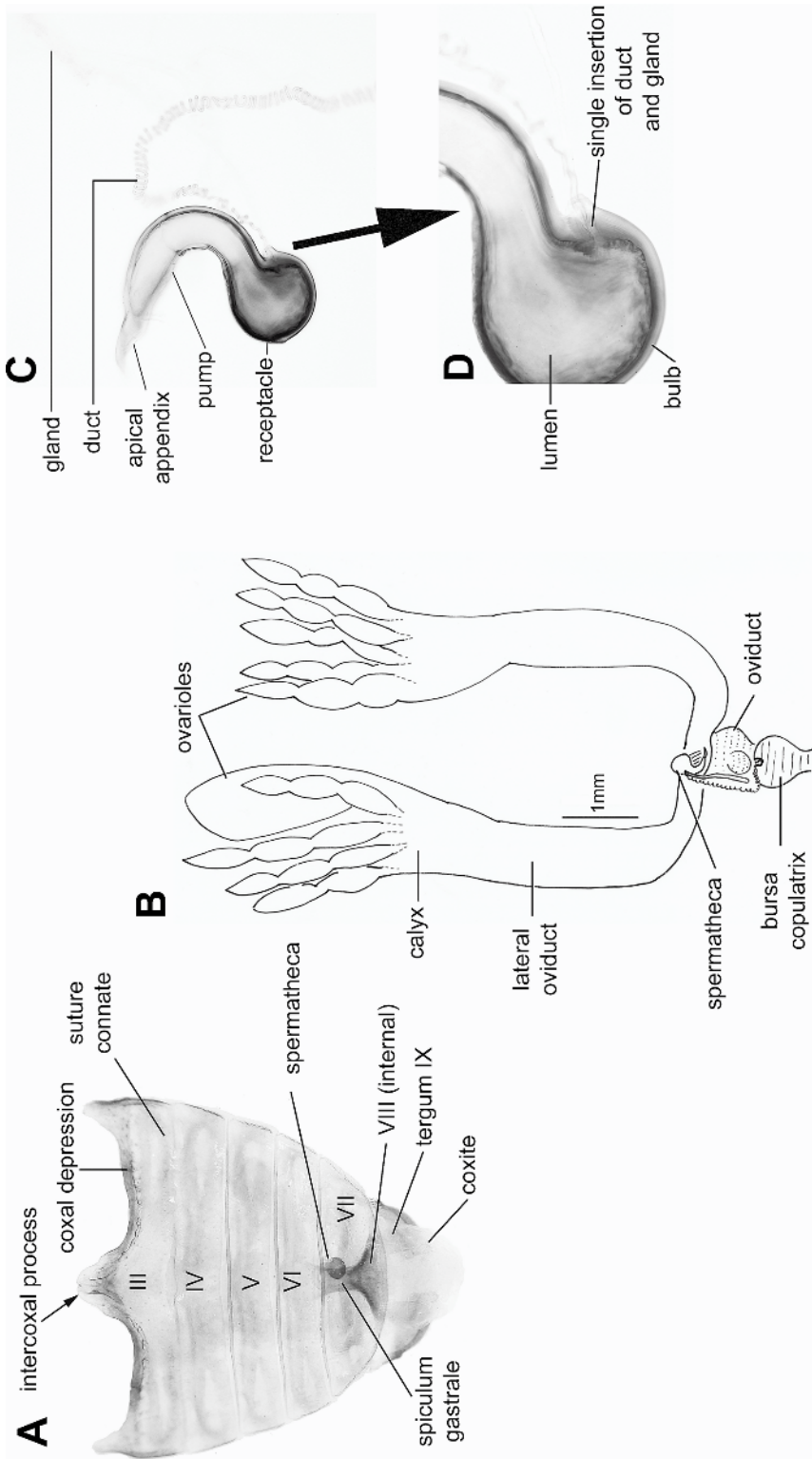


Fig. 39. *Hemisphaerota palmirarum*, female reproductive system. **A.** Abdomen, ventral view. **B.** Reproductive system. **C.** Spermathecal system. **D.** Spermatheca, entry of duct and gland.

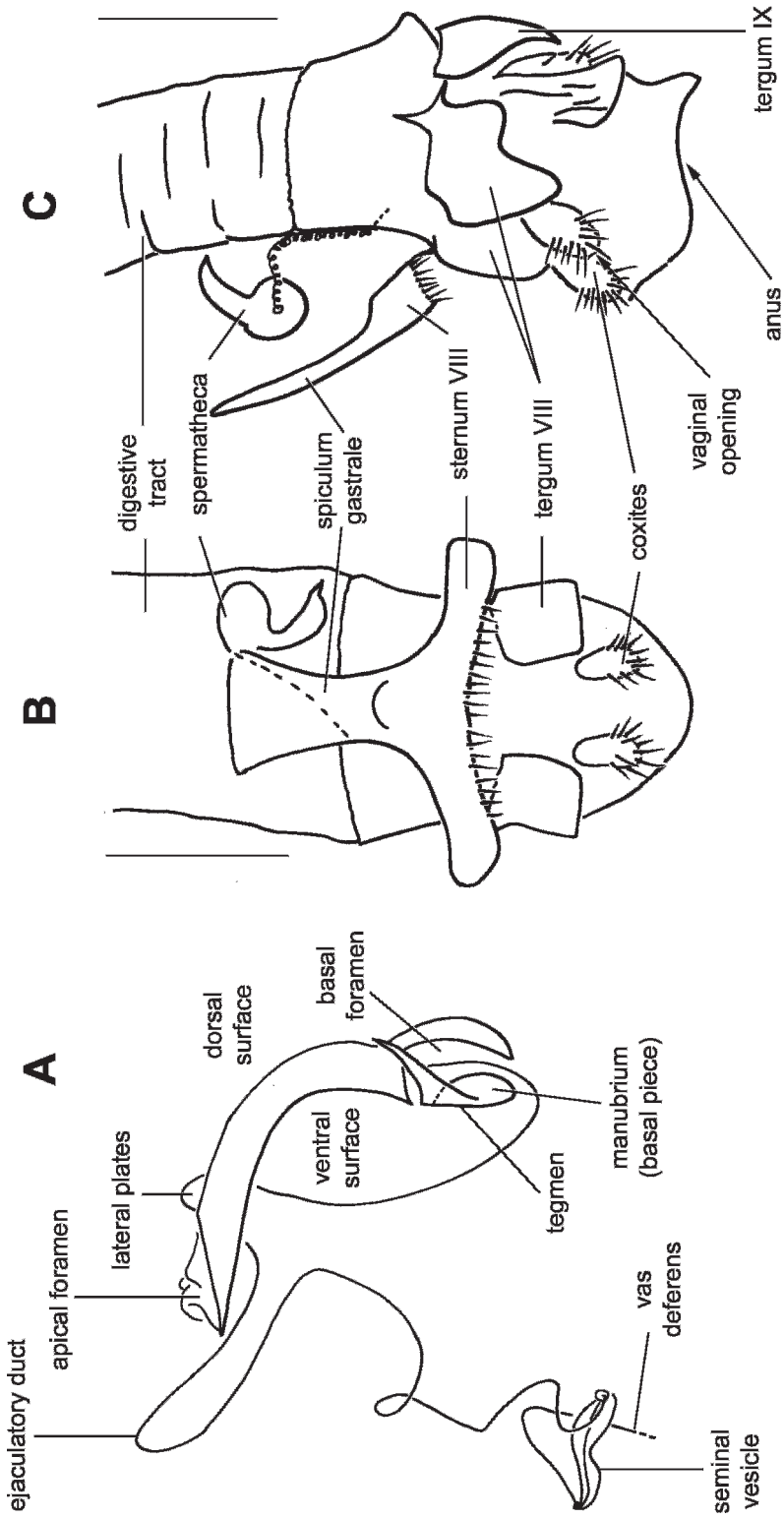


Fig. 40. *Hemisphaerota palmarum*, genitalia. A. Aedeagus, ventral view. B. Female, ventral view. C. Female, lateral view.

The cassidine head appears to have become shortened and/or retracted into the prothorax. It may be completely exposed or completely hidden in dorsal aspect. Exposure depends on several independent features: head length, head insertion into the prothorax, emargination or extension of the pronotal anterior margin (hiding the head dorsally), and extension of the prosternal anterior margin (partially or completely covering mouthparts ventrally). Researchers have tended to emphasize different aspects of head exposure; for example, Monrós and Viana (1951) focused on the pronotal emargination, whereas Würmli (1975) focused on head length. Promecothechini was diagnosed as having the head short due to retraction up to the eyes (Würmli, 1975).

Heads (figs. 29–30, 41–45) are commonly quadriform in dorsal aspect but may also be rounded (e.g., *Callispa*, *Delocrania*, *Hemisphaerota*, and *Spaethiella*). In lateral profile, the ventral surface is flattened or diagonal in shape, so that the posterior margin of the mouth is obscured or visible in anterior view (figs. 43, 44). The vertex may be short or long, and smooth, coarse, or punctate. Posteriorly it may be finely transversely striate with the “pars stridens” or stridulatory file (fig. 44A, C). The vertex is commonly dissected longitudinally by the mid-cranial suture, which terminates between the *antennal calli* or is continuous frontally with the mid-frontal sulcus. The antennal calli ranges from indistinct to well defined and protuberant.

Head Sutures. Frontal and ocular sutures or grooves are important landmarks in determining chrysomelid subfamily relationships (Schmitt, 1985a, 1985b, 1988; Askevold, 1990a, 1990b; Reid, 1995; Santisteban, 1997; Lingafelter and Konstantinov, 2000). In his review of head sutures and terms in Donaciinae, Askevold (1990b) determined that the frontal sutures (= frontoclypeal suture) form the lower \wedge shape in the X-shape grooves on some chrysomelid heads, namely *Sagra*. Gular sutures converge anteriorly but never meet, terminating at the posterior tentorial pits. In some taxa (e.g., *Poecilaspis*) they extend to the margin of the mouth. Gular sutures vary in their length, curvature, and orientation so the gular size is

also variable. The *transfrontal suture* (Konstantinov and Vandenberg, 1996) may be present or absent in Cassidinae. The *coronal suture* (Snodgrass, 1935) has been variously termed in Chrysomelidae: epicranial suture (Rivnay, 1928), median longitudinal groove (Schmitt, 1989), orbital sulcus (Staines, 1989), frontal furrow (Santisteban, 1997), frontal groove (Riley, 1985), median groove (Reid, 1995), and midcranial suture (Lingafelter and Konstantinov, 2000). Alexander Konstantinov’s (personal commun.) distinction of the coronal suture into two sections, the midcranial suture posteriorly and the midfrontal sulcus anteriorly, is followed here. Schmitt (1989) indicated the midcranial suture as present in Criocerinae, Donaciinae, and Cassidinae. This sulcus is interrupted in *Sagra tristis*, which Schmitt (1989) interpreted as a remnant of the condition in other subfamilies. Lingafelter and Konstantinov (2000) however coded the suture as absent in Sagrinae. Reid’s (1995) character 8 involving the coronal suture is refined here as three characters: presence/absence of the mid-cranial suture (char. 29), presence/absence of frontoclypeal sutures (char. 37), and presence/absence of antennal tubercles (char. 48). The relationship between the positions of the tubercles and suture is unclear so these are treated as separate characters. It is also ambiguous whether the X-grooves and the coronal groove are homologous so these are also treated separately.

The midfrontal sulcus is commonly present in cassidines, but it is absent in *Prosopodonta* and *Pharangispa*. Some cassidines have the sulcus everted as the coronal carina (char. 32). In some (e.g., *Asmangulia* and *Cephalodonta*) the coronal carina and midcranial suture are present. This carinate projection has been referred to as a rostrum (Würmli, 1975). The midcranial suture may be slightly concave or deeply sulcate, and short or long.

Eyes may be small or large relative to the head. They are situated anterolaterally, with the facets directed dorsally, ventrally, laterally, and anteriorly. Eye shapes include round and irregular quadrate forms with the margins straight or sinuate. Individual facets may be flat or convex, giving the eye a granular appearance. Usually the eyes are widely separated by the frontoclypeus, but in

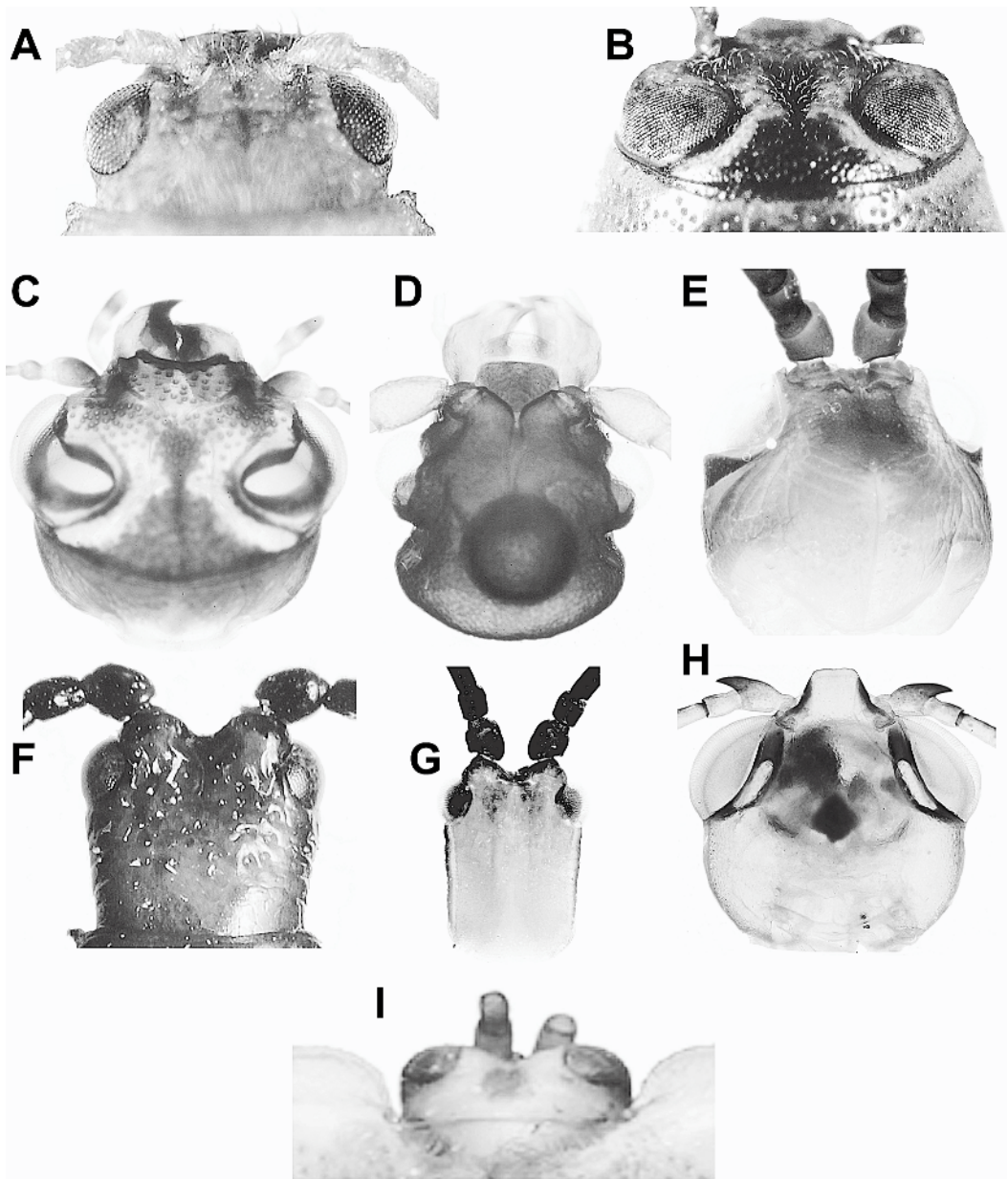


Fig. 41. Head, dorsal view. **A, D.** Chrysomelidae. **A.** *Ophraella* sp. 1. **B.** *Pachybrachis circumcincta* (in situ). **C.** *Pachybrachis circumcincta* (cleared). **D.** *Plataumaris rufa*. **E, L.** Cassidinae. **E.** *Alurnus bipunctatus*. **F.** *Aproida balyi* (in situ). **G.** *Aproida balyi* (exposed). **H.** *Arescus* sp. 1. **I.** *Aslamidium* sp. 3.

Plesispa their medial margins are very close due to a narrowed frontoclypeus. The eye margin can be elevated medially (e.g., *Notosacantha*), posteriorly (e.g., *Delocrania*), or

frontally (e.g., *Calliaspis*). The elevation is slightly different among these taxa; for example, *Notosacantha* has a sclerotized ridge around the orbit, whereas in *Imatidium*, the

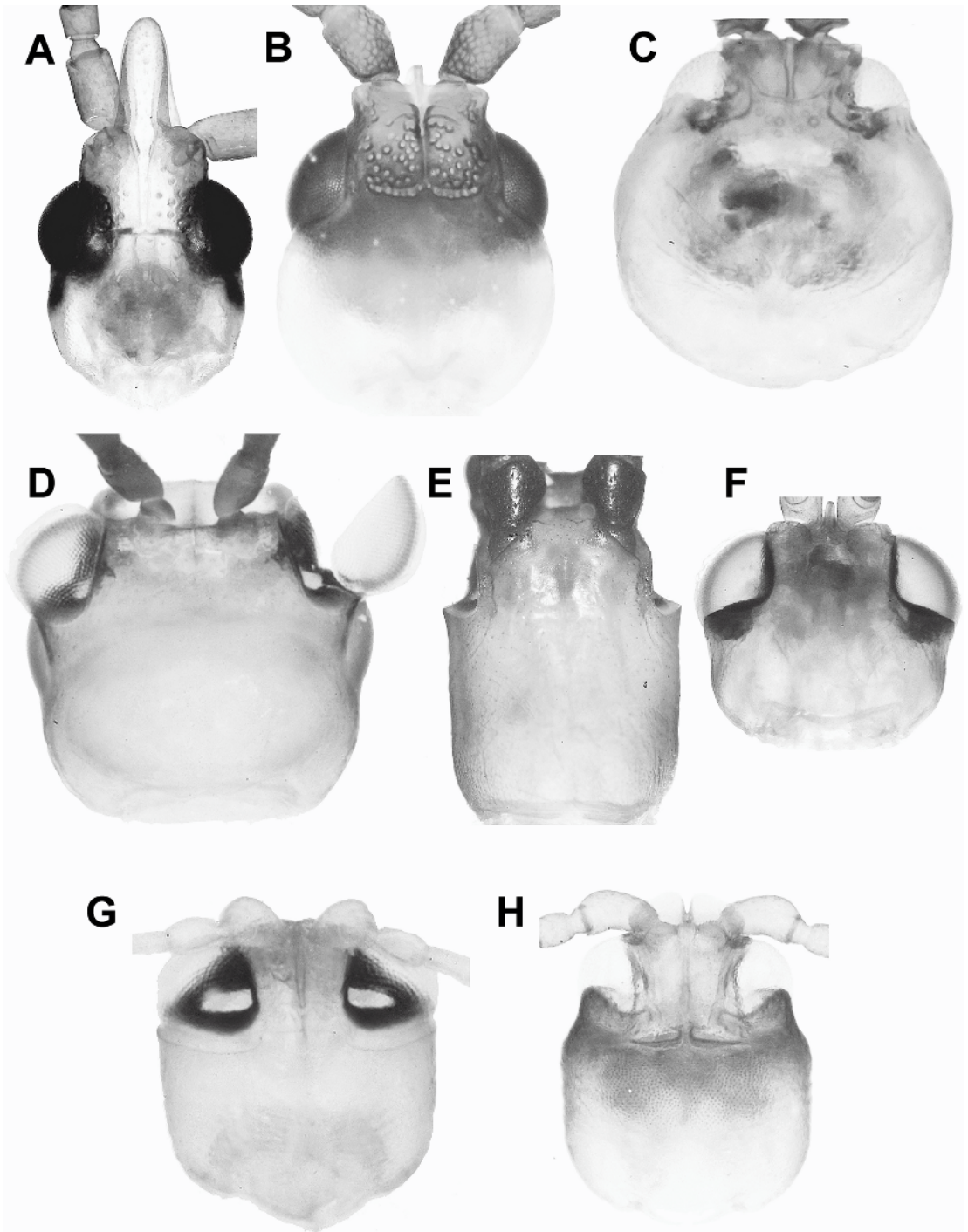


Fig. 42. Head, dorsal view. A. *Callistola speciosa fasciata*. B. *Ceratispa palmicola*. C. *Delocrania panamensis*. D. *Demotispa* sp. 1. E. *Exothispa reimeri*. F. *Hispodonta chapuisi*. G. *Metriona bilimeki*. H. *Notosacantha badia*.

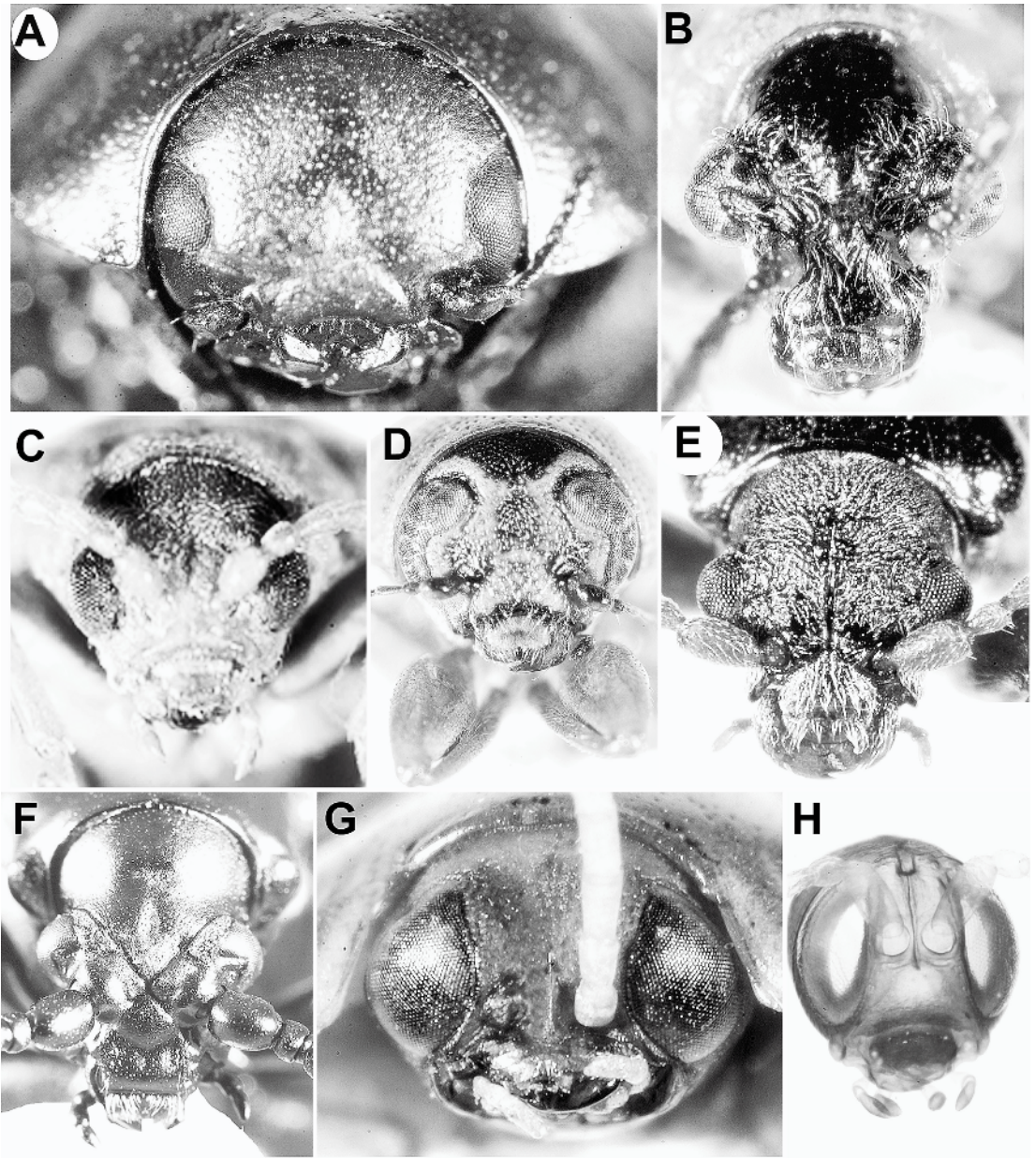


Fig. 43. Head, anterior view. A. *Lamprosoma* sp. 1. B. *Lema trivittata*. C. *Ophraella* sp. 1. D. *Pachybrachis circumcincta*. E. *Plataumaris rufa*. F. *Sagra* sp. 1. G. *Calliaspis rubra*. H. *Jonthonota maculata*.

eye orbit is elevated so much so that the entire eye is projected and the anterior eye margin forms a discontinuous line with the anterior margin of the head. In *Callistola*, *Chalepus* and *Xenochalepus* the vertex is protuberant, projecting the margin toward the antennal insertions.

Frons and Clypeus (figs. 43–45; chars. 67–68). This region is variable and complex. Some cassidines appear to lack both frons and clypeus so that the mouth and antennal insertions are proximate or are separated by a thin sclerite. The clypeus is commonly fused to the frons, forming the frontoclypeus.

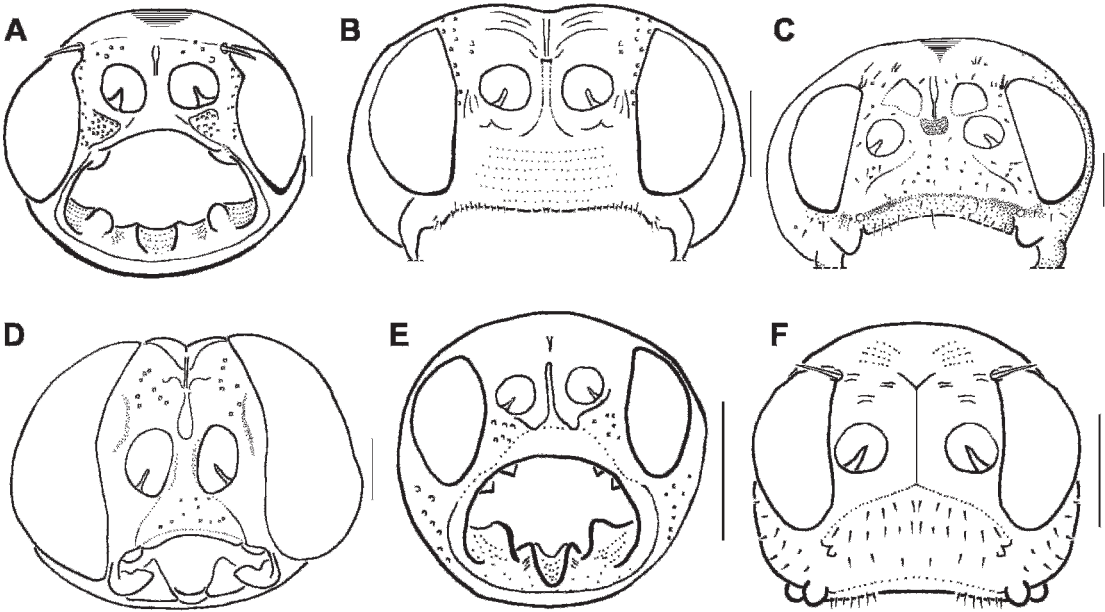


Fig. 44. Head of Cassidinae, anterior view. **A.** *Botryonopa foveicollis*. **B.** *Callistola speciosa fasciata*. **C.** *Physonota* sp. **D.** *Plautyauchenia deyrollei*. **E.** *Prosopodonta dorsata*. **F.** *Stolas lebasi*. Scale bars = 0.5 mm.

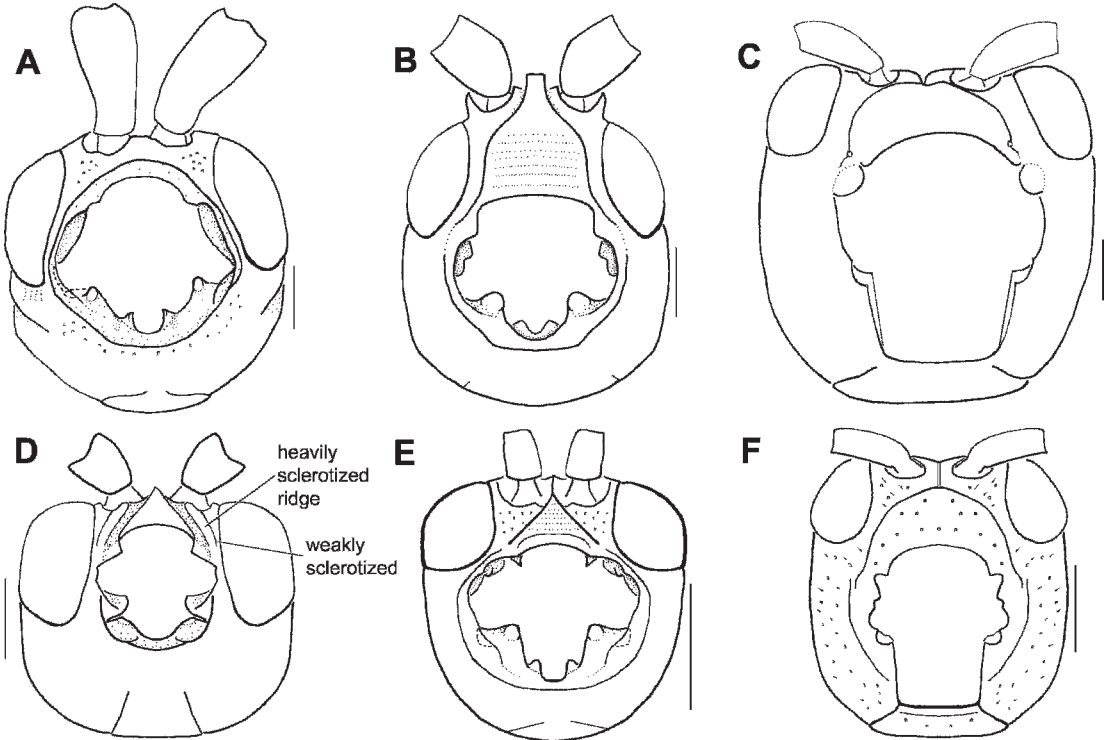


Fig. 45. Head of Cassidinae, ventral aspect. **A.** *Botryonopa foveicollis*. **B.** *Callistola speciosa fasciata*. **C.** *Physonota* sp. **D.** *Plautyauchenia deyrollei*. **E.** *Prosopodonta dorsata*. **F.** *Stolas lebasi*. Scale bars = 0.5 mm.

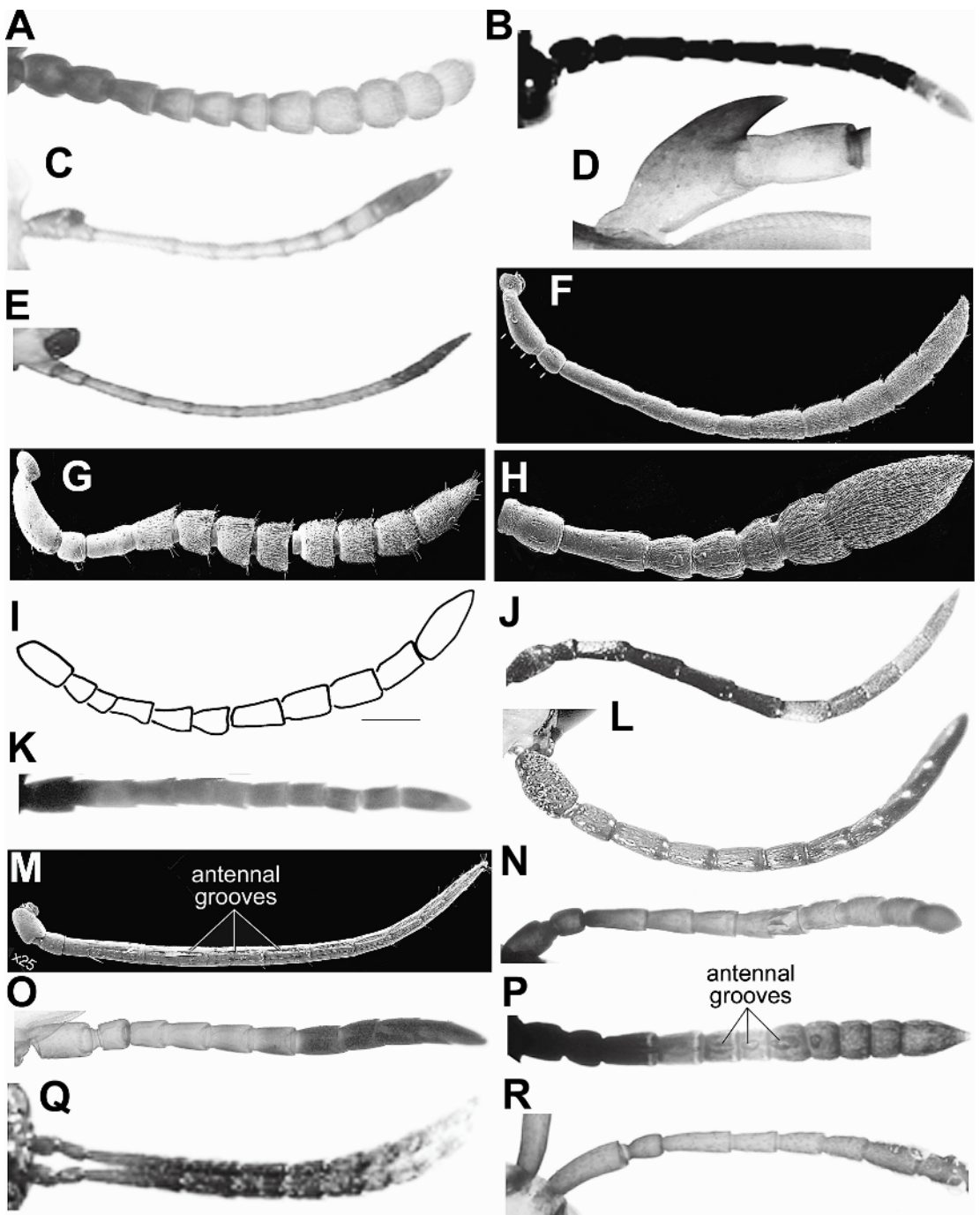


Fig. 46. Antennae of Cassidinae. **A.** *Anisotena inaequalis*. **B.** *Aproidea balyi*. **C.** *Arescus* sp. 1. **D.** *Arescus* sp. 1, antennomere I. **E.** *Aslamidium* sp. 1. **F.** *Aspidimorpha miliaris*, scanning electron micrograph. **G.** *Asteriza flavicornis*, scanning electron micrograph. **H.** *Baliosus californicus*. **I.** *Basipta stolidi*, scale bar = 1mm. **J.** *Botryonopa foveiocollis*. **K.** *Callispa bowringi*. **L.** *Callistola speciosa*. **M.** *Calyptocephala brevicornis*. **N.** *Cephaloleia* sp. 1. **O.** *Ceratispa* sp. 1. **P.** *Chalepus acuticornis*. **Q.** *Cyperispa thorachostachyi kolombangana*. **R.** *Dactylispa angusta*.

Sometimes the *epistomal suture* between the frons and clypeus is barely discernible, but most often it is not apparent. The frontoclypeal length varies, influencing the position of the mouth and the gular length. Borowiec's (1993) character 3 has two clypeal states, long and short, however these are not so discrete, but variation in clypeal length is conveyed here as relative to hypostomal length (char. 65). Borowiec (1995: 545) stated "horizontalization of the clypeus is a linear trend in Cassidinae." Further study and detailed illustrations are needed to understand this trend. The clypeus may be discernible by a faint groove or suture, or by a slight change of angulation, however in many cases it cannot be defined since the *anterior tentorial pits* are not obvious. Sagittal sectioning may be necessary to determine locations of these structures. The frontoclypeus may be distinct, with developed margins. Anteriorly it may be dissected by the midfrontal sulcus. Its surface may be flat, depressed, or protuberant, and its texture may be smooth, striate, wrinkled, or punctate, and sparsely to densely pubescent.

Antenna (figs. 46–50; chars. 48–64). Cassidine antennal morphology has been used in a limited way in the past. Traditional characters include close insertions of antennae, relative proportions of antennomeres, presence of grooves, weakly or strongly developed club, and fusion and loss of distal antennomeres.

Position. The close insertion of the antennal tubercles (char. 51) was treated as a synapomorphy of Cassidinae (Chen, 1985; Schmitt, 1989; Reid, 1995) but it also applies in Galerucinae (e.g., char. 10 of Lingafelter and Konstantinov, 2000). Monrós (1959) used the cephalic width as a measure of interantennal distance.

Cassidine antennal insertions vary relative to the eye margin and in interantennal distance. *Length* is also variable and is measured relative to pronotal length. Uhmman (1954) described the "twisting" of the antenna to distinguish among species of *Botryonopa*, but this is a difficult feature to observe (Würmli, 1975). Antennomeres vary in relative proportions, relationship to each other (how they fit), shapes (cylindrical or compressed), numbers (fusion and loss),

pubescence, striations, and grooves (presence, number, and extent). Relative proportions of antennomeres were first used by Baly (1969a). Monrós (1959) also used antennal length (relative to body length) for diagnoses. Hincks (1952) included five antennal features in his key to cassidine tribes: (1) presence or absence of parallel longitudinal grooves on distal antennomeres; (2) antennomere shape cylindrical (round cross-section) or broader at apex; (3) division of the antenna into proximal and distal portions, based on shape and length; (4) presence or absence of pubescence; and (5) relative lengths of the second and third antennal segments. Of these features, I use the first, second and fifth as characters in this study. Hincks' (1952) third and fourth characters are difficult to apply consistently. Striated antennomeres are more widespread than as originally defined; for example, they also occur in *Xenochalepus* (C. Staines, personal commun.) and *Emdenia* (L. Borowiec, personal commun.).

Number of Antennomeres. Antennomere number is surprisingly variable at generic and species levels. For example, coelaenomerine genera have 6–11 antennomeres (Gressitt and Samuelson, 1990); cephaloleine genera have 10 antennomeres (*Calliaspis* Dejean; Borowiec, 2003) or 11 antennomeres in others; and uroplatine genera vary with 3–8 segments (Staines, 1986a, 1989). These variations may be due to loss or fusion of antennomeres. The degree of fusion also varies; for example, sutures are apparent but reduced in *Acanthodes* Baly (Uroplatini). *Acanthodes* displays intraspecific variation, with some having up to nine antennomeres fused together (Baly, 1864a). Fusion of distal antennomeres appears to have also occurred in *Octotoma*, *Callistola*, and *Microrhopala*. Distal antennomeres may also be thickened and have the appearance of a gradual club, for example, Chalepini (Staines, 1993), *Brachycoryna* (Staines, 1986a) and *Notosacantha* (Borowiec, 1995).

Antennomere I (scape) is the most divergent morphologically from other antennomeres. It is variable in shape, length, sensilla (presence, density, arrangement, and types), and surface texture. In *Delocrania* its shape is highly irregular, with the mesal surface having horizontal ridges (appearing

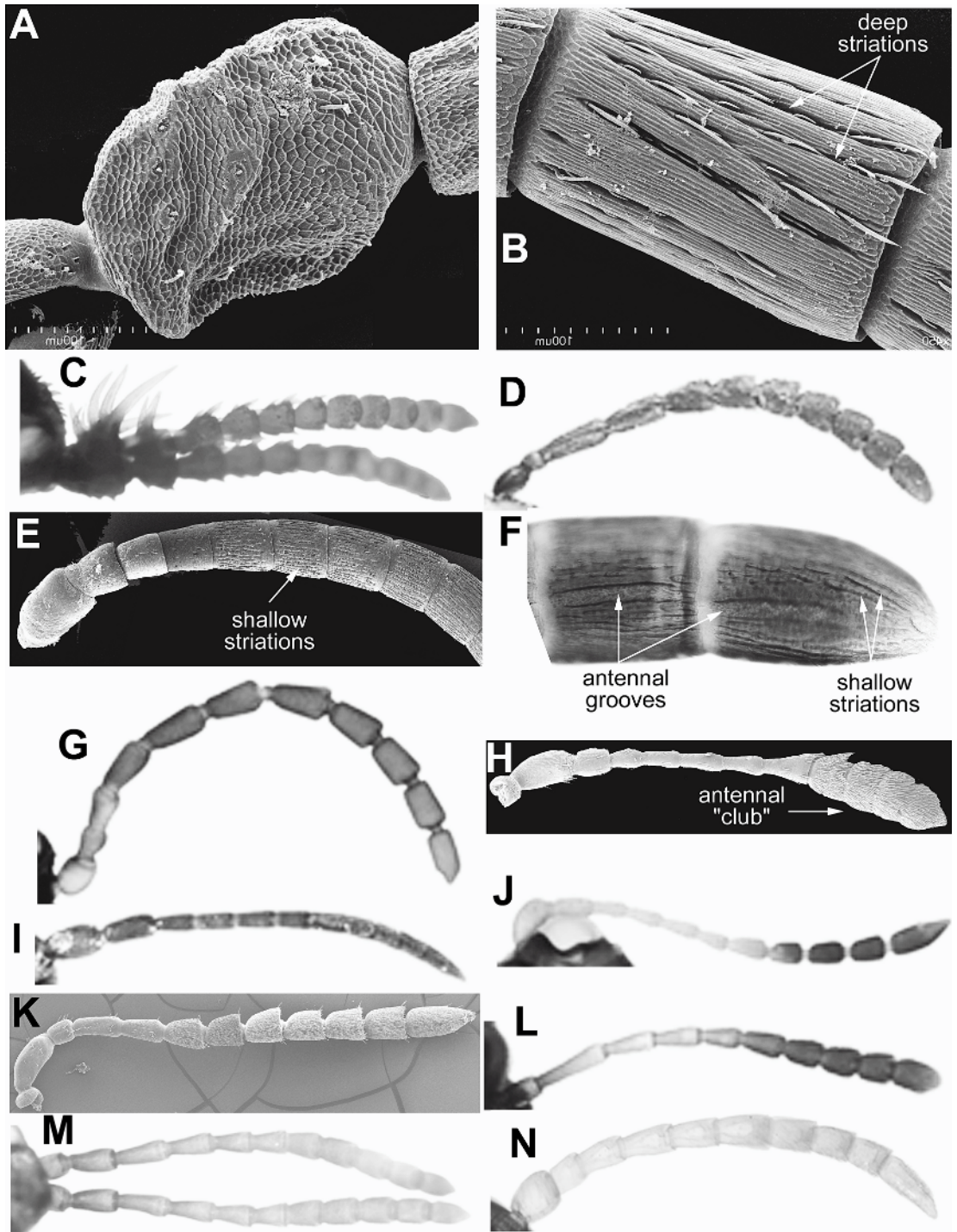


Fig. 47. Antennae of Chrysomelidae. **A.** *Delocrania panamensis*, antennomere I. **B.** *Delocrania panamensis*, antennomere VIII. **C.** *Dorcathispa* sp. 1. **D.** *Echoma dichroa*. **E.** *Epistictina viridimaculata*, scanning electron micrograph. **F.** *Epistictina viridimaculata*, apex. **G.** *Lema trivittata*. **H.** *Notosacantha badia*, scanning electron micrograph. **I.** *Palmispa parallela*. **J.** *Philaspis bivulnerata*. **K.** *Physonota exclamationis*, scanning electron micrograph. **L.** *Prosopodonta dorsata*. **M.** *Sceloenopla mantecada*. **N.** *Spaethiella* sp. 1.

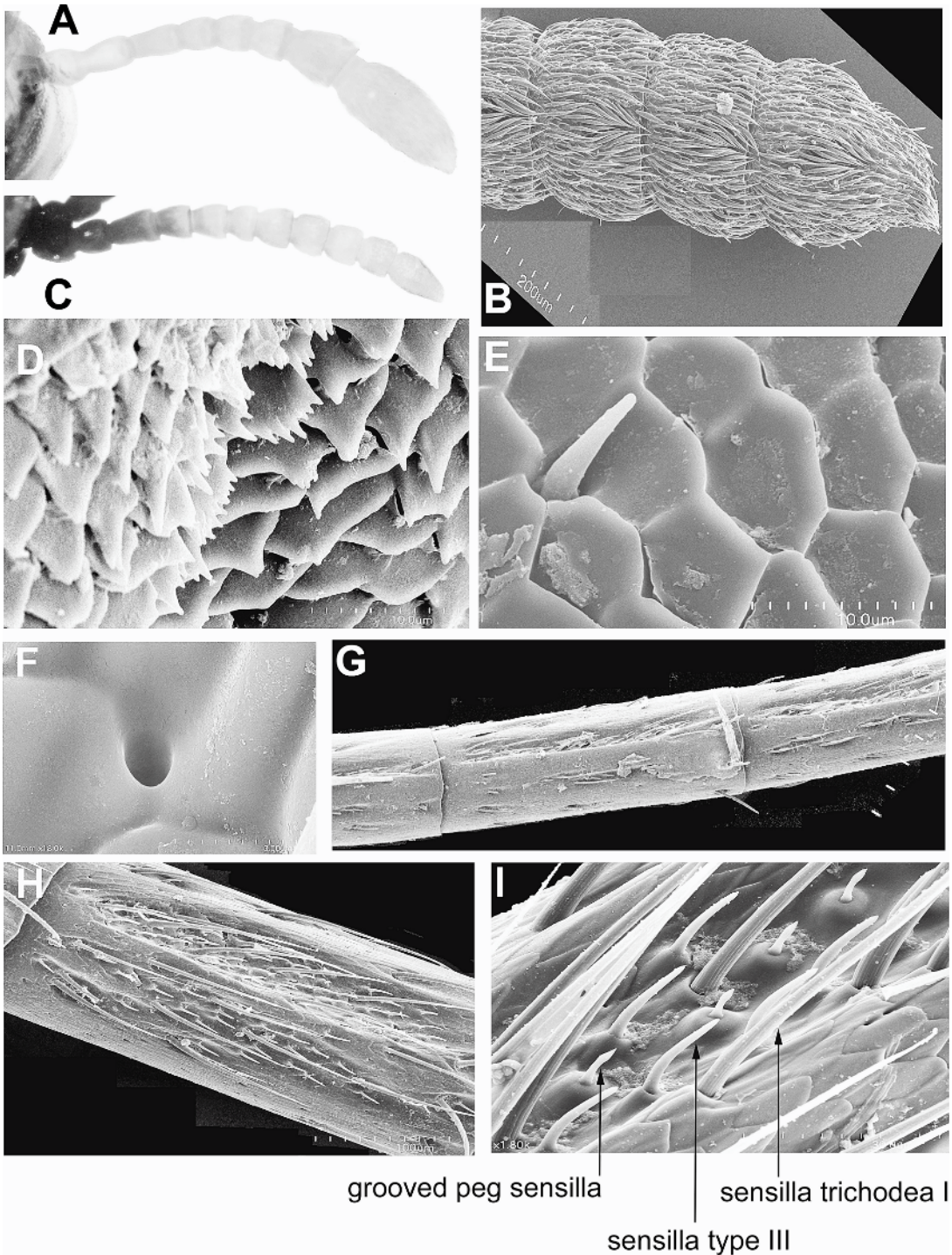


Fig. 48. Antenna of Cassidinae, surface features. **A.** *Uroplata girardi*. **B.** *Uroplata girardi*, apex. **C.** *Xenochalepus* sp. 1. **D, E.** *Asteriza flavicornis*, surface of scape. **F.** *Baliosus californicus*, pore on antennomere VII. **G.** *Calyptocephala brevicornis*, groove on antennomere VI. **H.** *Calyptocephala brevicornis*, groove on antennomere X. **I.** *Calyptocephala brevicornis*, sensilla within groove on antennomere X.

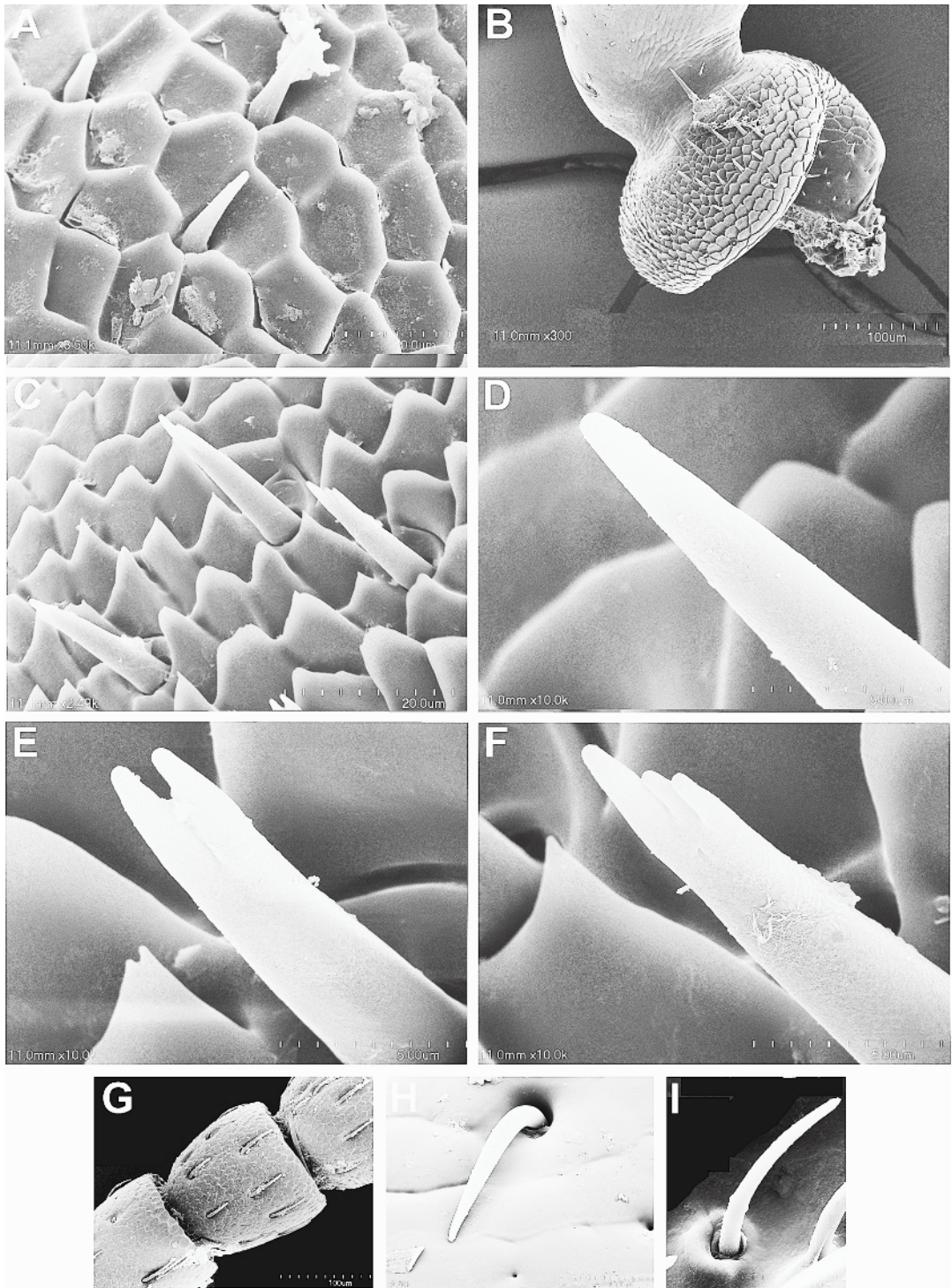


Fig. 49. Antenna of Cassidinae, scanning electron micrographs. **A.** *Baliosus* sp., antennomere III. **B.** *Physonota* sp., base of antennomere I. **C.** *Physonota* sp., base of antennomere I. **D.** *Physonota* sp., simple sensilla. **E.** *Physonota* sp., bifid sensilla. **F.** *Physonota* sp., trifid sensilla. **G.** *Microrhopala vittata*, antennomere IV. **H.** *Chalepus* sp. 1, sensilla trichodea I on base of antennomere IV. **I.** *Calyptocephala brevicornis*, sensilla trichodea I on antennomere III.

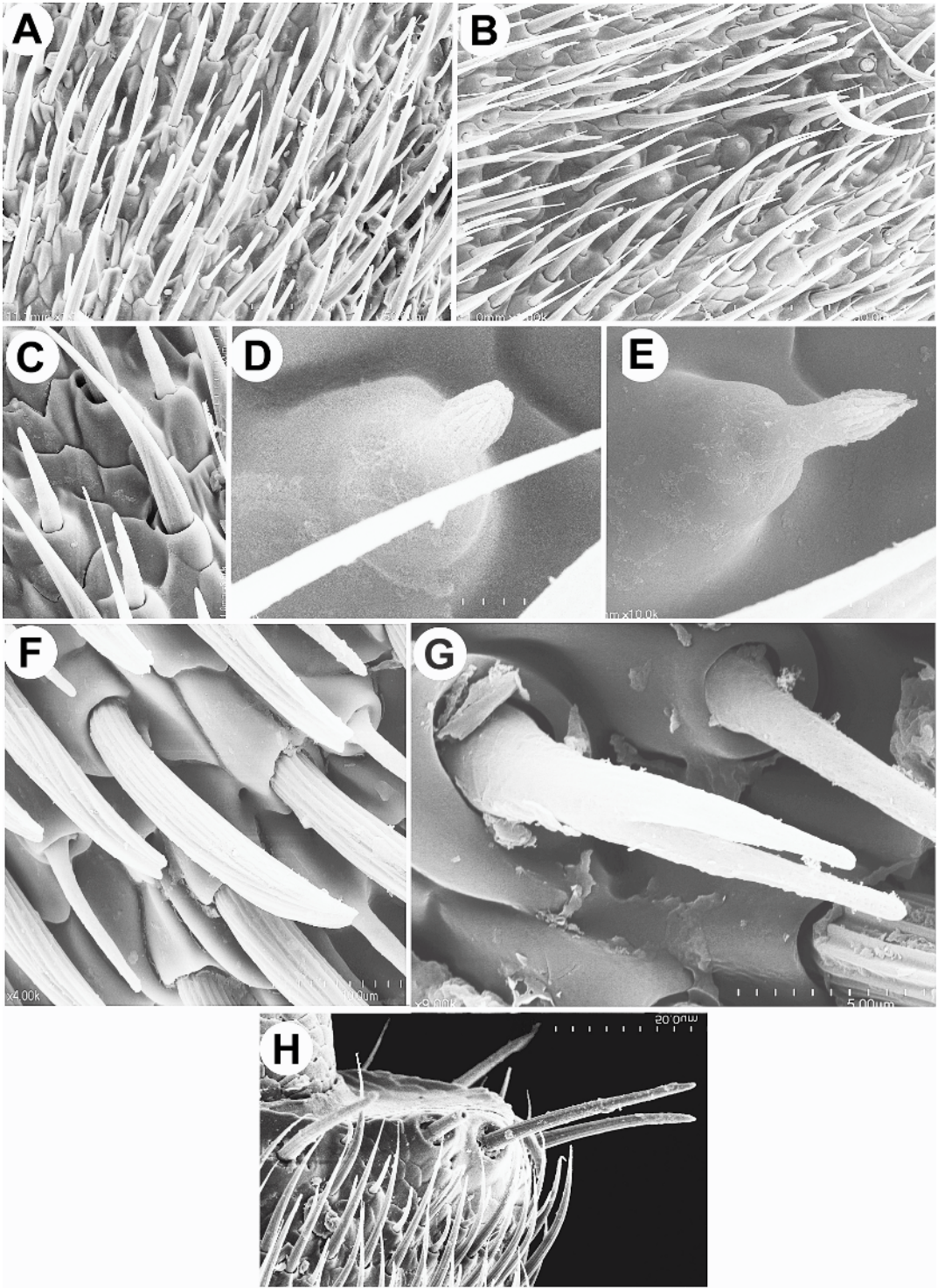


Fig. 50. Antennal sensilla, scanning electron micrographs. **A.** *Baliosus* sp. 1, antennomere 6. **B.** *Physonota* sp. 1, antennomere VI. **C.** *Physonota* sp. 1, antennomere VIII. **D.** *Physonota* sp. 1, grooved peg sensilla (short), antennomere VIII. **E.** *Physonota* sp. 1, grooved peg sensilla VIII (long), antennomere VIII. **F.** *Notosacantha badia*, sensilla trichodea II on antennomere. **G.** *Notosacantha badia*, sensilla type VI on antennomere 8. **H.** *Asteriza flavicornis*, sensilla chaetica on antennomere VII.

like a stridulatory file). In some cassidines, the apical margin is projected into a spine of variable length (e.g., *Arescus*, *Asmangulia*, and *Hispellinus*). This spine may be forked (e.g., *Hispa donckieri* (Pic)) or unforked (e.g., *Hispa atra* Linnaeus) (Gressitt, 1950). This projection was suggested to be sex-related (Würmli, 1975). In a few genera, the apical and basal margins are sinuate. Other antennomeres generally resemble one another in shape; that is, elongate and cylindrical with the apex slightly wider than the base. Distal antennomeres tend to be shorter, giving the antenna the appearance of gradual thickening distally.

Surface Texture. Cassidine antennal microsculpture includes pores, grooves, pits, striations, and diverse sensilla. Pits vary in their sizes, shapes, and presence on different antennomeres. *Callistola* antennae appear to be uniquely densely pitted. Gressitt and Samuelson (1990) characterized *Pharangispa* by the numerous sensory pits on antennomere XI. Shaw (1961) placed *Capillocassis* close to *Trichaspis* Spaeth based primarily on the presence of large sensory pits on the underside of distal antennomeres.

Sensilla. A few galerucine sensilla were studied (Ritchey and McIver, 1990; Baker, 1987) and these provide a guide to cassidine sensilla types. *Sensilla trichodea I* (fig. 50A–C) is the most common type on the cassidine antenna. It occurs on most antennomeres but varies markedly in numbers from base to apex, increasing sharply in density between antennomeres IV and V. This sensillum is long, slender, and tapered, and it is aligned to the long axis of the antenna. Its surface may be smooth or ridged, with ridges ranging from barely perceptible to distinct. The basal attachment is variable, being simple or slightly depressed. This sensillum probably serves a mechanoreception function. *Sensilla trichodea II* is also very common and is long and stout with well-developed ridges. Its base commonly has a crescentic pore on the anterior side, and its apex is slightly narrowed and compressed, with the apical margin straight or sinuate. This may also serve a mechanoreception function. *Sensilla basiconica* occur on all taxa examined. These are smooth, medium-sized, and stout, and they are found basally on antennomeres I–II.

The most common form has a simple apex, but within *Physonota* sp. 1 (of the taxa sampled here) (figs. 49B–F), two variations were found with bi- or tri-furcated apices. The split apex is suggestive of an aperture, and a closer examination of this tip is needed to determine if one exists. *Sensilla type 3* (fig. 48H) is found on all taxa and on all antennomeres. They are medium-sized, tapered to a simple apex, curved towards the antenna, and with a smooth surface. The basal attachment may be flat or prominent. They are found as singles or in fields, especially within grooves of some taxa. *Grooved peg sensilla* (fig. 48I, 50D–E) are double-walled, single branched, olfactory sensilla. They are slightly mushroom-shaped, with a slender basal stem and an inflated grooved apical portion. Some are short, lacking the stem. The shape of the basal disc varies from a rounded protuberance to a prominent angular base. *Sensilla Type 6* (fig. 50G) is unique to *Notosacantha*. It is medium-sized and double-branched, with the bifurcate section being longer than the basal stem. It is loosely set in a prominent socket and the surface is entirely porous. These wall pores suggest a chemosensory function. This sensilla type does not appear to be documented for any insects. *Sensilla chaetica* (fig. 50H) are the largest sensilla on the cassidine antennae and occur in all species examined. Within the antenna, they are found in a sparse row along the apex of distal antennomeres, oriented perpendicularly to the antenna. They are long, tapered, and unbranched; the surface has faint longitudinal ridges, and the base is in a circular, depressed, porous pit. These pits may represent an olfactory pore plate.

Antennal Grooves. These occur on some antennomeres in a few tribes. On basal antennomeres, grooves are short and incomplete, not spanning the length of the antennomere. Grooves tend to be longer distally, and terminal ones span the length of the antennomere. Fields of mixed sensilla types occur within these grooves (fig. 48F–H). The number of antennomeres involved varies among taxa. For example, grooves occur on antennomeres VII–XI in *Stenispa*, *Anisostena*, *Ceratispa*, *Cyperispa*, and *Palmispa*; on antennomeres VIII–XI in *Calli-*

stola; on antennomeres V–XI in *Ischyrosomyx* and *Calliapsis*; and on antennomeres III–XI in *Calyptocephala*. Grobbelaar (1993) illustrated similar antennal grooves in some Galerucinae s.l., but Lingafelter and Konstantinov (2000) did not discuss this feature. Antennal grooves occur in *Emdenia* Spaeth (L. Borowiec, personal commun.), currently classified in the tribe Cassidini. Its larvae resemble those of *Basiprionota* (C. Reid, personal commun.) more than those of other Cassidini, so its tribal placement may need reevaluation. Sensory pits, sensory fields and other antennal structures of cassidine antennae are interesting and could be phylogenetically significant.

MOUTH (figs. 30–32, 51–54; chars. 69–83)

Position. Cassidines have the mouth positioned ventrally, in contrast to the prognathous condition in other chrysomelids. Their mouth position varies from extreme anteroventral to a posteroventral position; for example, the *Exothispa* mouth is in an extreme anterior position whereas others have the mouth in an extreme posterior position. As a consequence of this shift in position, tracing the areas of the gena, vertex, frons, and corona on the cassidine head is problematic. I refer to the dorsal surface of the head as the vertex, the laterofrontal areas as the gena, and the area between the antenna and clypeus as the frontoclypeus. As a consequence of hypognathy, the landscape of the head has completely altered, making comparisons and homologies with prognathous heads difficult. Several mouth and head characters defined for hypognathous heads are inapplicable on prognathous heads. This positional variation also influences the development and relationships of the antennal insertions, frons, clypeus and gula.

Gressitt (1950) used some interesting mouth features (e.g., relationships to antennal insertions and to clypeus) in his key to Chinese hispinae tribes. A thorough comparative analysis of the cassidine head is needed to separate characters and states. The present study is only skimming the surface of this diversity.

Mouth Cavity (figs. 44A, D–E, 45). The shape of the cavity may be rounded

(fig. 45A) or irregularly quadrate. The margins may be simple (fig. 45C) or heavily sclerotized and protuberant (fig. 45A, B, E). The margin may be extended into the head, providing a shelf for mouthparts (e.g., figs. 44A, D, E, 45A). This shelf is variously modified with cavities that receive the mandibular, maxillary and labial articulations, and a detailed study is needed to determine the homology of articulations and sockets.

Mouthparts are complex and varied in Cassidinae and provide rich ground for characters. Material for disarticulation of the head and mouthparts was not available for many species examined here, and this region is a source of missing information in my dataset. Mouthpart structures are described only briefly here.

The cassidine *labrum* (fig. 51; chars. 76–78) has shifted ventrad, resulting in a reorientation of its surfaces: the dorsal surface has become the anterior or external surface, the distal margin has become the ventral margin, and the posterior margin has become the dorsal or internal surface. Cassidine labra are deeply inserted into the head, leaving a short exposed section that may be quadrate, hemispherical or trapezoidal. They may be narrow and overlap only the mandibular apices, or they may be wide and extend to the mandibular bases. They are also symmetrical, with the lateral margins parallel, sub-parallel, or rounded. The apical margin may be simple (fig. 51D) or emarginated (fig. 51A, E), and narrowed (fig. 51E) or thickened (fig. 51B). When the distal margin is emarginate, the emargination may be broad or narrow and shallow or deep. The external (anterior) surface of the labrum may be asetose (fig. 51C) or setose (fig. 51B, D, E); setae may be soft or bristle-like and randomly scattered at the apex or in paired lateral groups. *Botryonopa* (fig. 51B) has the apical margin thickened and with two types of setae; long flexible setae occur in a narrow band across the upper portion while short, closely spaced, bristle-like setae occur in the lower portion. A few genera have the labrum carinate dorsally, with one or two carina extending from apex to the exposed basal margin, or diagonally from apex to lateral margins (e.g., fig. 51C). This carina variation was proposed as character 4 in Borowiec

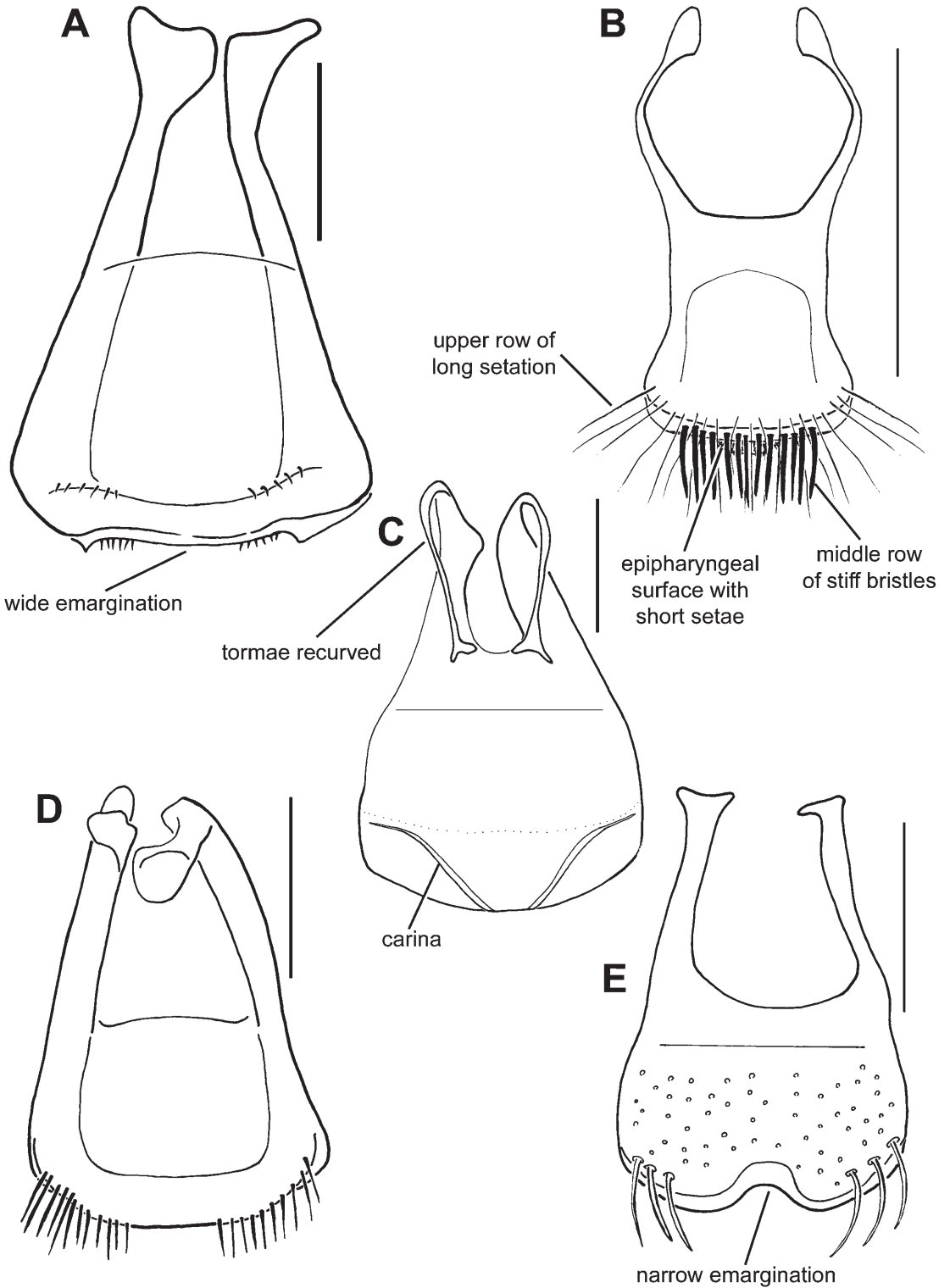


Fig. 51. Labrum of Cassidinae, anterior view. **A.** *Arescus* sp. **B.** *Botryonopa foveiocollis*. **C.** *Callistola speciosa fasciata*. **D.** *Prosopodonata dorsata*. **E.** *Stolas lebasi*. Scale bars = 0.5 mm.

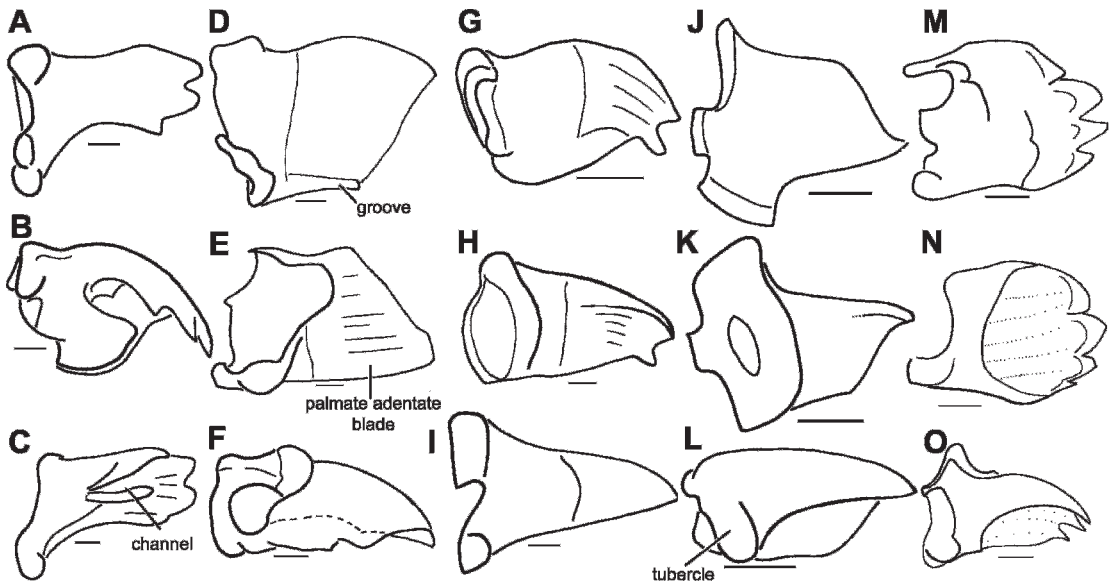


Fig. 52. Mandible of Cassidinae. **A.** *Arescus* sp., ventral view. **B.** Dorsal view. **C.** Posterolateral view. **D.** *Botryonopa foveicollis*, ventral view. **E.** Dorsal view. **F.** Anterolateral view. **G.** *Callistola speciosa fasciata*, ventral view. **H.** Dorsal view. **I.** Anterolateral view. **J.** *Prosopodonta dorsata*, ventral view. **K.** Dorsal view. **L.** Anterolateral view. **M.** *Stolas lebasi*, ventral view. **N.** Dorsal view. **O.** Anterolateral view. Scale bars = 1 mm.

(1995) and is used here as character 77. Some cassidine labra are modified with a thickened epipharyngeal surface, for example, *Hemisphaerota* (fig. 31C, D) and *Botryonopa* (fig. 51B). In *Hemisphaerota*, this thickened epipharyngeal surface spans the labral width and its surface is smooth. In *Botryonopa*, the epipharyngeal surface is exposed as a narrow, rounded thickening located medially along the labral margin, and it is densely microsetose.

Mandible (figs. 31E, F, 52; chars. 79–82). Migration of the mouth ventrad has altered the articulation, shape and position of the cutting edge of the cassidine mandible. The dorsolateral socket has moved to an anterior position and the ventrolateral condyle has moved to a posterior position. The cutting edge is mesal, not apical. Generally, cassidine mandibles overlap, with no obvious asymmetry except for slight size differences. Many genera have the mandibles trigonal in shape with a broad base and narrowed apex (e.g., fig. 52G–I), often with a single incisor alone, or with the incisor combined with a secondary dens or a sub-apical notch. Some trigonal-

shaped mandibles may be slightly constricted medially or may have the dorsal (inner) surface shallowly convex. In a few genera, the mandibles are extremely thick throughout with the mesal margin wide, flattened, and transversely grooved; these mandibles abut directly, suggesting a grinding surface. Some taxa have the internal (dorsal) mandibular surface with paired, heavily sclerotized ridges that form a groove or channel (e.g., fig. 52A–C). Many genera have the mandibles flattened, and palmate-shaped (e.g., fig. 52M–O), with the internal surface depressed and the mesal margin developed in three to nine dens of varying sizes. Palmate mandibles often have the external surface with a thickened medial or basal ridge or one to three basal tubercles.

The dramatic variation observed in adult mouthpart morphology across Cassidinae is paralleled by similar variation in larval mouthparts. Given the wide taxonomic and morphological diversity of host plants and plant parts selected as food within Cassidinae, it is intriguing if and how host choice has affected mouthpart morphology.

Maxilla (fig. 53). This has a cardo, one- or two-segmented galea, a one-segmented lacinia and a four-segmented palpus. The cardo is usually constricted medially; the basal portion may be deflected into the head, leaving a quadrate apical section exposed. The stipes varies in shape and sclerotization, with the mesal margin longer than the external margin. Sclerotization may be uneven (e.g., *Callistola*) with a heavily sclerotized external portion and a lightly sclerotized mesal portion. The surface is commonly flat but may also have a prominent longitudinal ridge. The apical margin may project laterally beyond the lacinia. The palpomeres are commonly cylindrical and they vary in proportions with the distal most one being the longest. They are commonly setose, with setae varying in density and arrangement. In a few taxa, the palpomeres are flattened. The medial and lateral margins of palpomeres are usually similar in length, but in some the lateral margin is longer, giving a curved appearance to the palpus. The galea is cylindrical, and in two-segmented forms, the basigalea and distigalea vary in relative proportions and density of vestiture. Setation on the basigalea may be absent, scant, or dense. Setation on the distigalea may be scant (e.g., *Callistola*), confined to a narrow apical row (e.g., *Arescus*) or a mesal band (e.g., *Botryonopa*), or cover the entire surface and form a dense brush. The lacinia may be small and rounded, larger and rounded, or quadrate. The apex is commonly rounded. In *Botryonopa* (fig. 53B), it is flattened, and the enlarged surface is densely covered with short setation.

Labium (fig. 54). Cassidine labia comprise distinct menta, prementa, ligula, and a three-segmented palpus. The mentum may be quadrate, triangular, or rounded, with lateral margins parallel, subparallel, or diverging apically. The surface is generally smooth, sometimes with a few sparse setae. The apical margin of the mentum may be continuous with, slightly narrower than or slightly wider than the basal margin of the prementum. In *Exothispa* (fig. 54F) the apical margin is slightly projected laterally. The prementum is quadriform and may be longer than wide or wider than long. The surface is usually flattened and with sparse setation. The labial

palpus is generally present and three-segmented with palpomeres varying in their relative proportions. In *Choeridiona* Baly, this palpus is absent (Gressitt, 1950). Palpomere I is usually the shortest. Palpomere II or III may be the longest. Palpomeres may be cylindrical or, more rarely, flattened. In *Cephaloleia* (fig. 54C) the palpus is flattened, and the external margin of palpomere II is almost twice as long as the mesal margin. The palpus insertion can vary from mediolateral to basal in position. The cassidine ligula is relatively large compared to other chrysomelids (e.g., fig. 54A) and ranges in general shape, sclerotization and surface pubescence. It can be rounded or triangular and lightly to heavily sclerotized. The apical margin may be acuminate or rounded, but never bilobed. The ligular surface is commonly flat and can be glabrous or sparsely to densely setose. The ligula of *Exothispa* is slightly depressed medially (fig. 54F).

ENDOSKELETON OF HEAD

Stickney (1923) found that the tentorium is generally membranous in the heads of *Anoplites gracilis* and *Chelymorpha argus*. The absence of the clypeal sclerite was not discussed but the term "postclypeus" was introduced for the frontoclypeus. Although Stickney's (1923) illustrations indicate some variation in head endoskeleton, I have not explored this feature here because of lack of materials for the sagittal sectioning needed to examine it.

PROTHORAX (figs. 55–66; chars. 84–113)

This segment varies across Cassidinae in general shape, margin form, development and number of angles, orientation of various sections, prosternal process form, coloration (dorsally and ventrally), and texture patterns (dorsally and ventrally). Some pronota are transparent, but with cuticular patterns within the sclerite (e.g., *Coptocycla*). The presence of the anterior and posterior trichobothria has been useful for diagnosing cassidine tribes (Hincks, 1952; Würmli, 1975; Staines, 2002b). The prothorax can be longer or shorter than the pterothorax.

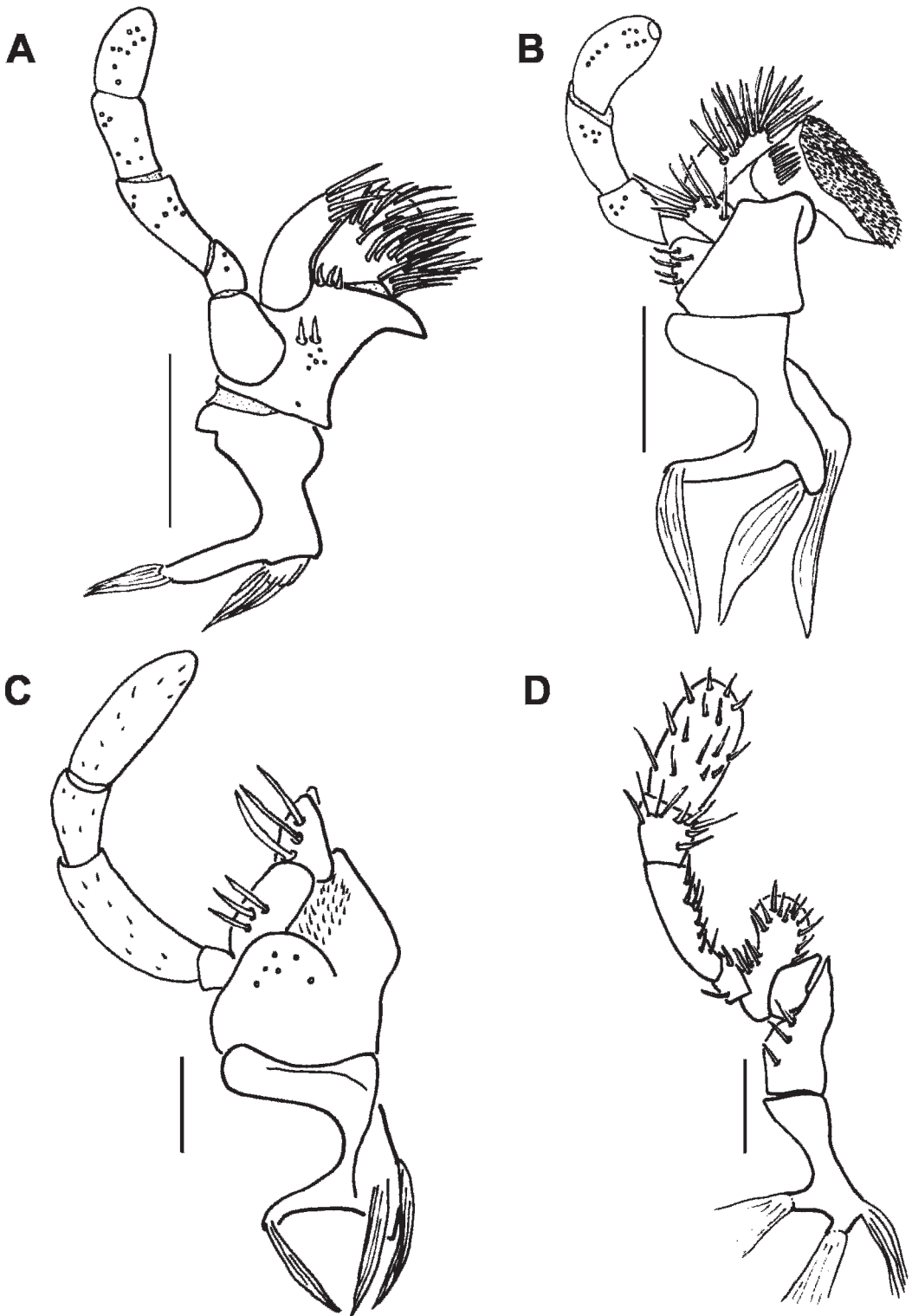


Fig. 53. Maxilla of Cassidinae, external view. **A.** *Arescus* sp. **B.** *Botryonopa foveicollis*. **C.** *Callistola speciosa fasciata*. **D.** *Physonota* sp. Scale bars = 0.5 mm

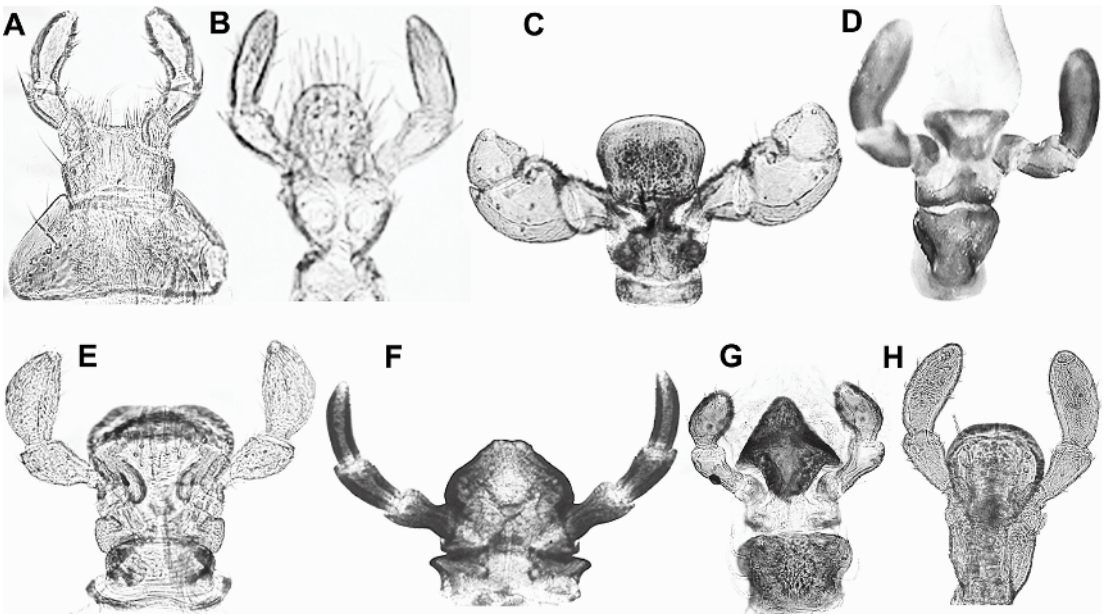


Fig. 54. Labium of Chrysomelidae. **A.** *Plateumaris rufa* (Donaciinae). **B, H.** Cassidinae. **B.** *Basiprionota chinensis*. **C.** *Cephaloleia* sp. **D.** *Botryonopa foveicollis*. **E.** *Calliaspis rubra*. **F.** *Exothispa reimeri*. **G.** *Eurispa vittata*. **H.** *Hispodonta chapuisi*.

Pronotum (figs. 55–59, chars 84–102). Pronotal shape in dorsal aspect ranges from transverse rectangular (almost square) to hemisphaerical. It has anterior (= apical) and posterior (= basal) margins and anterolateral, posterolateral, and posterior angles. Lateral margins may be absent, slightly developed or greatly explanate. In pronota with a deeply convex anterior margin, anteromedial angles are also present. In pronota with bisinuate basal margins, medioposterior angles are formed (e.g., fig. 55C, D). The length of pronotal margins varies in relative proportions; frequently the apex and base are more or less equal in width or the base is wider than the apex. In *Basipta* (fig. 55D) the pronotum has the apex appearing wider than the base, but the basal margin is actually much longer than the apical margin. In lateral aspects, cassidine pronota appear flattened (e.g., *Callistola*), shallowly arched (e.g., *Spilophora*), or strongly arched with the basal margin highly elevated from the apical margin (e.g., *Oxynodera*).

The anterior pronotal margin may be simple (fig. 55A, B) or expanded (fig. 55D, 56B, E). In many species, this margin is either straight

or broadly concave but in some it is broadly and deeply convex, partially or completely covering the head (fig. 56E). The relationship between the marginal extension and head retraction into the prothorax must be studied further since these two distinct processes may have occurred together. In convex anterior margins, the prothorax has both anterolateral and anteromedial angles, and the head is exposed dorsally. Because of variations in the marginal extension, the anterior prothoracic foramen can appear wide, bounded completely by the anterior margin, or narrow and bounded by the discal margin. In some genera (e.g., *Elytrogona* and *Hilarocassis*) the anterior margin is thickened and slightly upturned.

Ventrally, the basisternum may be very narrow longitudinally so that the anterior margin is very close to the procoxal margin (e.g., fig. 64A–C). More commonly, the basisternum is well developed and long, with the anterior and procoxal margins well separated (e.g., fig. 64C). In *Basiprionota*, the basisternum is very long and partially covers the venter of the head, hiding the mouth completely. In *Paraselenis*, the prepectus is approximately three times longer

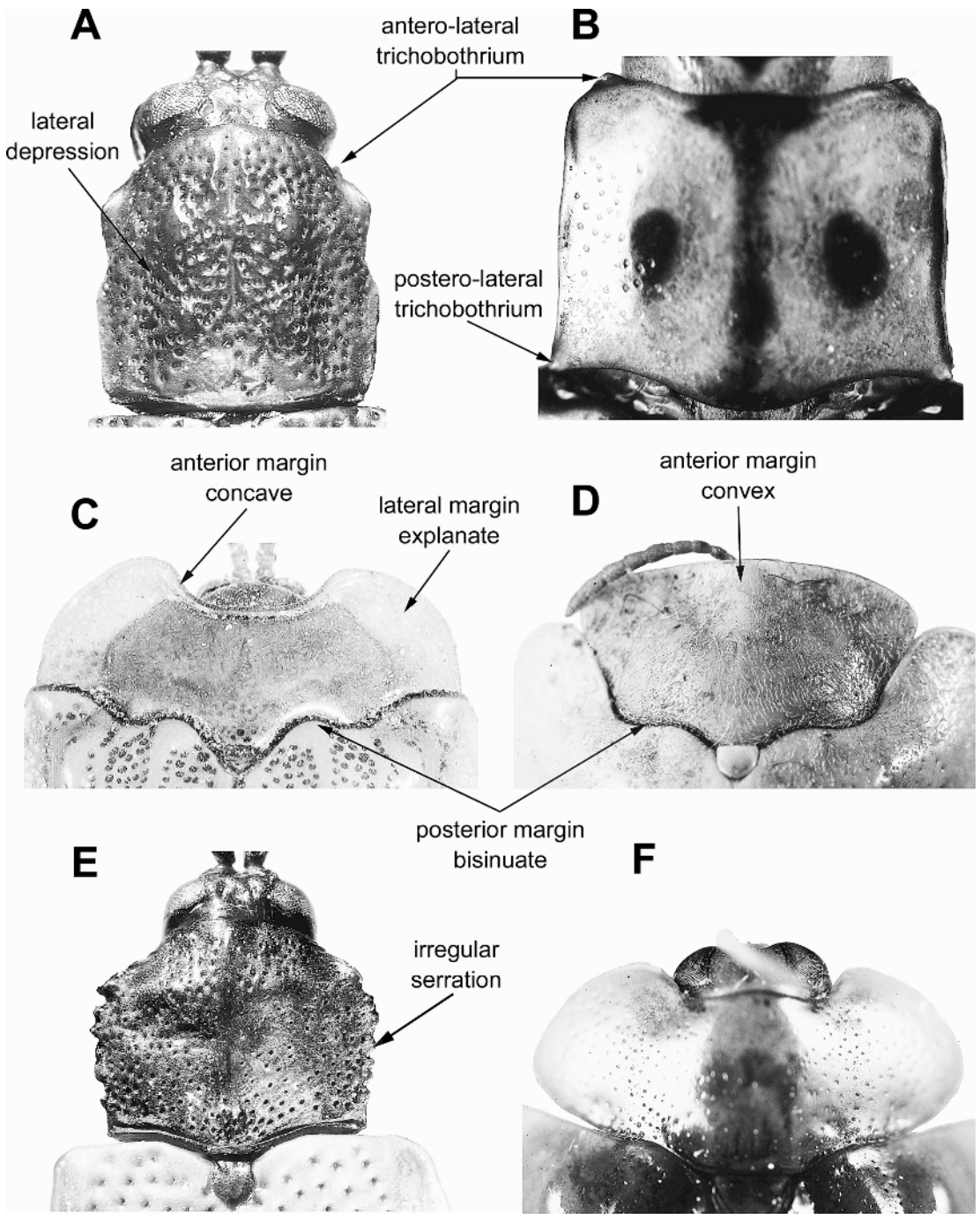


Fig. 55. Pronotum of Cassidinae, dorsal aspect. A. *Anisodera guerini*. B. *Arescus* sp. C. *Basiprionota quadriimpressa*. D. *Basipta glauca*. E. *Botryonopa foveiocollis*. F. *Calliaspis rubra*.

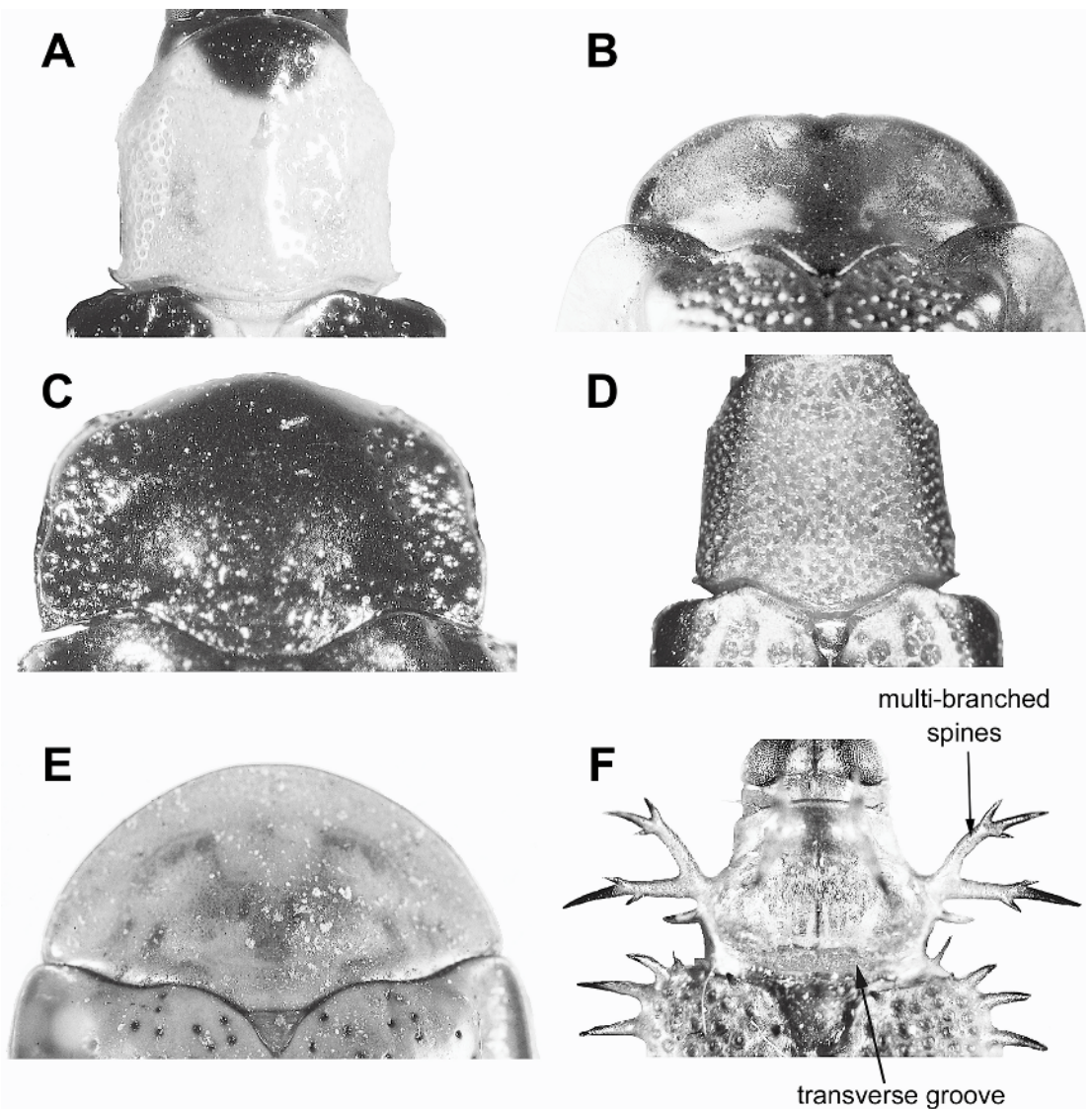


Fig. 56. Pronotum of Cassidinae, dorsal aspect. **A.** *Callistola speciosa*. **B.** *Canistra plagosa*. **C.** *Cephaloleia* sp. **D.** *Ceratispa palmicola*. **E.** *Conchylotenion hybrida*. **F.** *Dactylispa* sp.

than the length of the hypomerall lobe. The mouth may be partially hidden in other taxa because of a medial extension of the anterior margin. This flange over the mouth has been called a “chin plate” (Würmli, 1975), or *prosternal collar*. The prosternal collar often has a transverse groove posteriorly that defines it from the rest of the prosternum. It may be short or long, and the surface texture may be smooth or transversely wrinkled. In *Basipta*, the prosternal collar

covers the mouth up to the labrum, and it is unclear how the animal feeds, if at all.

The anterior pronotal margin may be smooth, spinose, setose, or serrate. *Asamangulia* has the pronotal disc aspinose but the lateral and anterior margins spinose; these spines branch basally. In *Cyperispa* the anteroventral margin has a single median tooth and a row of evenly spaced, erect hairs.

The *lateral margins* of cassidine pronota are commonly margined but some (e.g.,

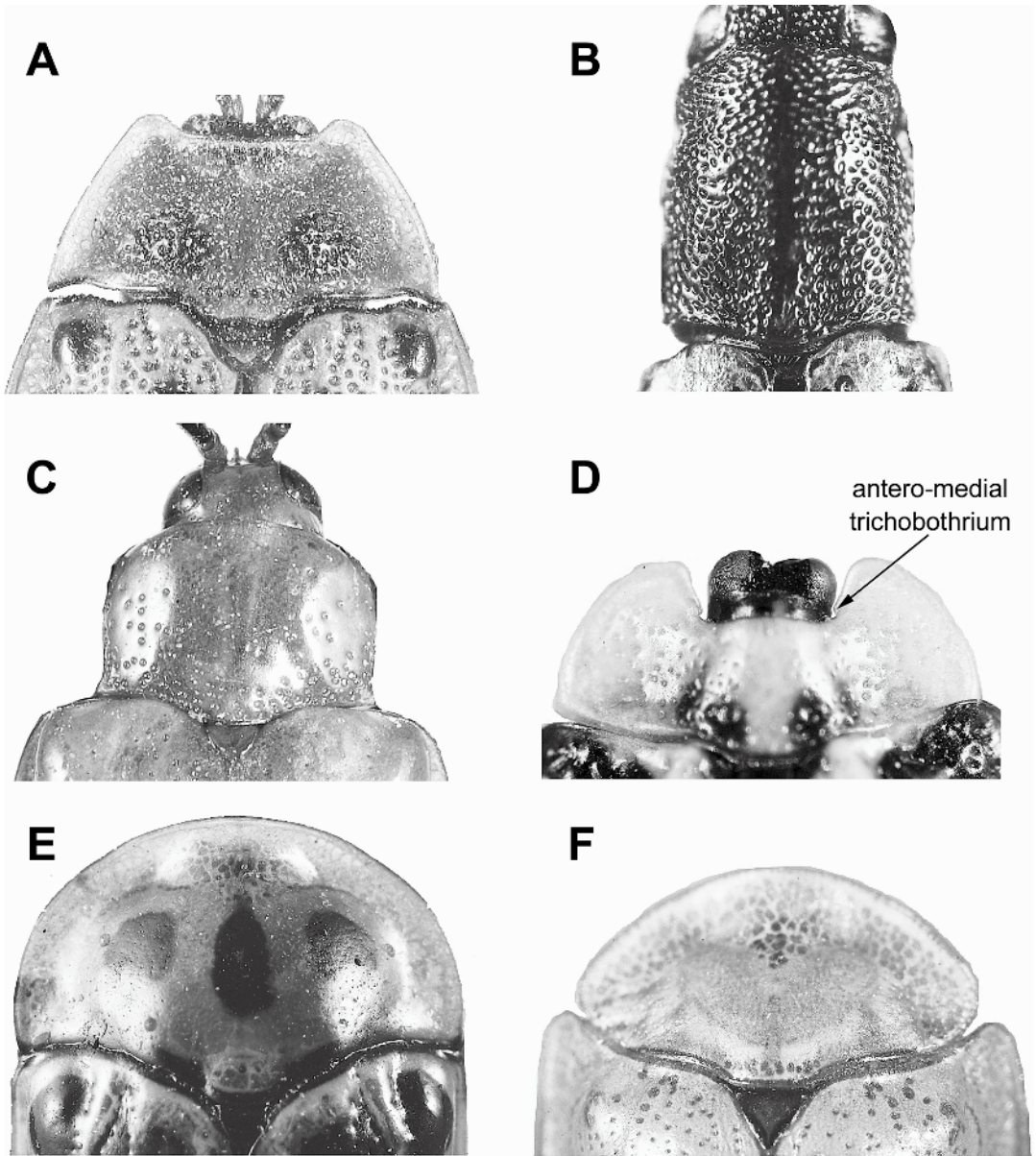


Fig. 57. Pronotum of Cassidinae, dorsal aspect. A. *Epistictina viridimaculata*. B. *Eurispa* sp. C. *Hispodonta chapuisi*. D. *Imatidium fasciatum*. E. *Ischyrosomyx oblonga*. F. *Jonthonota novemmaculata*.

Promecothea) have rounded sides that are also protuberant medially. In margined forms, margins are usually complete, extending from the anterior margin to the basal margin, and simple or slightly thickened (e.g., *Chelymorphia*). More rarely, some margined forms have the margin incomplete (fig. 60A,

D). The margin is evanescent posteriorly in *Chalepus*, evanescent medially in *Cyperispa*, and evanescent anteriorly and posteriorly in *Exothispa*. Margin development varies widely, as in the elytra. Some have a very narrow bead or gutter along the edge of the pronotal disc. In others, the margin is explanate, and

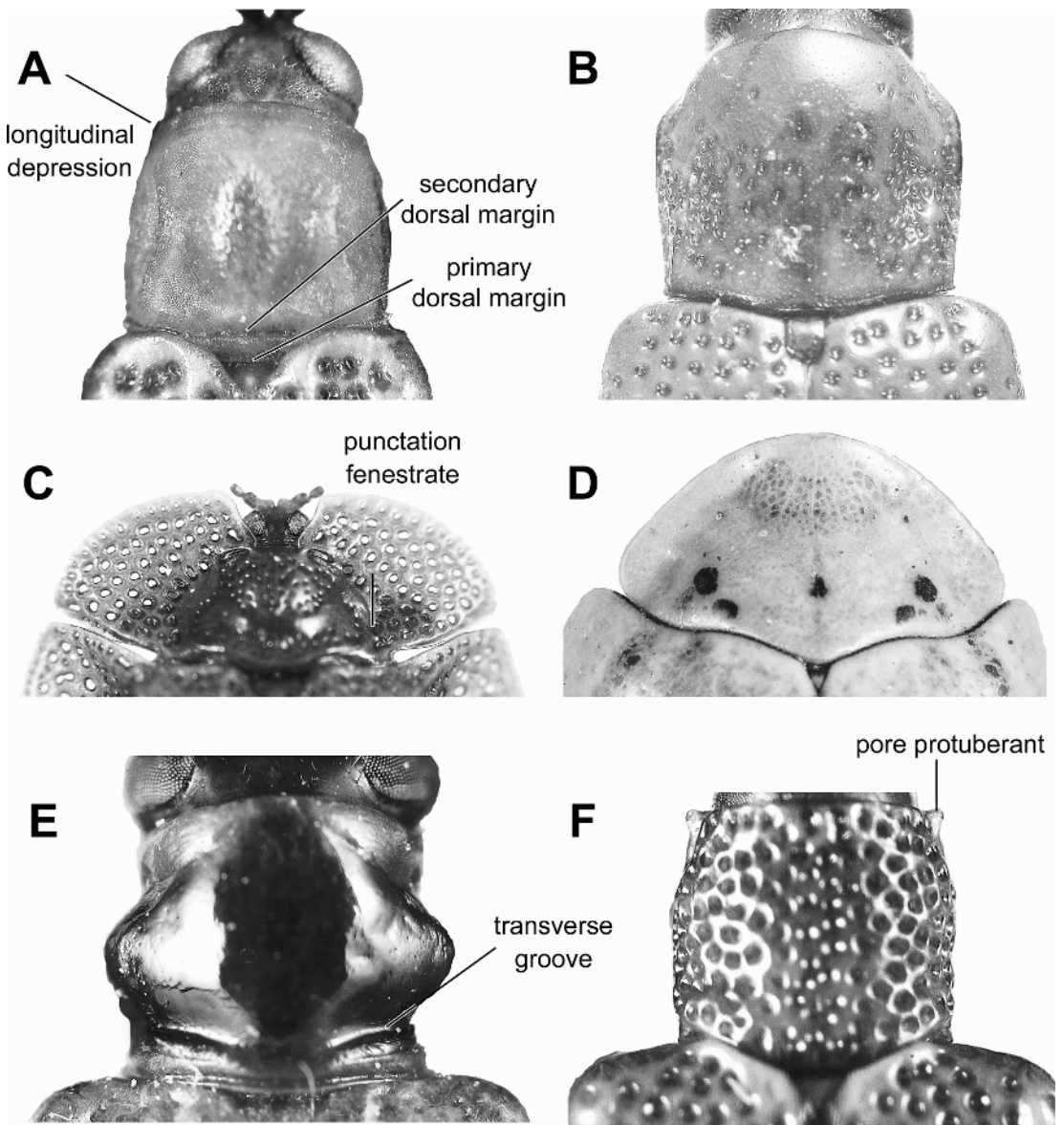


Fig. 58. Pronotum of Cassidinae, dorsal aspect. **A.** *Klitispa opacicollis*. **B.** *Lasiochila gestroi*. **C.** *Notosacantha badia*. **D.** *Physonota alutacea*. **E.** *Promecotheca papuana*. **F.** *Scoloenopla mantecada*.

its width can be less than, equal to, or greater than the width of the disc. Development of the explanate margin is also accompanied by enlargement of the hypomeron ventrally. Laterally, some pronota have a humeral protuberance (e.g., *Sagra*, *Plateumaris*), defined by a shallow projection of the disc and margin and/or with a slight depression behind the humerus (e.g., *Plateumaris*). The

surface texture of the lateral margin includes setation, serration, and spines. In *Anisodera* (fig. 55A, 60A), the marginal surface texture is irregular. Lateral margins of *Botryonopa* (fig. 55E) have large, irregular serration. *Dactylispa* has spinose lateral margins (fig. 56F).

Posterior (= Basal) Margin. This may be tranverse (fig. 55A, 58A, B), appearing trun-

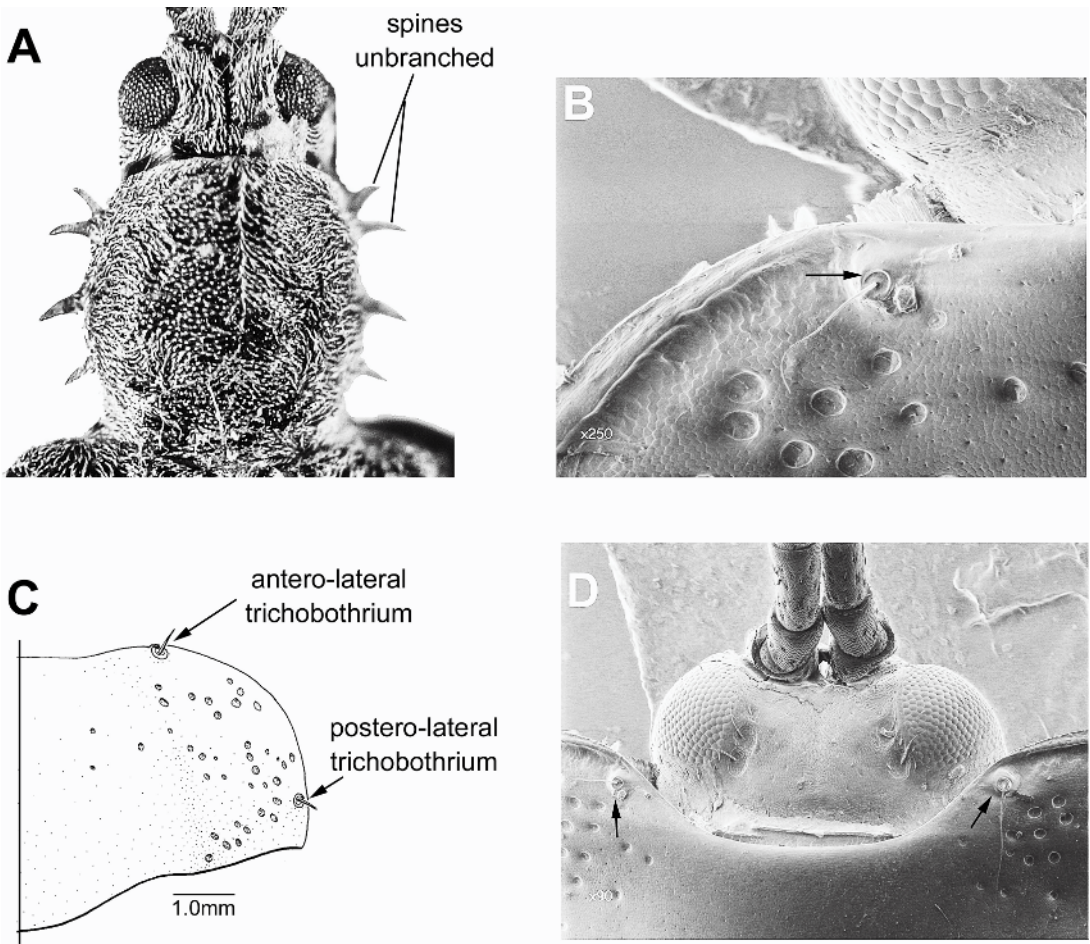


Fig. 59. Pronotum of Cassidinae, dorsal aspect. **A.** *Trichispa* sp. **B.** *Hybosa* sp., anterolateral trichobothrium. **C.** *Calyptocephala nigricans*, anterolateral and posterolateral trichobothrium. **D.** *Calyptocephala nigricans*, scanning electron micrograph showing anterolateral trichobothrium.

cate at the posterior angle. The posterolateral angle may or may not be projected, and with a single trichobothrium (fig. 55B) (char. 9 of Borowiec [1995] = char. 101 herein). Where projected, this angle may be directed laterad, or posteriad (e.g., *Chelymormpha*). In cassidines with bisinuate posterior margins (fig. 55C, D, 56B), the latter may be distinguished into two sections separated medially by the medioposterior angle. Both sections may be concave, corresponding with convexities of the elytral basal margin (e.g., fig. 55C, 56B) or the outer section may be straight and the inner section may be convex (e.g., fig. 55D). The posterior margin may be inflected, forming a secondary dorsal margin (fig. 58A). This secondary

margin corresponds to the elytral basal margin while the true basal margin is hidden under the elytra. In these cases, the primary pronotal posterior margin is exposed medially at the mesoscutellum.

The pronotal posterior angle may be absent (i.e., the margin is straight) or present; when present it is rounded or acute and may overlap the mesoscutellum. In *Dorynota*, the anterior margin of the mesoscutellum is expanded and overlaps the pronotum at this point. The posterior margin is commonly smooth (e.g., *Basipta*) but can also be crenulate (e.g., *Basiprionota*).

Pronotal Disc. Where the pronotum has explanate margins, the disc and margin may

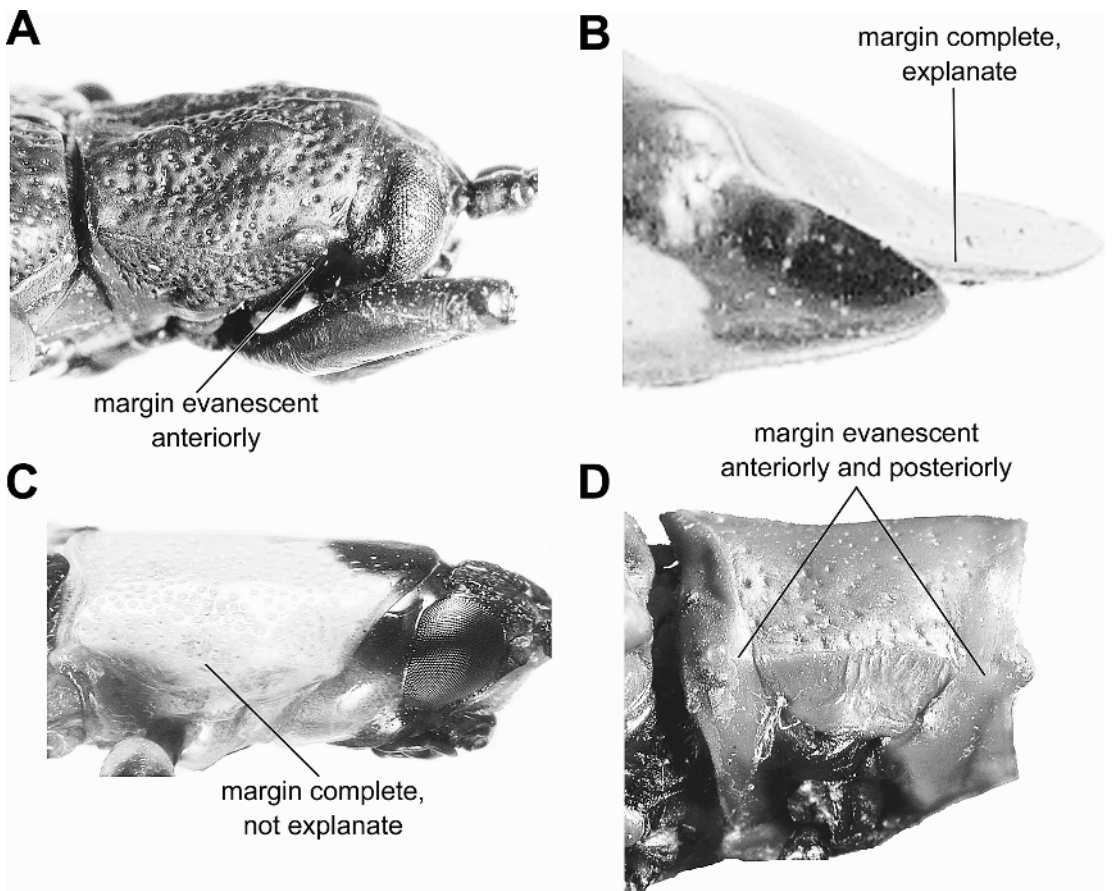


Fig. 60. Pronotum of Cassidinae, lateral view. **A.** *Anisodera guerini*. **B.** *Aspidimorpha quadrinodosa*. **C.** *Callistola speciosa fasciata*. **D.** *Exothispa reimeri*.

be clearly defined by changes in angulation, a discal margin, ridges, wrinkles or punctation. When they are not easily demarcated dorsally, one must examine the venter of the prothorax to determine the hypomeron, tergosternal suture and prosternum.

Pronotal surface texture varies across Cassidinae from smooth to having irregular patterns of depressions or protuberances, to having various patterns of punctation and vestiture. *Botryonopa* has a slightly carinate medial longitudinal line and a shallow, uneven, transverse medial depression. In *Asa-mangulia* and *Dactylispa*, a slight transverse medial projection and the inflection of the basal margin create two parallel transverse grooves. There is a transverse basal depression in *Cephalodonta* (weakly developed) and *Dactylispa* (well developed; fig. 56F).

Exothispa has a slight transverse, sub-basal ridge. *Klitispa* has a deep, narrow transverse slit in the sub-basal medial area, and paired arcuate ridges running longitudinally in the lateral areas. *Lasiochila* has short depressions running longitudinally in the posterolateral area.

Punctation can vary greatly, being shallow or deeply impressed and even fenestrate (e.g., fig. 58C), small or large, with regular round forms or irregular shapes, widely separated or adjoining, and in many different distribution patterns over the pronotal surface. *Ceratispa* has a highly regular arrangement of evenly spaced, round, similar-sized punctures. Punctuation patterns on the disc and explanate margin can be independent; for example, *Calyptocephala* has a smooth disc and a shallowly impunctate margin. In

Arescus, the disc has fine, shallow dispersed punctations, whereas in *Anisostena* it has deeply impressed, closely spaced punctation.

Dorcathispa has one of the most complicated pronotal surfaces of any cassidine. The lateral margins are evanescent anteriorly and have multibranching spines medially. The disc also has a pair of subapical multibranching spines and a pair of sharply defined protuberant discs medioposteriorly. The anterolateral and posterolateral angles both have protuberant trichobothria with a single long bristle. Erect, somewhat flattened setae are also dispersed on the body, including the pronotum especially along the anterior and posterior margins and in a medial field.

Pubescence. Generally pronotal pubescence is restricted to trichobothria located on the angles with single or multiple bristles. *Basipta* has fine, dense, recumbent hairs oriented anteromedially. *Asamangulia* has erect, somewhat flattened setae with swollen apices similar to that of *Dorcathispa*; these are distributed on the disc and along the anterior margin of the pronotum. *Eurispa* has a deeply punctate pronotum, and the lateral and anterior punctures have a single, recumbent, anteriorly directed hair. In *Trichispa*, the body is generally clothed in dense recumbent pubescence.

Trichobothria (figs. 33A, 55A, B, 58F, 59B, E). Hincks (1952) distinguished the tribes Spilophorini and Imatidiini by, among other features, trichobothria on the anterior pronotal angles alone (e.g., *Imatidium*) and on both anterior and posterior pronotal angles (e.g., *Calyptocephala*). No other tribes within Cassidinae s.str. possess this structure. Within the Hispinae s.str., the occurrence of these trichobothria on the pronotal angles is widespread and has been useful in tribal diagnoses (e.g., Würmli, 1975), with some taxa having "sensory tufts" with multiple pores and/or multiple bristles. These sensory tufts, or clusters of trichobothria, occur on both the anterior and posterior corners of Hispini, on only the anterior corners of Aroidini, Anisoderini, and Eurispini (Würmli, 1975), and on only the posterior angle of *Alurnus*. *Alurnus* has three pores, each with a single bristle. Anterior and posterior trichobothria can occur together (e.g., *Asamangulia*) or independently. They

are only on the anterolateral angles in *Baliosus*, on the anteromedial angles in *Calliaspis*, and on the posterolateral angles in *Callispa*. The pore base may be flat, protuberant or even slightly elongated. Cases where trichobothria occur on both anterolateral and anteromedial angles are not known. I follow Borowiec (1995; chars. 8, 9) and treat these as independent characters (chars. 99–101) based on their topographic differences.

The *hypomeron* may be oriented vertically (e.g., *Ceratispa*), or more commonly, ventrolaterally (e.g., *Calyptocephala*). In the former condition, the procoxae may be in a lateral position so that the profemur can be retracted vertically against the propleuron (e.g., *Hemisphaerota*). The propleuron surface can be indented, often in conjunction with changes in the orientation of the mesopleuron, and together they form a cavity where the legs are retracted (e.g., *Pachybrachis*). The hypomeral surface texture varies from smooth (e.g., *Calyptocephala*) to wrinkled (e.g., *Desmonota*) to punctate (e.g., *Callistola* and *Ceratispa*).

Prosternum (figs. 61–65; chars. 103–113). The length of the prepectus in cassidines is usually longer than that of the hypomeral lobe; however in a few taxa (e.g., *Ceratispa*) the latter is longer than the former. The anterior prosternal margin may be smooth, serrate, dentate, or with a row of fine hairs; the edge may be simple or thickened, and continuous or with an anterior convexity called the prosternal collar. This collar forms a broadly rectangular flange, which overlaps the mouth. In *Basiprionota*, the collar is greatly expanded anteriorly, covering the mouth as far as the labrum. In expanded margins, the edge may be directed anteriorly or anteroventrad, with a slight groove behind the collar. The prepectus (section of prosternum anteriorly of procoxae) is usually as long as or longer than the length of the hypomeral lobe behind the procoxae, but in *Delocrania* it is shorter than the length of the latter. The anterolateral section of prepectus is oriented vertically (*Sagra*, *Plateumaris*) or ventrally (in the same plane as process). In *Deloyala*, a pair of weakly-developed carina extend from the hypomeron, longitudinally alongside the eye and gena. In *Dorynota*, this point

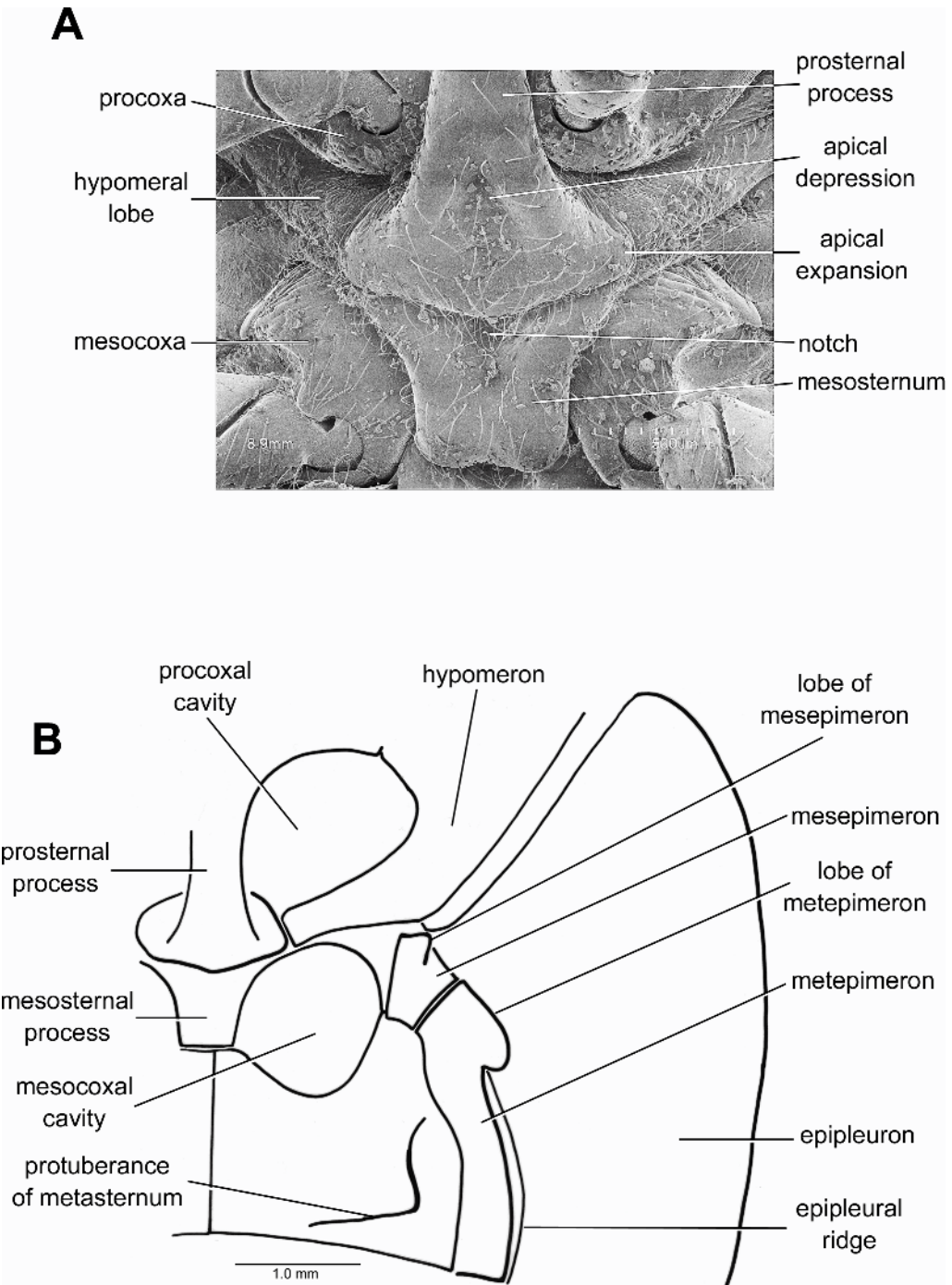


Fig. 61. *Basipta glauca*. **A.** Prosternal process, scanning electron micrograph. **B.** Meso- and metasternum.

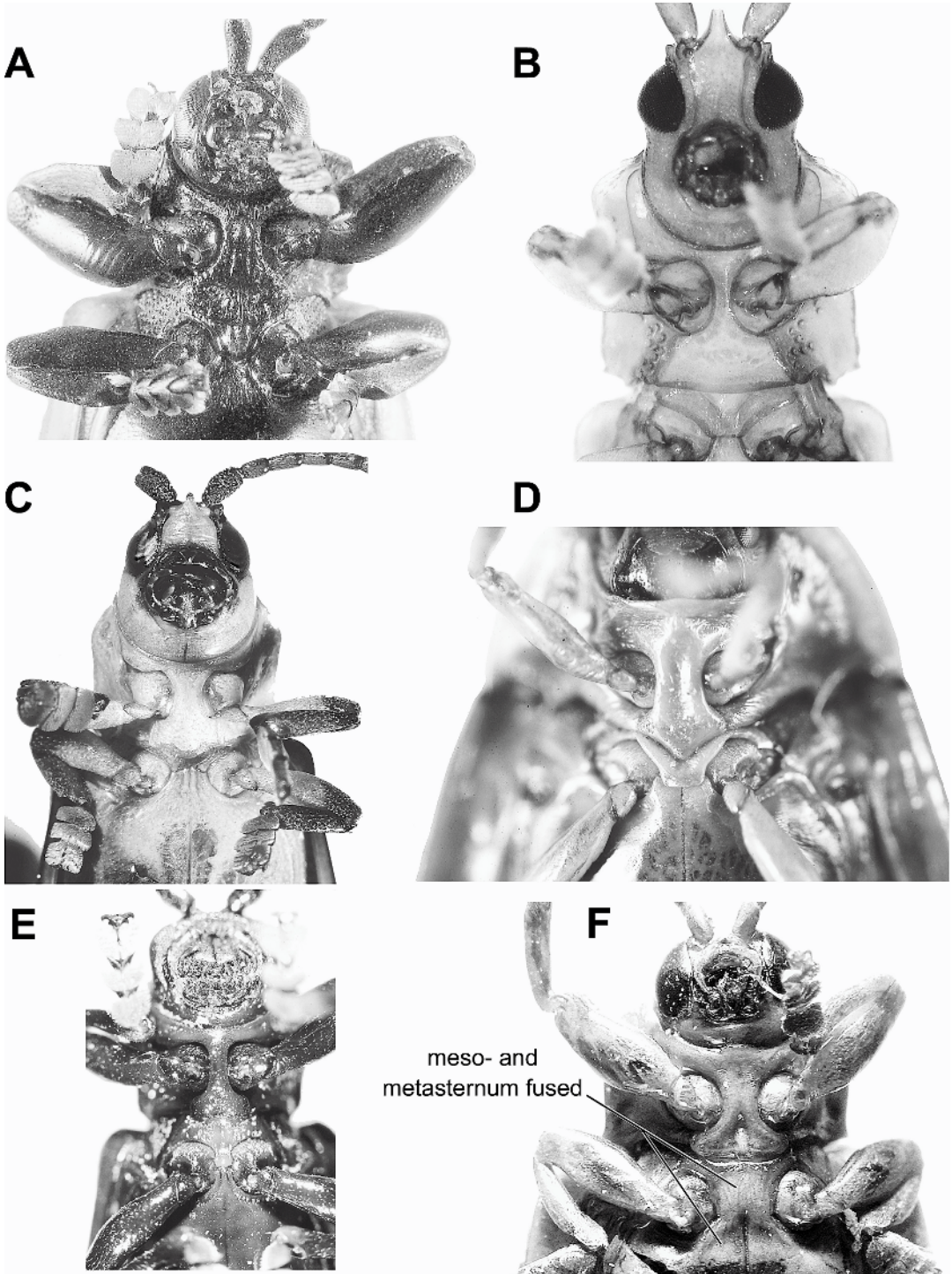


Fig. 62. Thorax of Cassidinae, ventral view. A. *Brontispa mariana*. B. *Botryonopa foveicollis*. C. *Callistola speciosa fasciata*. D. *Epistictina viridimaculata*. E. *Estigmene chinesnsis*. F. *Hispodonta chapuisi*.

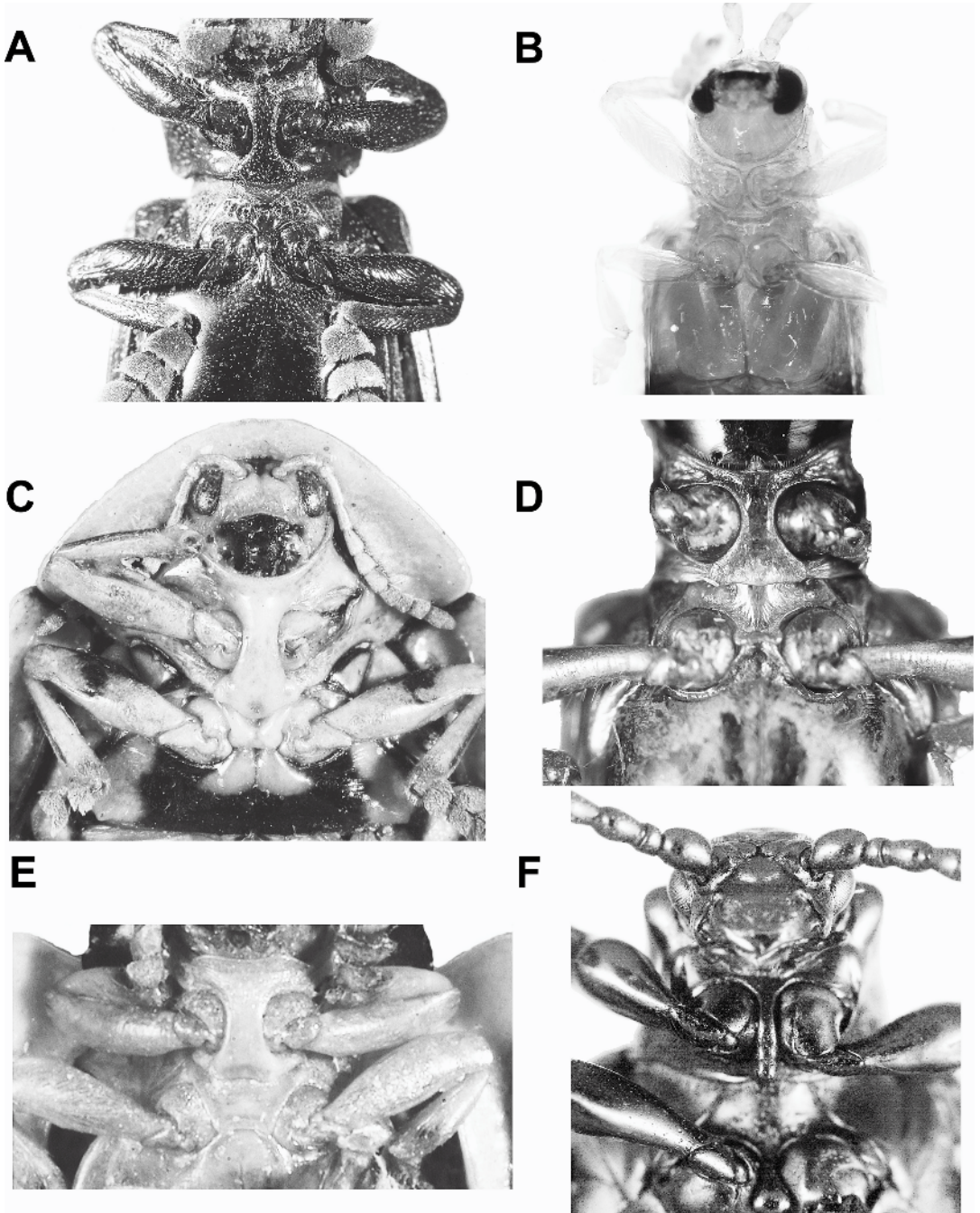


Fig. 63. Thorax of Chrysomelidae, ventral view. A, E. Cassidinae. A. *Lasiochila gestroi*. B. *Pharangispa palmicola*. C. *Physonota alutacea*. D. *Promecothea papuana*. E. *Spilophora aequatoriensis*. F. *Sagra* sp. (Sagrinae).

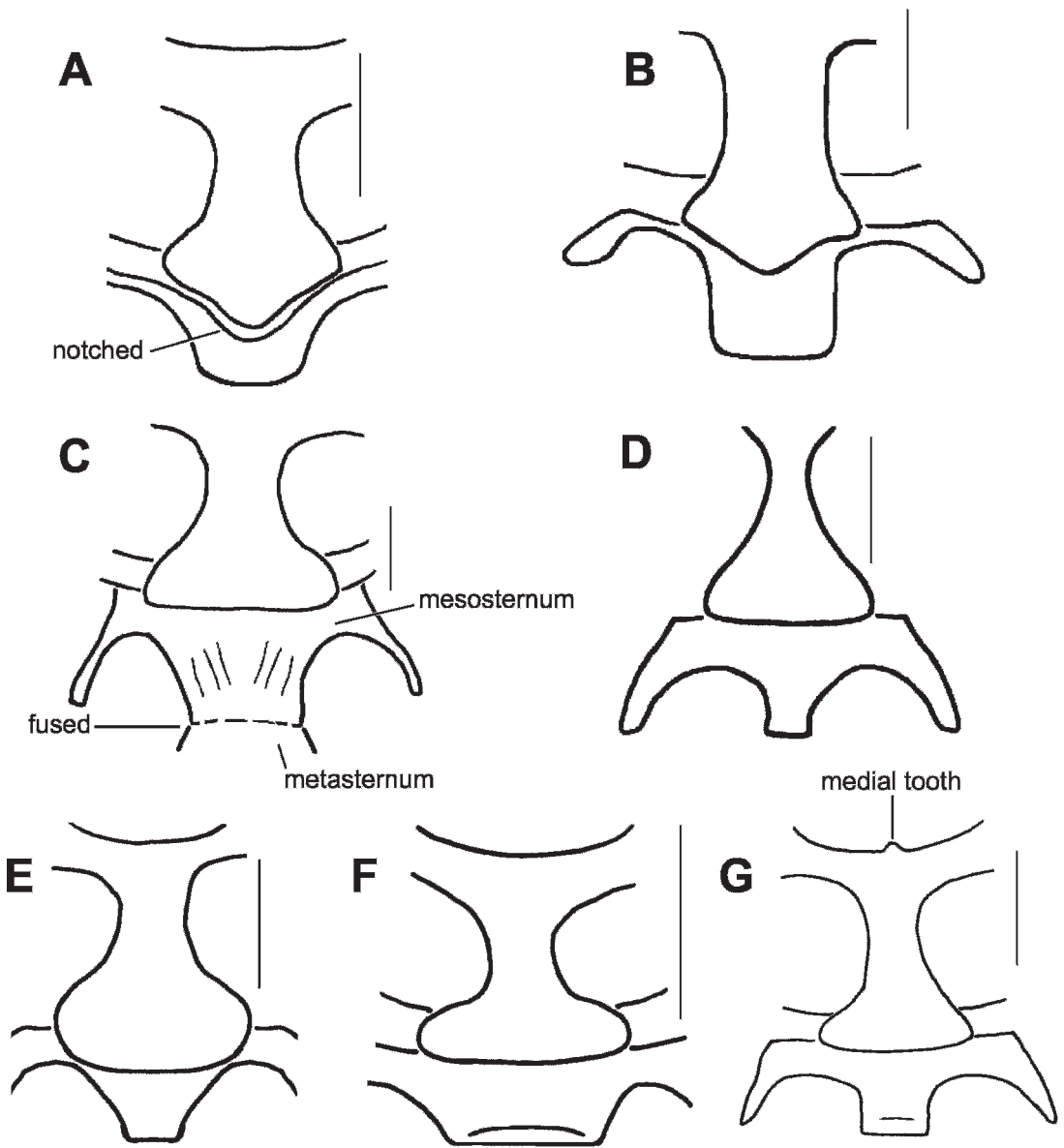


Fig. 64. Prosternal process in Cassidinae, ventral view. A. *Asteriza flavicornis*. B. *Basiprionota chinensis*. C. *Hispodonta chapuisi*. D. *Estigmena chinensis*. E. *Lasiochila gestroi*. F. *Notosacantha badia*. G. *Promecothea papuana*. Scale bars = 1.0 mm

on the hypomeron is slightly protuberant and forms a groove with the prosternal collar; these lateral grooves may hold the antennae but this has not been observed.

The *prosternal process* (figs. 33B, C, 61–64; chars. 108–113) varies in length, protuberance, and general shape especially in the

apical region. In most cassidines the base, stem, and apex of the process are in the same plane; however, some may have the medial section protuberant (e.g., *Arescus*). This differs from the condition in some outgroups (e.g., *Sagra*) where the apex is protuberant from the base and stem. The general shape of

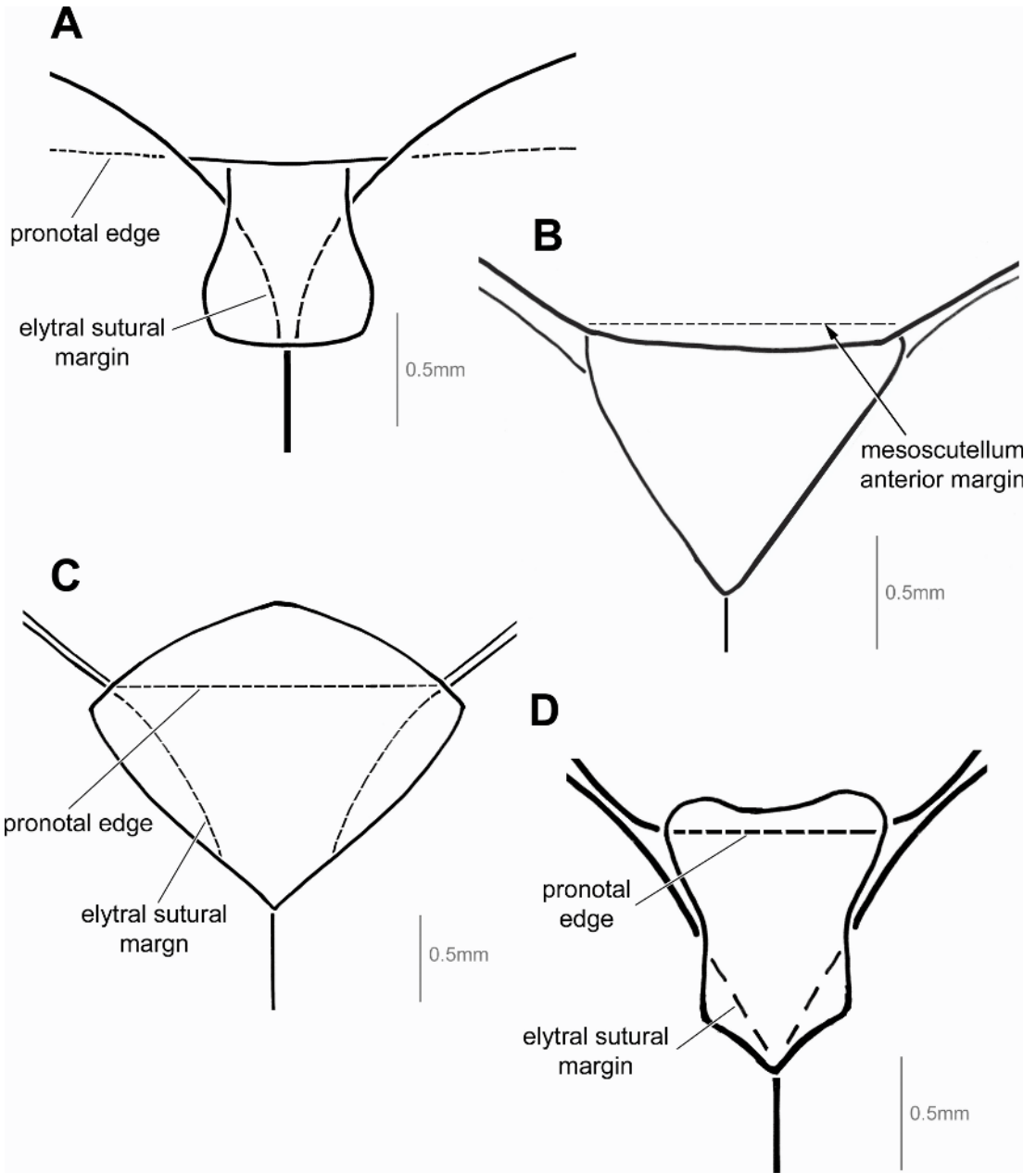


Fig. 65. Mesoscutellum of Cassidinae. Dashed lines represent underlying sclerite. **A.** *Aproidea balyi*. **B.** *Coptocycla dorsoplagiata*. **C.** *Dorynota* sp. **D.** *Spaethiella* sp.

the process apex varies across Cassidinae. Commonly, the apex is expanded laterally, extending below the procoxae and meeting the hypomerall lobe directly or overlapping the latter. The apex may also be simple, with

the process width being even from base to apex.

The process surface can be smooth or have grooves, wrinkles, punctures and pubescence. The base, stem and apex can also have

different patterns of textures. In *Botryonopa*, the base is smooth, the stem has a slightly convex line medially and longitudinally, and the apex has five short, deeply impressed, parallel, longitudinal grooves. In *Charidotella* and *Chalepus*, the process has sparse fine long hairs.

Tergosternal Suture (= notosternal suture; Chamorro-Lacayo and Konstantinov, 2004) (fig. 33B). This is usually apparent but is absent in *Plautyauchenia* and *Acromis*. It may be long, extending to the anterior margin (e.g., *Basiprionota*). In many other cassidines, it is short, terminating before the anterior margin. Its orientation may be longitudinal or anterolateral.

Procoxal Cavity. The position, shape, and orientation vary in subtle ways that are difficult to define. In *Hemisphaerota* the cavities are in a laterovertical plane, but more commonly the cavities are in the ventral plane. This must certainly affect the orientation of legs. The margins of the procoxal cavities are simple or marginate and protuberant. Procoxal cowlings are not prominent in cassidines.

Cassidine procoxae are closed posteriorly by the hypomerall lobe (= post-coxal bridge) and lateral expansions of the prosternal process apex. The point of contact between hypomerall lobe and process varies depending on their widths. The medial margin of the lobe may extend under the prosternal process, and its apex is therefore hidden. Its length and width vary, as does the surface texture, which may be smooth or wrinkled.

PTEROTHORAX (figs. 65–73; chars. 114–159)

Dorsally, the pterothorax appears to be fairly uniform but further study with additional taxa is needed. Ventrally, relative proportions, shape, form of margins, meso-coxal process form, ventral coloration and ventral texture patterns show much diversity.

Mesonotum. This region will not be described in great detail here, only to note that the mesoscutellum is usually elevated from the mesoscutum. The mesoscutum is commonly relatively weakly sclerotized and smooth. In *Plautyauchenia*, the mesoscutum is heavily sclerotized, deeply impunctate, and elevated from the mesoscutellum.

Mesoscutellum (fig. 65; chars. 114–117). This sclerite is always exposed in Cassidinae and shows variation in shape, margin exposure, and surface texture. It may be triangular (e.g., *Canistra*), rounded (e.g., *Aproidea*), or quadrate (e.g., *Calyptocephala*). In *Cephalodonta* and *Anisostena*, it is quadrate, with the apex depressed and the base protuberant. The pronotal basal margin may be inflected onto itself, creating a small cavity around the depressed mesoscutellum. The anterior margin of the mesoscutellum is usually straight, but it is convex in *Dorynota* (fig. 65C) and *Spaethiella* (fig. 65D) and overlaps their posterior pronotal angle. The lateral margins of the mesoscutellum may be expanded and overlap the sutural edge of the elytra (e.g., fig. 65A, C). The mesoscutellum surface can be smooth, punctate, pubescent, or finely microreticulate. In most cassidines, the surface is glabrous, but in *Trichispa* it is densely pubescent, like the rest of the body.

Mesosternum (figs. 62–64; chars. 118–122). The mesosternal surface may be flat (e.g., *Estigmena*) or deeply notched and receiving the prosternal process (e.g., *Canistra*). Anterolateral lobes of the mesobasisternum close the mesocoxae laterally. These lobes can be broad (e.g., *Basipta*) or tapered to a rounded point. The lateral portion of the mesosternum may be oriented vertically such that the mesosternum has a curved appearance from ventral to lateral. Mesosternal surface texture can be smooth, wrinkled, grooved, striate or punctate. In *Ceratispa* this surface is punctate anteriorly but smooth medially and on the mesosternal process. *Botryonopa* has the mesosternum with a deep medial trough, the apex slightly protuberant, and the surface with shallow lateral punctures and shallow medial longitudinal grooves. This medial trough is not regarded as homologous with the notched surface since it does not fit around the prosternal process, as in the latter condition.

The *mesosternal process* (figs. 62–64; chars. 120–121) may be short or long (relative to its width), with the posterior margin rounded (e.g., *Botryonopa*), broadly quadriform (e.g., *Anisostena*), tapered and acuminate (e.g., *Plautyauchenia*), or quadrate (e.g., *Callispa*). Overall, the process is commonly flat, but in *Estigmena* and *Dactylispa* the apex is pro-

tuberant from the base. It is frequently longer than wide; in *Callispa* it is wider than long. The surface may be smooth, wrinkled, punctate, or with shallow parallel longitudinal grooves (e.g., *Botryonopa*). The posterior margin of the process may be concave, convex, or straight. The mesosternal process is free in most cassidines, but in *Hispodonta* it is fused to the metasternal intercoxal process with the suture being poorly defined (fig. 62F). *Mesocoxal cavities* are usually rounded, with the intercoxal distance varying according to the width of the mesosternal process. The sclerites closing the cavity laterally also vary according to the development of the lateral lobe of the mesoscutellum.

Cassidine *mesopleura* (fig. 66) have the *mesepisternum* small and roughly triangular in shape and they are commonly exposed ventrally or, infrequently, hidden in lateral view by explanate pronotal and elytral margins. This sclerite may be curved or flattened, and positioned in a ventral or ventrovertical plane. Its surface texture includes smooth or punctate and glabrous or pubescent. In *Alurnus*, a thin transverse carina divides the sclerite into a narrow rectangular anterior section and broad triangular posterior section. In *Anepsiomorpha* a shallow gully runs alongside the lateral margin. The *mesepimeron* may be triangular or quadrate in shape, with the anterior margin hidden by the elytra (e.g., *Asmangulia*), meeting the epipleural ridge directly (e.g., *Alurnus*) or slightly expanded and overlapping the latter (e.g., *Acromis*). Surface texture varies as in the mesepisternum. The orientation may be ventral or mostly lateral.

The mesepisternum and mesepimeron are commonly separate sclerites, but in a few cassidines they are very tightly fitted together and appear almost fused. Hinck's (1952) proposed the fused state as a character but Borowiec (1995) considered this assessment incorrect. I agree with Borowiec (1995). Based on examination of both intact and cleared, disarticulated specimens, I have found no cases of fusion between the mesepisternum and mesepimeron. Both mesopleural sclerites may be smooth, wrinkled, punctate, and glabrous or pubescent. In *Asamangulia* the surface has fine microreticulations in addition to larger punctation.

Metapleuron (fig. 66, char. 123). The *metepimeron* is hidden under the elytra as in other beetles. The *metepisternum* is usually exposed, but in *Anisostena*, *Delocrania*, and *Dorcathispa* it is hidden because the elytra extends to the lateral margin of the metasternum. In *Anisostena* the elytra fits into a groove under the length of the lateral margin that completely covers the *metepisternum*. In *Delocrania* and *Dorcathispa*, the elytra abut directly with the metasternal lateral margin, hiding the metepisternum.

The surface texture of the metepisternum is usually smooth (e.g., *Acromis*), but it can be finely or coarsely punctate posteriorly (e.g., *Chalepus*) or throughout (e.g., *Charidotella*). Some cassidines have the anterior surface protuberant or the entire surface broadly depressed (e.g., *Chelymorpha*). In some taxa a protuberance from the anterior surface metepisternum overlaps the epipleural ridge, thus locking the elytra into position (e.g., fig. 66D). In *Basiprionota*, the lock is slightly different with a slight lobe from the lateral margin of the metepisternum extending over the elytral ridge. *Epistictina* has marginal lobes off both the mesepimeron and metepisternum that overlap the epipleural ridge. In *Paratrikona* and *Dorynota*, the lock is reversed with a lobe off the epipleural ridge nested in a cavity in the anterior mesepisternal surface.

The relationship of the meso- and meta-pleural sclerites provides a significant character in Cassidinae s.str. Spaeth, as translated by Hincks (1952), separated tribes (couplet 1) according to the fusion or separation of the metepisternum and mesepimeron, and diagnosed the fused state for Delocraniini, Hemisphaerotini, Imatidiini, Notosacanthini and Spilophorini. Borowiec (1995) indicated that Hincks' assessment was incorrect, and his character 0 treated the metepisternum as fused with the metepimeron in this group of tribes, and the metepisternal suture as lacking. In my examination of both intact and disarticulated specimens, I found that the mesepimeron and mesepisternum may be fused, with the mesopleural suture discernible or evanescent. However, I found these sclerites to be separated in *Calyptocephala* and *Spilophora* (Spilophorini), and in *Hemisphaerota* and *Spaethiella* (Hemisphaerotini), taxa indicated as fused by

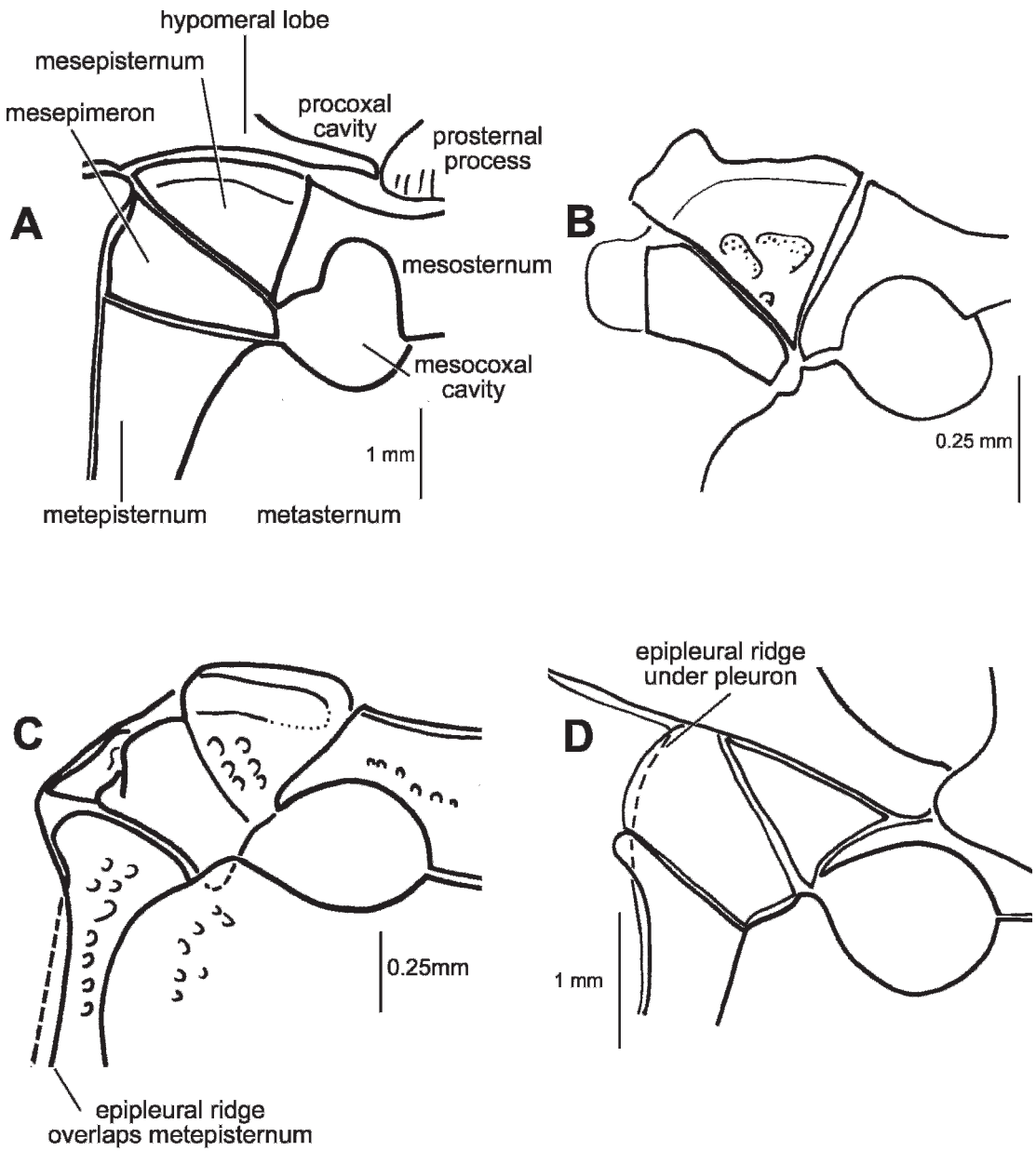


Fig. 66. Mesopleuron of Cassidinae. A. *Alurnus* sp. B. *Anoplites* sp. C. *Asmangulia cuspidata*. D. *Aspidimorpha miliaris*.

Hincks (1952). Borowiec (1995) also appears to be incorrect since I found the mesepimeron and metepisternum to be distinct sclerites throughout Cassidinae (e.g., *Hemisphaerota*, fig. 36B). Finally the term “metepisternal suture” should be referred to by the standard terminology, metapleural suture (Snodgrass,

1935: fig. 102). The metepimeron is usually covered by the elytra, with the elytral margin meeting a well-defined metapleural suture. This region of the cassidine body warrants further study.

Metasternum (chars. 124–127). This is usually rounded or flattened, with the ante-

rior and posterior margins sub-equal, and the medial and lateral lengths equal or sub-equal. More precisely, the base is slightly wider than the apex, with the lateral margins curved and slightly convergent anteriorly. In most cassidines, the lateral margin is slightly longer than the length along the medial line. In *Eurispia*, the medial length appears longer than the lateral marginal length. In *Elytrogona*, the metasternum is highly distorted and protuberant, with the lateral margin almost twice as long as the medial length. The median longitudinal groove is impressed (e.g., *Cephalodonta*) or faint (e.g., *Charidotella*), and it may extend from the anterior to the posterior margin or become evanescent before the anterior margin. The relative proportions of length and width vary, with some having the metasternum longer at the midline than half its width (e.g., *Callistola*), and others having the medial length shorter than half the width (e.g., *Calyptocephala*). In *Exothispa*, the anterolateral corner of the metasternum is projected into a rounded lobe that overlaps the mesepimeron. The metasternal surface is shallowly convex in some cassidines (e.g., *Callistola* and *Calyptocephala*). In some (e.g., *Cephalodonta*) the surface is rounded, with the lateral margins in the vertical plane. In *Basipta* the metasternal surface is protuberant posterolaterally. In addition to such protuberances, the surface may be punctate and/or striate (e.g., *Ceratispa*). In *Charidotella*, the lateral area has fine recumbent hairs and the post-coxal margin is lined with a row of punctures.

Anterior Metacoxal Process. In most cassidines, the process is flat or very weakly notched. In *Elytrogona* and *Stoiba*, it is deeply notched and receives the mesosternal process. These genera are flightless and this feature may be part of a syndrome of morphological changes in the pterothorax associated with flightlessness. Other changes include distortion of the metasternal surface, narrowing of the metasternal length (the lateral margin is twice as long as the medial length in *Elytrogona*), a deeply impressed medial longitudinal line, a long abdominal intercoxal process, an anterior lobe in the metepimeron that locks the elytra (*Elytrogona*), and wing reduction and loss in both genera.

Longitudinal compaction appears to be a trend in the cassidine thorax. This is achieved in two ways. First, the prosternal hypomeral lobe may overlap the mesosternum, reducing the longitudinal distance between the pro- and mesocoxa. In extreme cases, the hypomeral lobe may reach as far as the mesocoxal margins (e.g., *Acromis*). Second, the metasternal length varies, with the length along the medial line becoming shorter relative to the width. Thus, the distance between the meso- and metacoxae is shortened.

ELYTRA (figs. 67–69; characters 128–156)

Cassidine elytra are fully developed and completely cover the abdomen in dorsal aspect. Generally, the elytra are strongly sclerotized, heavy, and rigid, but *Promecotheca* has thin, soft elytra (fig. 14N). Elytral coloration varies widely, as discussed under the Biology section (figs. 9–14). Most elytra are opaque, but some metallic-golden forms can have transparent margins (e.g., fig. 9F). Diversity in coloration, shape, proportions, and surface texture makes the cassidine elytra complex but rich with potential characters. No elytral characters were used in Reid (1995) or Borowiec (1995); I present 39 elytral characters for Cassidinae.

Shape. In dorsal aspect (figs. 9–11), cassidine elytra have parallel, subparallel, wedge, or rounded shapes (Gressitt, 1963; Würmli, 1975). In parallel and subparallel forms (e.g., fig. 9H), the width-length ratio is approximately 1:3 or longer, with the width consistent from the base up to the apex; at the apex, the margins are sharply rounded. Frequently, this shape is associated with a flattened lateral profile and the apex is gently curved or declivous (e.g., fig. 12G). In wedge-shaped forms (e.g., *Chalepus*), the beetle is widest at the apex, and the apical margin appears abruptly truncated. In rounded forms, the width-length ratio is 1:1 to 1:1.5, with the beetle widest at the basal margin, humeral line, or midline, and the apical margin is always rounded (e.g., figs. 10 A, B, E, G, I, K).

In lateral aspect, the elytral profile may be flattened, rounded or arcuate (figs. 12G–K, 13, 14). *Elytrogona* has inflated globose elytra

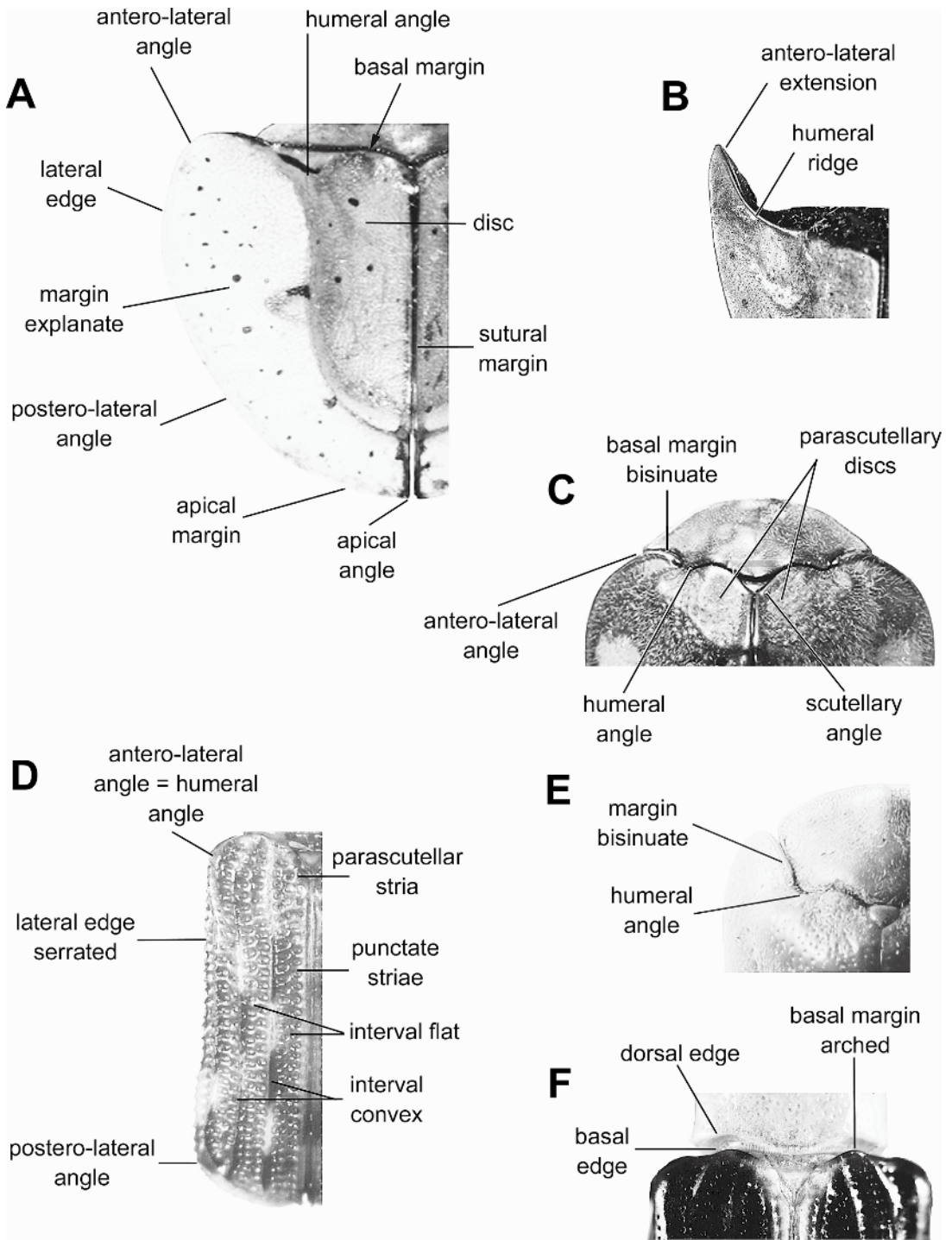


Fig. 67. Elytra of Cassidinae, dorsal aspect. A. *Acromis sparsa*, female. B. *Acromis venosa*, male. C. *Oxyndera biplagiata*. D. *Anoplites inaequalis*. E. *Basipta glauca*. F. *Callistola speciosa*.

(fig. 10J), which may be correlated with flightlessness (Chaboo, 2000). Arcuate forms are highest along the post-scutellar area (e.g., *Psalidonota*). This *post-scutellar protuberance* can be greatly extended, forming a spine (e.g., fig. 13I) or an umbo (e.g., fig. 14H). In addition to the post-scutellar spine, *Dorynota* has another distinctive elytral feature, a transverse ridge extending from the humerus across the margin to the anterolateral angle (fig. 8E). In *Canistra*, *Dolichotoma* and *Oxy-nodera*, there are paired flattened elytral discs adjacent to the mesoscutellum and extending to the post-scutellar protuberance. I term these *parascutellary discs* (fig. 67C).

Angles. Cassidine elytra have anterolateral, posterolateral, and sutural angles (figs. 67A–E). These angles vary in their extension and orientation and in the presence/absence of ridges, serration, spines and denticles. In most Coleoptera the humeral and anterolateral angles are usually coincident, but within Cassidinae, these angles are either separated (fig. 67A) or coincident (fig. 67D). In dorsoventrally compressed forms that lack explanate margins, they tend to be coincident. In forms with explanate margins, the humeral angle is produced at the epipleuron-disc junction. The humeral angle may be protuberant, forming a shoulder that obscures the anterolateral angle in dorsal aspect.

The separation between the explanate margin and the disc may be imperceptible, with little to distinguish the two areas dorsally. More commonly, their separation may be defined by marked changes in angulation between the disc and margin (e.g., *Aspidimorpha*), a protuberant humeral angle (e.g., *Exothispa*), and/or with a row of deeply impressed punctures (e.g., *Basipta* and *Conchylotenia*). The posterolateral angle is commonly rounded and not well defined. In a few genera this angle is drawn out as a single heavy spine (e.g., *Cephalodonta*).

Basal Margin. The elytral width at the base may be equal to the pronotum, producing a continuous lateral margin in dorsal aspect (e.g., fig. 7B, C, E, J–L; fig. 68C). The basal margin is wider than the pronotal base, in some cases up to twice as wide as the pronotal base (e.g., fig. 7A, D, 68I). The basal margin may be straight (fig. 68F), broadly arched (fig. 68J), bisinuate (fig. 68C,

G), or variously sinuate. In straight forms, the margin may be oriented transversely (e.g., *Delocrania*) or gently antieriad. Arched basal margins frequently overlap the pronotal basal margin, partially obscuring the latter (e.g., *Aproidea* and *Callistola*); in such cases, the elytral edge is inflected ventrad, and the pronotum forms a secondary dorsal edge with the elytra (fig. 67F). In some sinuate forms the elytral base at the epipleuron extends gently antieriad (e.g., *Spaethiella*) or sharply antieriad (e.g., *Goniochenia*). In bisinuate forms, the base is divided into two more or less equal sections with three angles, the anterolateral angle, a medial angle (which corresponds ventrally to the epipleural ridge) and a posterior angle (at the mesoscutellum) (fig. 67C, E). The two sections of the margin may be convex and tightly fitted with corresponding concavities in the pronotal basal margin (fig. 67C), or the outer section may be straight (fig. 67E).

The surface texture of the basal margin can be smooth (fig. 68A) or crenulate (fig. 68B). Crenulation can extend along the entire margin (e.g., *Basiprionota*, *Conchylotenia*, *Epistictina*), over short sections (e.g., *Aspidimorpha*), or from the mesoscutellum and tapering off near the anterolateral angle (e.g., *Asteriza*). Elytral basal crenulation appears to be independent of pronotal posterior marginal crenulation; for example, *Basiprionota* has both the pronotal posterior and elytral basal margins crenulate. *Dorcatthispa* has a row of long spines along the basal margin.

Lateral Margin. The development of the margin varies widely within Cassidinae. In many species (e.g., *Trichispa*) the lateral margin appears coincident with the edge of the elytral disc. In some species (e.g., *Alurnus* and *Odontota*) the margin forms a narrow gutter bordering the disc. Where the margin is coincident with the discal edge or it is very narrow, the epipleural ridge is coincident with the edge of the elytra ventrally.

Many cassidines have the margin explanate, and the extent of this margin varies widely. It may be as wide as the disc or wider than the disc (e.g., *Acromis*). Some genera, (e.g., *Omaspides*) exhibit interspecific variation in this relative ratio of disc-margin width. The marginal width may be consistent

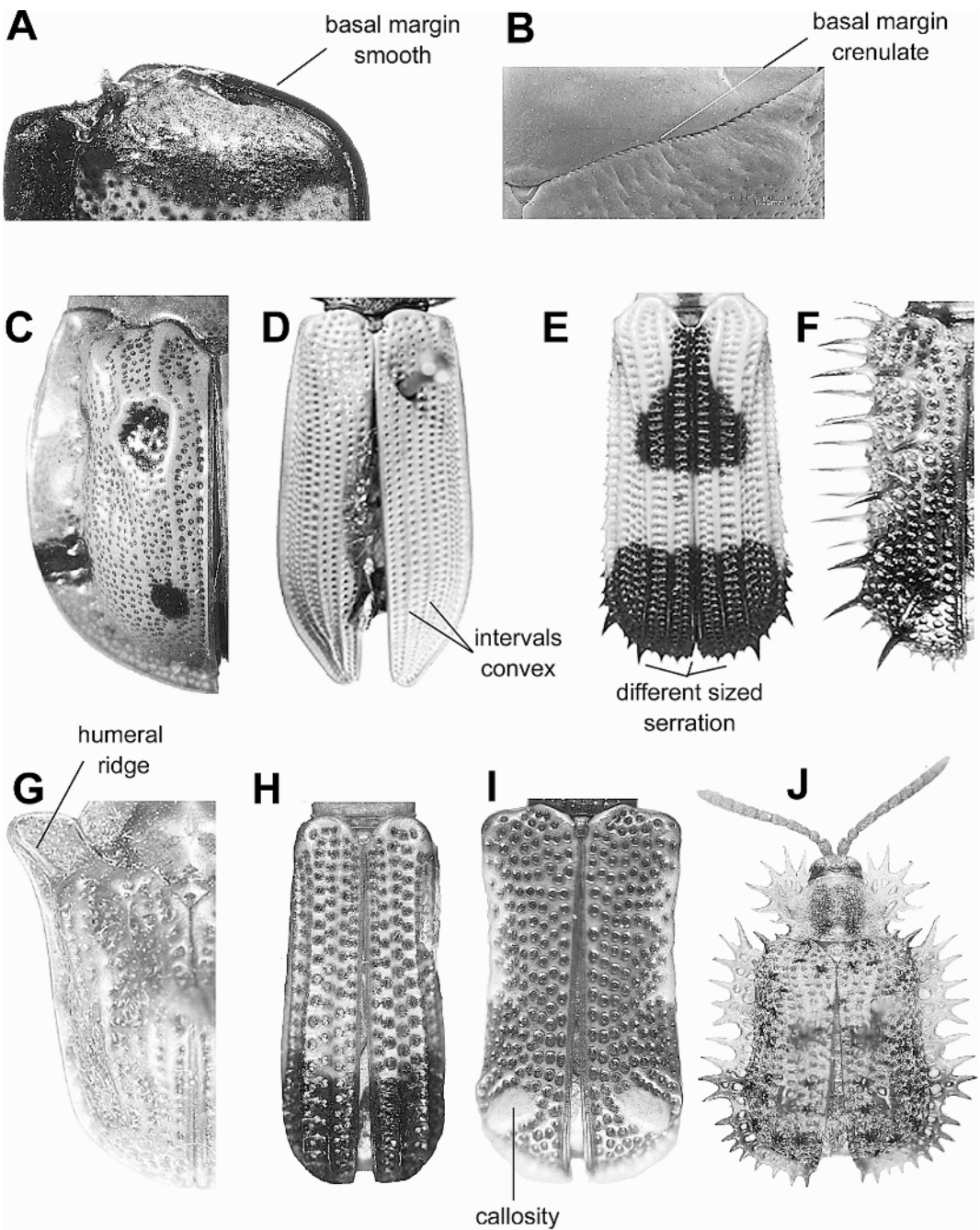


Fig. 68. Elytra of Cassidinae, dorsal aspect. A. *Canistra plagosa*. B. *Physonota* sp. C. *Basiprionota quadriimpressa*. D. *Botryonopa* sp. E. *Chalepus* sp. F. *Dactylispa* sp. G. *Dorynota* sp. H. *Klitispa opacicollis*. I. *Scoloenopla* sp. J. Undetermined sp.

from anterior to posterior or it may be widened or narrowed posteriorly. Its orientation, punctation and setation are variable. When the margin is explanate, the external elytral edge and the epipleural ridge are separated, with the latter in contact with the pleuron. In some cases, a sub-elytral cavity is created, bounded by the ventrolaterally or ventrally oriented elytral margin, the epipleuron and epipleural ridge. Hemisphaerotes retract their legs into this cavity, and early instar larva may be hidden here in subsocial cassidines. Crowson (1981) suggested that this explanate body form of cassidines probably helps to break up the outline in dorsal aspect and makes the animal difficult to lift once the margin is flattened against the substrate.

Males in the genus *Acromis* have elytra that are unique among cassidines in two ways. The lateral margin has a thin anterior section that will often tear during male combat for females; many museum specimens have holes in the elytra as a result (fig. 5B). The anterolateral angle is also greatly extended anteriorly, producing a spine-like lobe used in male combats (fig. 67B).

The surface texture of the lateral edge varies. In many cassidines, it is smooth. In *Baliosus*, *Chalepus* and *Uroplata*, the edge is entirely serrate and has a saw-like appearance. Lateral serration in *Demotispa* increases in density posteriorly. The lateral edge can also be spinose (e.g., *Dorcathispa*). *Trichispa* has a few short spines along the anterior section of the lateral edge, as well as sparse irregular serration in the posterior section. In *Dactylispa* the lateral edge is spinose from base to apex, with spines slender and twice as long as the interval between them. The lateral edge of *Delocrania* has a unique arrangement of pores with single bristles at regular intervals. In some *Dactylispa* and *Platypria* species the elytral texture is complicated with the margin highly sinuate, scalloped and spinose, and the dorsum has large porous punctation (fig. 68F).

Sutural Margin. The lateral profile of this margin may be flattened, arcuate, or rounded. In arched and rounded forms, the elytral dome is highest in the post-scutellar area, and the dome may also be extended into a spine

or umbo (e.g., *Batonota* and *Dorynota*). In *Elytrogana*, the dome is highest at the midpoint of the suture. The sutural margin is commonly flat but it is convex and carinate posteriorly in *Anisostena*.

The elytral suture of Coleoptera may have a tongue-and-groove mechanism for locking the elytra together. This mechanism is very tight in *Eytrogona* and *Stoiba*, making the elytra difficult to open, and it may be related to flightlessness in these genera. The sutural margin at the apex may be continuous or indented, and rounded or drawn out into broad lobes or spines. In some genera, the suture terminates in a short denticle (e.g., *Botryonopa*). In *Aproida*, the apical margin is drawn out into a heavy, posteriorly directed spine, and the sutural margin has a small, ventrally directed denticle.

Apical Margin (fig. 69A–E). The apex of the elytra may be rounded (fig. 69A), truncated (fig. 69B–C), or indented (fig. 69E). In truncated forms, the margin can be entirely or partly (medially) truncated. Wedge-shaped forms have the apical margins as the widest part of the elytra, and the posterolateral angles are developed. The apical angle may be extended into a single, heavy spine (fig. 69D). The sutural margin may also terminate with a small denticle (fig. 69E).

The texture of the apical margin may be smooth, serrate, or spinose. *Chalepus* and *Xenochalepus* have two distinct sizes of serration on the apical margin whereas *Demotispa* and *Uroplata* have one size of serration. *Dorcathispa* has a row of spines along the apical margin. *Promecothea* has some long erect hairs on the apex.

Surface Texture. Cassidinae elytra may be smooth, or punctate, spinose and tuberculate. Texture patterns between the elytra and pronotum, and between the elytral disc and margin appear to be independent. **Punctation** varies in sizes, shapes, individuality, degree of impression, and arrangement. Punctures can be round or irregularly shaped, and distinct or confluent. Punctures may be barely perceptible (e.g., *Alurnus*), shallow (e.g., *Hispodonta*), deeply impressed (e.g., *Sceloenopla*), fenestrate (e.g., *Cyperispa*, *Dactylispa*), or even porous (e.g., *Notosacantha*). They may be arranged in a confused way (e.g., *Alurnus*), in small, rounded regular

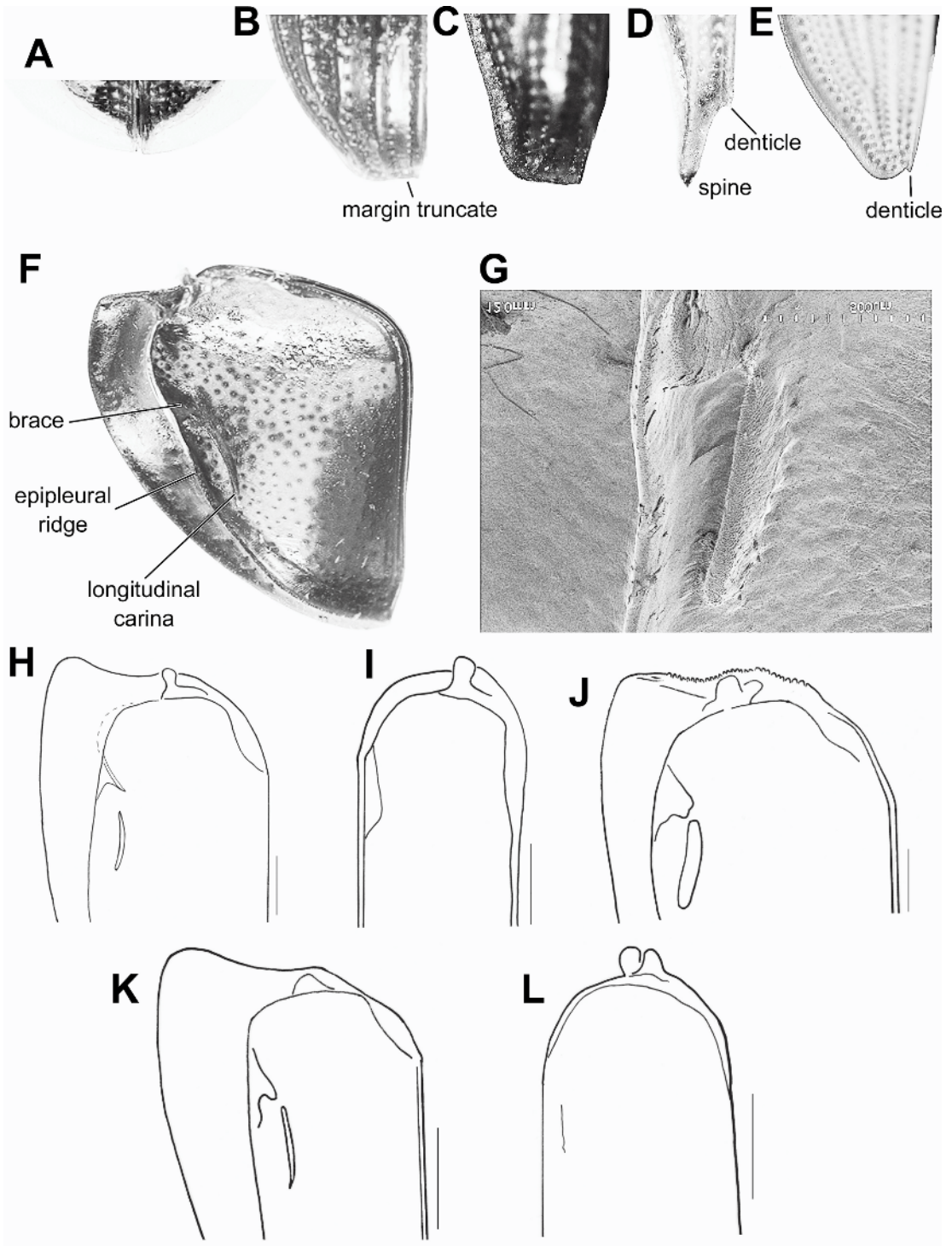


Fig. 69. Elytra of Cassidinae, dorsal aspect. A. *Coptocyclus dorsata*. B. *Callistola* sp. C. *Ceratispa* sp. D. *Eurispia* sp. E. *Botryonopa* sp. Ventral aspect, scale bars = 1 mm. F. *Canistra plagosa*. G. *Paraselenis flava*, scanning electron micrograph. H. *Agroiconota bivittata*. I. *Aproidea balyi*. J. *Asteriza flavicornis*. K. *Charidotella bicolor*. L. *Promecotheca papuana*.

clusters (e.g., *Agenysa*), or, more commonly, in well-defined discrete longitudinal rows along striae (e.g., *Dorcathispa*). Punctuation arrangements of the disc and margin are independent; for example, discal punctures of *Calyptocephala* are in rows, whereas marginal punctures are confused. In *Delocrania*, discal punctures are small and rows are difficult to distinguish whereas marginal punctures are large, deeply impressed and arranged in rows that are separated transversely by slightly carinate joints. In *Arescus*, punctuation is in rows medially but these rows become confused in the posterolateral area; in *Anisodera*, puncture rows are well defined basally and medially, but become obsolete posteriorly with the insertion of additional rows; in *Aspidimorpha*, the external punctures are in rows but medial punctures are confused. In *Conchylotenia*, punctures are widely separated and rows are vaguely defined. In *Prosopodonta*, the anterior and central parts of the discal surface are impunctate but puncture outlines are discernible within the cuticle. These puncture rows emerge at the surface apically.

Some cassidine elytra are spinose, tuberculate, and denticulate, or they even have these textures combined together with punctuation and pubescence. This produces much complexity to the general dorsal appearance. In *Asmangulia*, the basal and lateral margins are spinose whereas the dorsum is deeply punctate-striate and tuberculate. In *Dactylispa*, the disc has irregularly arranged, fenestrate punctures and spines in two sizes, long and short. The lateral and apical margins are also spinose. In *Trichispa*, punctures are fenestrate and irregularly arranged, and the disc and lateral and apical margins are spinose. Some punctures have a single pore with a short, stiff bristle; the bristle appears to be flattened with a slightly expanded apex. In spinose elytra, the spines are unbranched and vary in length and interval distance.

The elytra often have striae and intervals. Striae are regarded as external manifestations of the columella (internal connections between dorsal and ventral surfaces of the elytra) (Spilman, 1971). Intervals may represent the ancestral wing veins (Spilman, 1971) but elytra are so modified that it is impossible to be conclusive about the derivation of

intervals. Striae and intervals alternate and are generally numbered from the sutural stria laterad (e.g., Uhmman, 1954). In Cassidinae, when punctures are arranged in rows (punctate-striate), the striae and intervals can be detected. Intervals vary in number, development, convexity, and surface texture (smooth, tuberculate, or spinose). Interval widths are commonly more or less equal to those of striae, but they are almost twice as wide as the latter in *Prenea*.

Where striae are apparent, the first one is often less than half the length of a complete stria and has been referred to as the scutellary striole in Cassidinae (Würmli, 1975) (fig. 69D) and scutellar stria in other Coleopteran families (see Will, 2002). These terms are not precise since the mesoscutellum lacks striae. For precision and consistency of homology statements, Will (2002) argued for the use of the term “*parascutellar stria*”, which I follow here. The presence of the parascutellar stria has been noted in Anisoderini, Aprodini, Botryonopini, Callispini, Callohispieni, Cryptonychini, Eurispini, Leptispini, and Oncocephalini (Würmli, 1975) and Prosopodontini (Maulik, 1931a), and its absence has been noted in Exothispini, Promecothecini, Coelaenomenoderini and Gonophorini (Würmli, 1975). Presence/absence of the parascutellar stria has not been commonly used in the taxonomy of Cassidinae s.str., although it is mentioned in the description of *Oocassida* (Maulik, 1919). The number of punctures within the parascutellar stria varies among genera; for example, 2 found in *Octotoma*, 3 in *Conchylotenia*, 4 in *Chalepus*, 7 in *Anisodera*, 9 in *Charidotella*, and 13 in *Demotispa*, and 15 in *Callistola*. The number of punctures within the parascutellar stria can also vary between two elytra; for example, *Estigmene* has seven punctures on the left elytron and four on the right one.

Intervals. These may be smooth or coarse (dentate, serrate, spinose, or setose), and flat or convex. Patterns of surface texture and convexity can vary within the length of the interval and between intervals. In *Lasiochila* each interval is convex. In *Anisostena*, *Anoplites*, *Baliosus*, *Callistola*, *Klitispa*, *Sceoloenopla*, and *Uroplata*, the intervals have an alternate arrangement of smooth and convex forms; intervals I, III and V are smooth and

flat; intervals II, IV, and VI are smooth basally but convex beyond the humerus. These intervals may also be carinate posteriorly and connected at their apices by a single transverse carina. This transverse carina and intervals IV and VI are usually dentate; in *Klitispa* they are smooth. In *Anisostena*, interval III terminates immediately before this transverse carina. In *Anisodera*, only alternate intervals appear convex in their posterior sections. In *Xenochalepus* all intervals are smooth; the second interval (= the first convex one) is convex, prominent and shiny black; the sixth interval is slightly carinate basally but flat distally; the eight interval is slightly carinate from base to apex; all other intervals are flat; only the second interval is shiny black whereas all others are matte black. In *Chalepus* only the second interval (= the first convex one) has serration at its apex.

Some cassidines can have the disc with irregular convex lines and wrinkles, or with a net-like arrangement of ridges. *Octotoma* has carinate wrinkles. *Anepsiomorpha* has short, irregular, slightly convex lines, whereas *Agenysa* and *Poecilaspis* have a convex net-like pattern. *Notosacantha* also has a somewhat carinate, irregular lattice. These patterns are diverse and are not considered homologous. A second net-like pattern is also discernible within the elytral disc (e.g., *Aspidimorpha*) or within the elytral margin (e.g., *Paratrikona*).

Pubescence. Most cassidines are glabrous. In *Dorcathispa*, deep elytral punctures have a single long bristle, usually on the margin of the puncture. The bristle is stiff and erect, with a somewhat flattened appearance and a slightly inflated apex. *Delocrania* has single, long bristles at regular intervals along the lateral edge. In *Demotispa*, each tooth of the saw-like apical margin has a single long subapical bristle. The body of *Trichispa* has short, dense pubescence over the entire body, including the elytra. Fine pubescence occurs in *Cyperispa*, *Oxynodera*, and *Promecothea*. In *Cyperispa* hairs are bent and form a sparse fringe along the lateral edge and are denser at the discal apex. In *Promecothea*, pubescence is erect and concentrated at the discal apex.

Michalski (1995) first described the thickened transverse brace and the longitudinal

carina often found on the internal side of the epipleural ridge structure in *Stolaini*. In the anterior third or midway along the venter of the elytra, a thickened transverse brace and a longitudinal carina are often found on the internal side of the epipleural ridge (fig. 69F–L). The carina varies in length, sometimes extending close to the brace, but not connecting with, the brace. In some cassidines, the carina joins the brace, and together they form a groove bordered internally by the carina, anteriorly by the brace, externally by the epipleural ridge, and open posteriorly. The elevation of both carina and brace varies, as does the distance between the carina and epipleural ridge. The carina height is short in *Chirida* but taller in *Asteriza*. Usually the carina is close to the epipleural ridge, positioned less than one fifth of the elytral width from the ridge. In *Stenispa* the carina is more distant from the ridge, positioned at about one fourth of the elytral width. Both the carina and brace may be entirely or partially covered with dense microtrichia.

Elytral Locking Mechanisms in Cassidinae. Morphological devices for locking the Coleopteran elytra to the body include a metepisternal muscle controlling the elytra (Breed, 1903), a tight sutural groove (Packard, 1898; Sharp, 1899; Breed, 1903; Breed and Ball, 1915), binding spicules (on the venter of the elytra) (Hammond, 1988; Samuelson, 1994, 1996; Bouchard and Gorb, 2000), insertion of the elytral anterior margin under the mesoscutellum (Breed and Ball, 1915), and insertion of the elytral epipleural ridge under or over ridges on the metepisternum (Breed and Ball, 1915).

Although a special metepisternal muscle has not been described in Cassidinae, many other elytral locks appear in the group. Morphology of these structures is described above. The *sutural groove* can be extremely tightly fitted in *Elytrogona* and some *Stoiba* species. A *mesepimeral lobe lock* holds the epipleural ridge in *Aspidimorpha* (fig. 66D). A *metepisternal anterior lobe lock* overlaps and holds the epipleural ridge (e.g., *Basipta*). The *metepisternal lateral margin lock* overlaps and holds the epipleural ridge in *Basipri-nota*. The *metasternal lateral marginal lock* performs a similar function in *Anisostena*.

The *epipleural ridge lock* inserts under or over ridges or cavities on the metepisternum (e.g., *Dorynota*). The *longitudinal ventral carina* (fig. 69F–L) near the epipleural ridge may lock the elytra to the metathoracic pleuron and/or to the pleuron of the first abdominal segment; the micro-trichiate surface may enhance the locking mechanism. Basolateral patches of *binding microtrichia* have been described in 27 species of Cassidinae (Samuelson, 1994, 1996). These frictional surfaces vary in their distribution, size, and general shapes and in the density and directionality of microtrichia (Hammond, 1979; Samuelson, 1994, 1996). Finally, the *bisinate basal margin* in some genera (fig. 69C, E) may also check elytral opening.

HINDWINGS (figs. 70–72; characters 157–159)

In the first broadly comparative study of hindwings in Chrysomeloidea, Jolivet (1954) sampled 24 species in 32 genera from 17 cassidine tribes. His illustrations show variation in wing development, coloration, vein development, cell development and sizes, and vein connections. The anal field development appears to vary, with reductions in *Leptispa filiformis* Germar and *Octhispa (Hepthispa) limbata* Baly. Suzuki (1969a, 1969b, 1970a, 1970b, 1994) has described additional taxa in his discussions of chrysomelid hindwing evolution. In *Cassidinae*, hindwings have been described for *Alurnus* spp. (Suzuki, 1994), *Jonthonota mexicana* (Sanderson and King, 1951), *Thlaspidea cribrosa* (Boheman) (Suzuki, 1994), *Chrysochus auratus* (Wilson, 1934), and *Acromis sparsa* (Chaboo, 2001). Chen (1940) proposed that Cassidinae s.str. and Hispinae s.str. share vein Cu1 continuous with anal cell 2, and he pointed out that the anterior cross vein is usually normal in Cassidinae s.str. but often atrophied in Hispinae s.str. Reid (1995) identified seven characters (chars. 18–24) from the hindwing for his higher-level phylogenetic analysis, and these were homogenous for Cassidinae.

The hindwing is commonly fully developed in Cassidinae. The veins Cu, Sc, RA, r3, MP, CuA, AA and AP₃₊₄ are usually present. The radial cell (rc) is developed and varies in shape (triangular or rounded) and size. The cell is relatively large in *Arescus* (fig. 70K),

small in *Asmangulia* (fig. 70L), and barely discernible in *Delocrania* and *Philaspis*. The cell is commonly closed, but it may be open due to reduced sclerotization of RA₃₊₄. The former positions of RP₁ and RP₂ may be marked as dusky lines, while RP₃₊₄ and r4 are absent. The presence or absence of trichiation on the veins has been used to identify species (Riley et al., 2001).

Cassidines show greatest heterogeneity in the development of veins MP4, CuA, and AA, and in cubital anal cells 1 and 2. These veins and structures are all present in *Hemisphaerota palmarum* (fig. 34B). Reductions of these veins results in open cubito-anal cells. CuA cell 2 is more commonly open than CuA cell 1, for example, *Anisodera* (fig. 70H) and *Oediopalpa* (fig. 72F). In some taxa, the veins are further reduced and both cells are lacking, for example, *Anoplites* (fig. 70I) and *Calyptocephala* (fig. 71I).

Jolivet and Hawkeswood (1995) listed *Delocrania* and *Elytrogona* as apterous, whereas *Stoiba*, *Fornicassis*, *Cassida (Pilemostoma)* and *Cassida (Mionycha)* are micropterous. Based on specimen examinations, I determined that *Elytrogona* species range from brachypterous to apterous (Chaboo, 2000), all *Delocrania* species have fully developed wing, and *Stoiba* species range from fully developed to micropterous wings.

Wing coloration (tinting) varies across the wing, with duskiness or stains marking original position of lost veins. The apical field is generally darker than the proximal portion, and the areas around the radial cell and central field can be particularly dark. The terminal portions of veins AA, AP, CuA, MP4, and the medial spur may taper off into duskiness.

LEGS (fig. 73; characters 160–188)

In his key to cassidine tribes, Hincks (1952) defined four characters from the leg: claws divergent (commonly) or parallel (a synapomorphy for Dorynotini); tarsomere III with apical margin expanded and hiding the claw base (a synapomorphy for Eugeny-sini); claw base simple or appendiculate; and inner and outer basal margins of claws simple, striate, or appendiculate. Monophyly of Botryonopini is based on its femoral tooth (Maulik, 1919; Würmli, 1975), and mono-

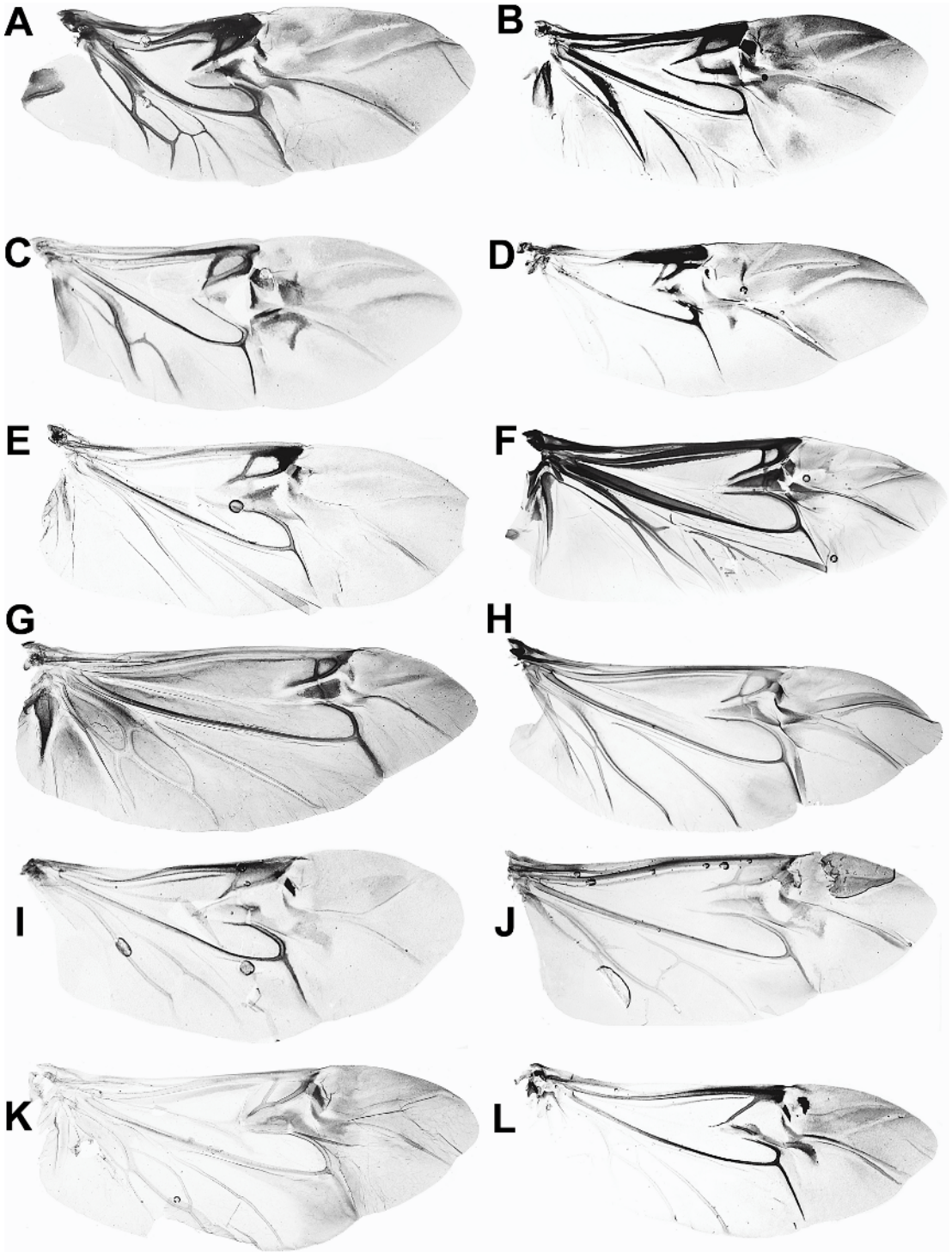


Fig. 70. Wings of Chrysomelidae. A. *Lamprosoma* sp. 1. B. *Lema trivittata*. C. *Ophraella* sp. 1. D. *Pachybrachis* sp. 1. E. *Plataumaris* sp. 1. F. *Sagra* sp. 1. G, L. Cassidinae. G. *Alurnus bipunctatus*. H. *Anisodera guerini*. I. *Anoplites inaequalis*. J. *Aproida balyi*. K. *Arescus* sp. 1. L. *Asmangulia* sp. 1.

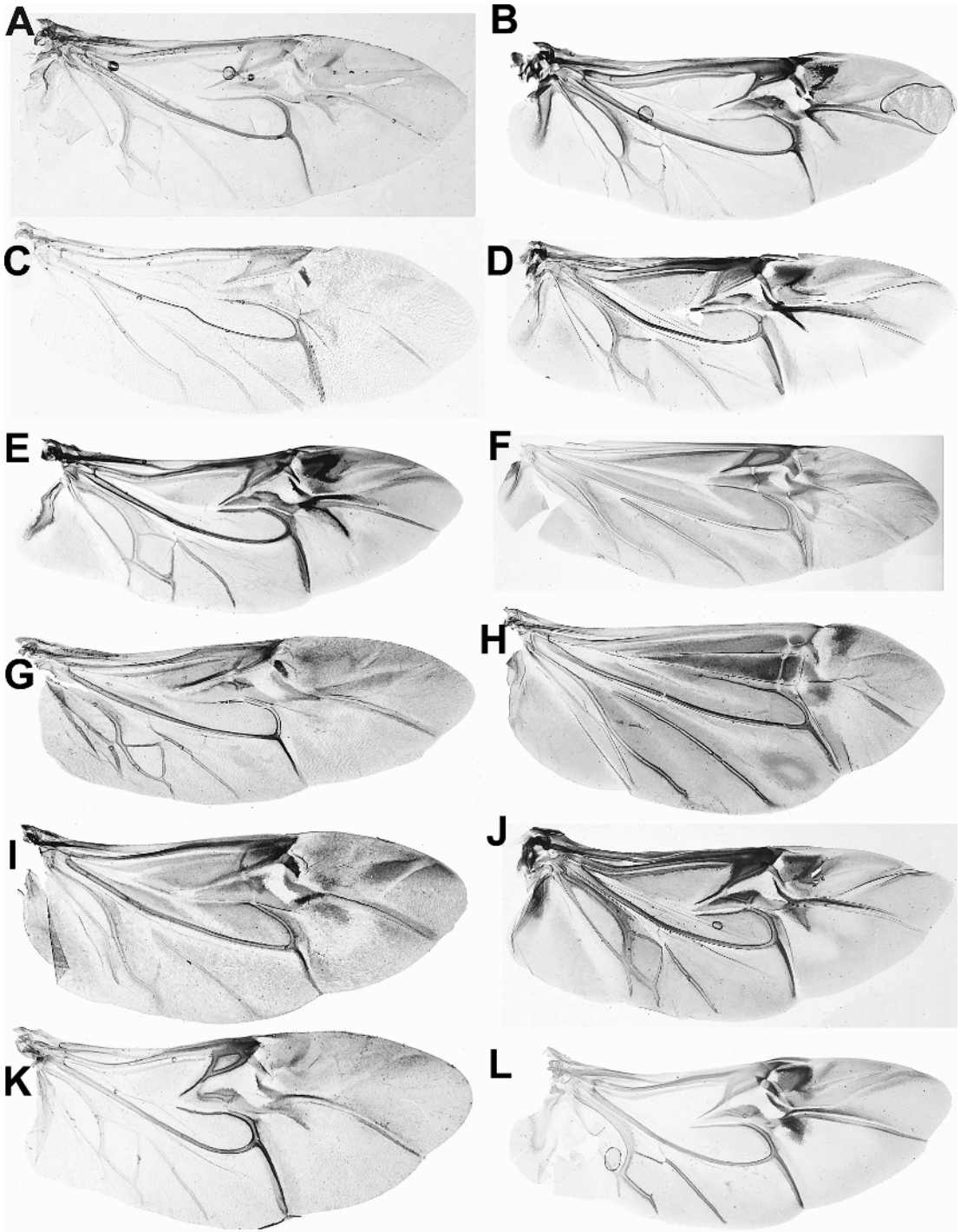


Fig. 71. Hindwings of Cassidinae. A. *Aspidimorpha miliaris*. B. *Asteriza flavicornis*. C. *Baliosus californicus*. D. *Basiprionota chinensis*. E. *Batonota* sp. 1. F. *Botryonopa foveicollis*. G. *Calliaspis rubra*. H. *Callistola speciosa fasciata*. I. *Calyptocephala nigricans*. J. *Canistra plagosa*. K. *Charidotella bicolor*. L. *Coptocyclus dorsoplagiata*.

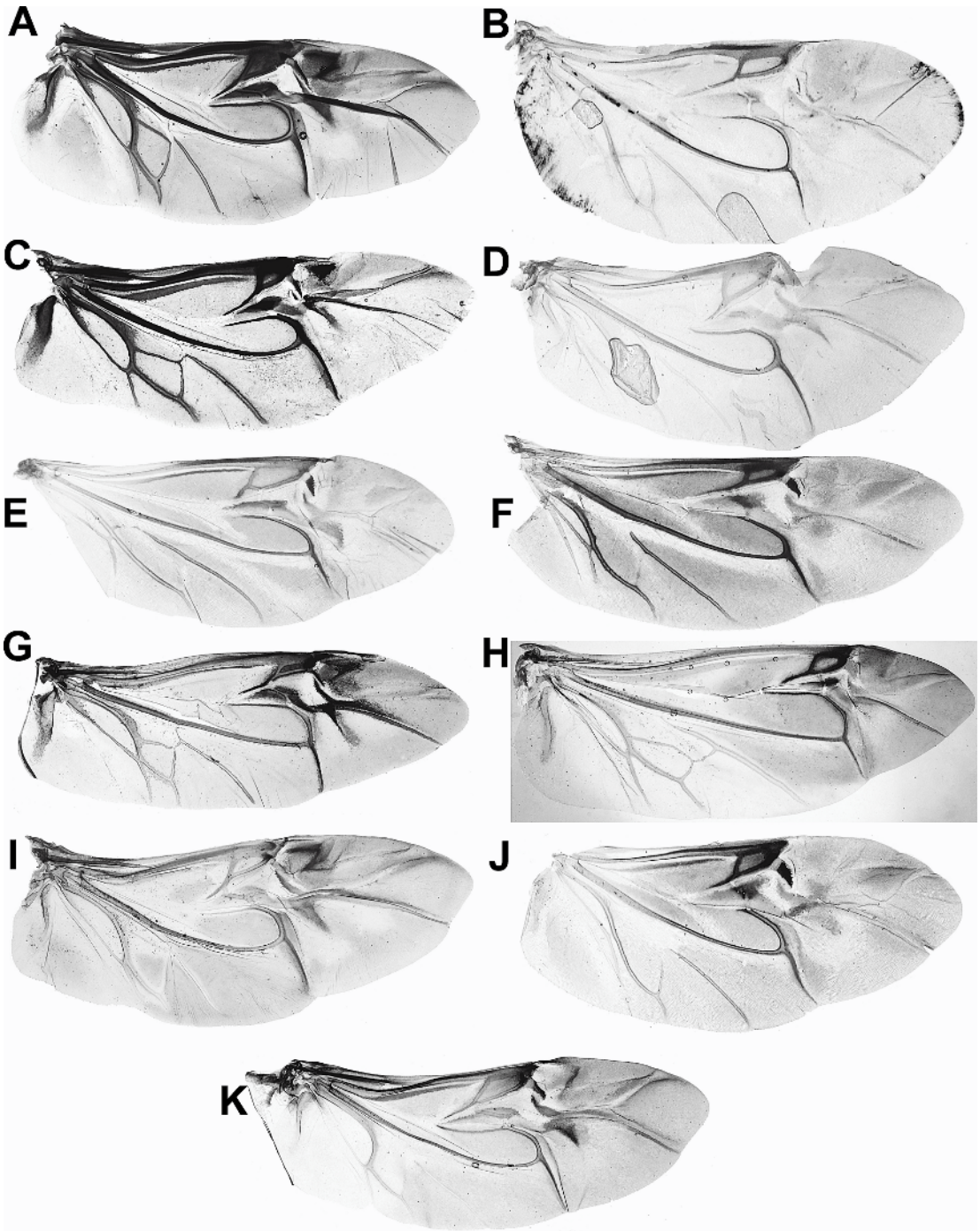


Fig. 72. Hindwings of Cassidinae. **A.** *Dolichotoma* sp. 1. **B.** *Imatidium capense*. **C.** *Ischyrosomyx oblonga*. **D.** *Jonthonota maculata*. **E.** *Odontota dorsalis*. **F.** *Oediopalpa guerini*. **G.** *Physonota* sp. 1. **H.** *Plautyauchenia deyrollei*. **I.** *Prenea strigata*. **J.** *Spilophora aequatoriensis*. **K.** *Syngambria bivulnerata*.

phyly of Promecothecini is based on its long, toothed hindfemur (Würmli, 1975).

Reid (1995) considered chrysomelid leg morphology to be relatively unvariable, and he defined three characters (chars. 28–30): the presence/absence of the tarsal empodium, bifid tarsal setae, and spatulate tarsal setae. His tarsal empodium character is not discussed here since Cassidinae and my sampled outgroups lack this feature. In their analysis of galerucine-alticine relationships, Lingafelter and Konstantinov (2000) proposed eight leg characters: relative proportions of tarsomeres; mesocoxal position and separation; distinction of the trochantin; intermetacoxal distance; metafemoral spring; and metatibial cross-section and metabial notch. These sources provide a starting pointing for searching for leg characters in Cassidinae.

Leg morphology appears heterogenous across Cassidinae, but all members have lost tarsomere IV (perhaps by fusion to the base of tarsomere V). The pro-, meso-, and metalegs do not differ greatly except in overall length, with the metalegs being slightly longer than the preceding legs. The femur is usually the longest segment, but the tibia is as long as or longer than the femur in Notosacanthini, Hemisphaerotini, Delocraniini, and Ischyrosomychini.

Coxae. The pro-, meso- and metacoxae vary in their relative sizes, shapes, prominence, and in intercoxal distance. Procoxal cavities are always closed behind by the hypomerall lobe and lateral extensions of the prosternal process, although the latter can appear very narrow (e.g., *Arescus*). Of the three pairs of legs, the inter-metacoxal distance is the shortest, separated by a narrowed abdominal intercoxal process. Intercoxal distances of the pro- and mesocoxae vary according to the development of the prosternal process. These coxae are proximate in *Arescus* due to the slender intercoxal processes, but they are more distant, almost laterally positioned in *Chalepus* and *Cyperispa*. *Procoxae* vary in shape and prominence. In most taxa, they are slightly elongate (pear-shaped) and well inserted into the coxal cavity. In a few taxa, they are globular and conical (e.g., *Arescus* and *Exothispa*). Margins of the procoxal cavities may be simple or emarginated, as discussed above. *Mesocoxae*

may also be rounded or transversely elongate. In most cassidines, they are inserted into the mesocoxal cavities. In *Arescus*, the mesocoxae are rounded, appearing globose, and protuberant. Mesocoxal cavity margins may be simple or rimmed. *Metacoxae* appear homogenous across Cassidinae.

Trochanters are usually somewhat flattened and triangular and do not appear to vary between legs, except perhaps in relative proportions. Across Cassidinae, trochanteral morphology is also similar, but in *Delocrania*, trochanters are elongate (especially the pro-trochanter) and flattened, and they appear almost as long as the coxae. In *Calyptocephala*, the metatrochanter is slightly prolonged as a medial lobe beyond its margin with the metafemur. The trochanteral surface is commonly smooth or with sparse ventral setation. *Mecistomela* has tufts of setae on its trochanters (C. Staines, personal commun.).

Femur (chars. 163–164). This is always the thickest segment of the cassidine leg, and is slightly inflated medially. In *Aproidea*, it is protuberant medioventrally, appearing slightly tuberculate. Femoral length is greater than or equal to tibial length. The cross-sectional profile may be rounded or triangular. In triangular forms, the ventral surface is somewhat flattened, with inner and outer margins weakly to strongly developed. These margins are rarely spinose (e.g., *Asamangulia*). In *Botryonopa*, the femur is compressed laterally so that the base is narrowed, and a narrow groove runs along the length. The margins of this groove are blade-like. Cassidine femora can be smooth, wrinkled or punctate, and sparsely to densely setose. Femoral setation may be unevenly distributed. *Dorcatthispa* is unusual in having both femoral and tibial surfaces spinose throughout and with erect, flattened setae similar to those found on the rest of the body. *Anisostena* has a rounded femur, with spines unevenly distributed on the medioventral face; these spines are generally short but vary slightly in sizes, and they taper off distally. In *Asamangulia*, these femoral spines are fewer, and are better developed on the pro- and meso-coxae. The tibial and femoral surfaces in *Callistola* and *Ceratispa* are shallowly punctate. *Botryonopa* (Maulik, 1919; Würmli, 1975) and *Ceratispa* have an apical femoral tooth.

Tibia (chars. 165–169). Tibial length was discussed above with femoral length. Cassidine tibiae generally have a triangular profile with the ventral surface rounded or flattened and with two margins, and the dorsal surface is rounded, angular, and ridged. In *Aproida*, they have a quadrate appearance. Tibiae are narrowest at the base and evenly tapered distally, reaching twice the width of the base. Cassidine tibiae are commonly straight, but they are strongly bowed in a few genera (e.g., *Botryonopa*) (Würmli, 1975). In *Anisostena* and *Prosopodonta* the bowed tibia and the spinose femur together resemble a nutcracker. *Asmangulia* legs have straight pro- and metatibia, but a bowed mesotibia. The *tibial apex* is inflated in *Prosopodonta*. All tibial apical margins in *Arescus* are rimmed with a row of short spines. *Notosacantha*, *Ceratispa*, and *Callistola* have a single spine on the mesal side of the apical margin. In the latter two genera this spine is small and pointed whereas in *Notosacantha* it is longer and hook-like. *Oediopalpa* has the mesotibia with an apical spine. These apical spines are not considered homologous with the sub-apical lobe in *Sagra*.

The dorsoapical surface of the tibia may be flattened or notched. The tibial notch or excavation notch receives the tarsus; it varies in size and depth, and its margin appears variously carinate. The margins may be slightly carinate in various combinations; for example, in *Asamangulia*, the basal margin is developed and slightly hooklike. *Arescus* has an unusual tibial apex where the notch appears enlarged because of the expansion of the anterior margin of the proleg (in dorsal aspect) and the posterior margin of the meso- and metalegs. This expansion is thin and gives the apex an asymmetrical appearance. Additionally the margin has a row of short spines. The tibial notch surface is commonly smooth, but it is finely microreticulate in *Botryonopa*. In *Ceratispa* both medial and external margins have a deep notch, with the medial notch slightly longer than the external notch. The external notch receives the tarsus but the medial one does not correspond with any particular structure. Tibiae may be smooth (e.g., *Arescus*), but they are more commonly sparsely setose proximally and more densely

setose distally, especially in the apicoventral area. In some species tibiae may be slightly transversely or longitudinally wrinkled.

Tarsomeres (chars. 170–188). Cassidines share the tarsal formula 4-4-4, because tarsomere IV is lost on all legs. Tarsomeres I, II, and III vary in shapes, lateral margins (expanded; rounded or straight), basal margin (rounded or sinuate), and apical margin (straight or bilobed and degree of lobation). *Tarsomere* I is usually the shortest and narrowest, almost half the width of tarsomere III, and the apex is usually slightly wider than the base. In *Arescus*, it is as long as tarsomere II. In *Cyperispa*, it is expanded and as long as tarsomere II. Its *lateral margins* are commonly not expanded and are straight. In *Delocrania*, they are expanded and tarsomere I is as wide as tarsomere II. In *Eurispa*, the overall shape varies between legs, being expanded on the proleg but not on the metaleg. In some cassidines, the lateral margins of tarsomere I are of different lengths, with the posterior margin longer than the anterior margin, so the segment has an asymmetrical appearance (e.g., *Basipta* and *Cyperispa*). Tarsomere I is large in *Leptispa*. This segment may be symmetrical or asymmetrical in dorsal aspect (e.g., *Eurispa*). *Callistola* has several unusual features on its tarsus: tarsomere I is expanded and slightly asymmetrical, tarsomere II has the apical margin slightly concave and lateral margins parallel, and tarsomere III has enlarged lobes that overlap tarsomere V. The *basal margin* is indented in *Klitispa* and it corresponds with an indentation of the tibial apex. Apical margins are usually straight or slightly sinuate. Tarsomere I is usually evenly rounded in lateral profile.

Tarsomere II is usually intermediate in size and shape between tarsomeres I and II. The *apical margin* may be straight, slightly concave, or deeply bilobed with lobes initiating medially. *Lateral margins* are commonly rounded or, more rarely, parallel-sided (e.g., *Alurnus*). The *lateral profile* is commonly evenly rounded, but it has a slight medial longitudinal groove in *Alurnus*.

Tarsomere III is commonly the widest tarsal segment, almost twice as wide as tarsomere I, and it has the apical margin deeply bilobed. It is rarely narrow and with

the apex not bilobed (e.g., *Stenopodius*). Staines (1988) amended the key of Arnett (1973) with this feature. Tarsomere III may also be bilobed or simple in other chrysomelids (e.g., Donaciinae; Monrós, 1959). The lobes are commonly symmetrical but they are asymmetrical in *Anisostena* in which the posterior lobe is longer than the anterior lobe. In *Ceratispa* the dorsal medial margin of the lobes appears slightly expanded and fits closely around tarsomere V, unlike in other cassidines.

Tarsomere IV is fused to tarsomere V, and the suture is commonly lost. In a few taxa the sutural line is faintly discernible, for example, *Basiprionota* (Chen, 1973, 1985). Crowson (1981) suggested that this unique loss within Chrysomelidae might be related to the broadening of the other tarsomeres and the shortening of tarsomere V in cassidines.

Tarsomere V is elongate and either evenly cylindrical or gradually widened anteriorly. Its length varies widely; it can be short (e.g., *Notosacantha*) with the apex and claws hidden between the lobes and setation of tarsomere III. When long, the apex extends well beyond tarsomere III (e.g., 73A–E) and the claws are exposed. In some long forms, tarsomere V is arched. In Eugenyssini, the distal margin of tarsomere V is expanded dorsally and overlaps the claw bases that are therefore hidden from view (Viana, 1968). Tarsomere V may have some *ventral projections*. *Baliosus californicus* has a pair of apicobasal triangular projections whereas *Uroplata girardi* and *Chalepus* have a single process, approximately half the claw length, and positioned medially between the claws and the claw bases.

Tarsal Setation. All tarsomeres are generally sparsely setose dorsally, with a small concentration of bristles medially on the anterior margins where they overlap the following segment (e.g., *Botryonopa*). Dorsal setation is fine and soft and longer than ventral setation. Legs in *Basipta* generally have dorsal setation longer and denser than is common and its tarsomeres have a medium dense cover. Ventrally, tarsomeres I–III are flattened and densely setose, forming the *tarsal pad* (Stork, 1980; Mann and Crowson, 1981a; Chen, 1985; Verma, 1999; Schmitt, 1989). These setae may be bifid (fig. 73U)

and adhesive. The presence of bifid tarsal setae has been argued as the fundamental character supporting monophyly of Bruchidae, Sagrinae, Criocerinae, Donaciinae, Cassidinae s.str. and Hispinae s.str. (Stork, 1980; Mann and Crowson, 1981a; Schmitt, 1989). Schmitt (1989) refined this concept by pointing out the variation among these tarsomeres. In Bruchidae, Sagrinae, Criocerinae, and Donaciinae bifid setae occur only on the third tarsomere, whereas Cassidinae has them on tarsomeres I–III. Reid (1995) also suggested variation among subfamilies. Bifid tarsal setae and the adhesive oils that they secrete are discussed under Biology.

Claws (chars. 185–188). Cassidinae commonly have two claws, which are usually divergent (100° – 180°). Parallel claws have been argued as a synapomorphy for Dorynotini (Monrós and Viana, 1949; Hincks, 1952), but they appear within many other genera of Hispinae s.str. Some genera exhibit a single claw, for example, *Hispellinus* Weise, *Acymenychus* Weise (Lopatin, 1984), some gonophoriine genera (Würmli, 1975), *Eurispini* (Gressitt, 1963), and Hemisphaerotini (Monrós and Viana 1951). Bifid tarsal claws, known in other chrysomelids (e.g., *Ophraella*) have not been described in Cassidinae. Cassidine claws are usually separated but they may be basally connate (e.g., *Monochirus*; Maulik, 1919). Connate claws are also known in other chrysomelids (e.g., *Lema*; Monrós, 1959). Cassidine claw bases are commonly exposed, but they are hidden in eugenysines (described above).

Claws tend to be tapered distally and pointed, but they are broadened apically in *Acymenychus* (Maulik, 1919). Cassidine claws are commonly symmetrical, but asymmetrical ones have been reported in *Asamangulia* (Maulik, 1919), some genera in Dorynotini, Hemisphaerotini and Cassidini (Monrós, 1949; Riley, 1986), and in *Dactylispa* (personal obs.). The claw ventral margin may be blade-like, or flattened and with inner and outer margins. The ventral margin has a single tooth in genera of Eugenyssini and Stolaini. In many Aspidimorphini, Cassidini, and Charidotini, the claw base may be pectinate (comb-like) (Riley, 1985), with pectens varying in length, size, general shape,

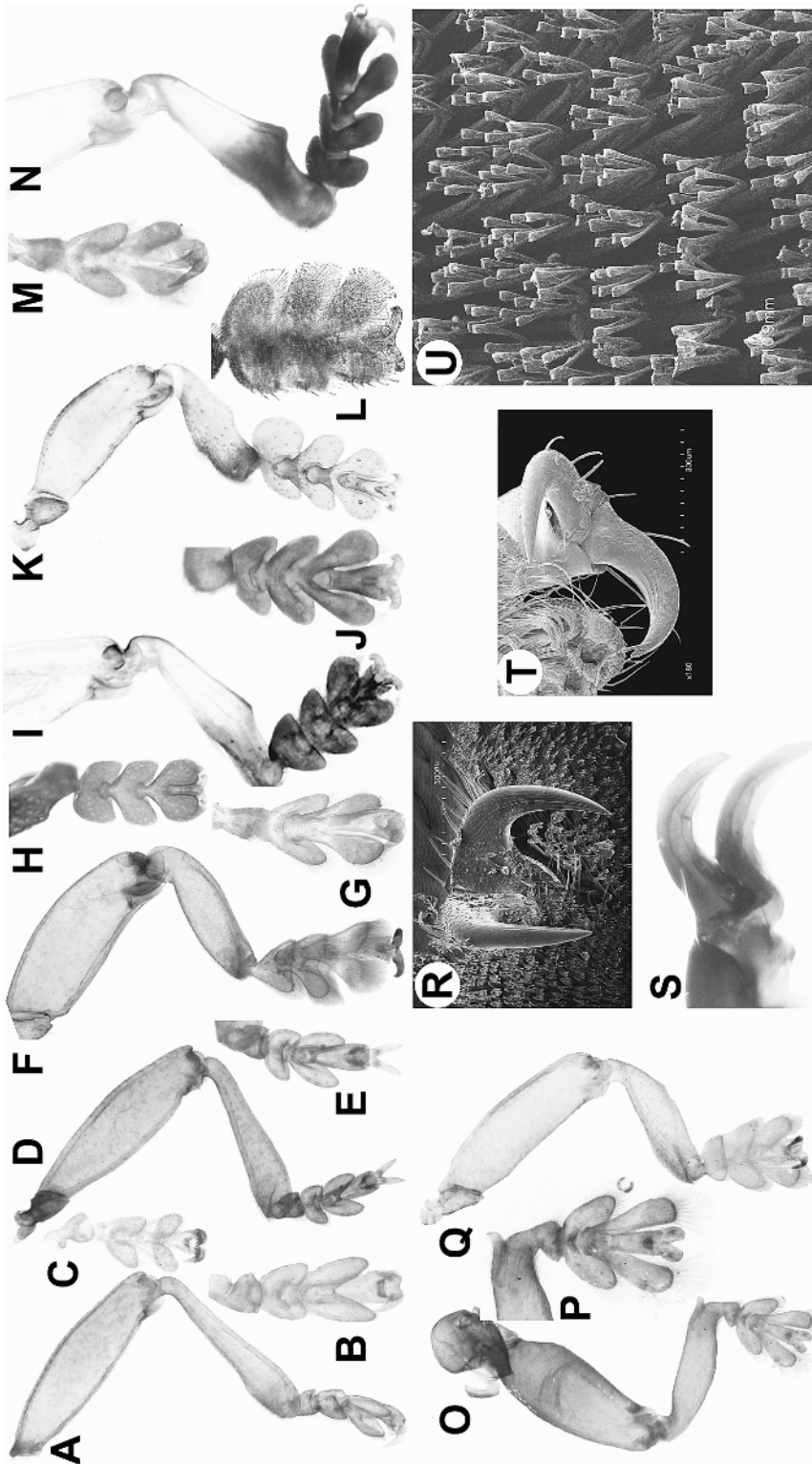


Fig. 73. Prolegs and protarsi of Cassidinae. A, B. *Anoplitus inaequalis*. C. *Aspidomorpha militaris*. D, E. *Baltosus californicus*. F, G. *Calliaspis rubra*. H. *Callistola speciosa fasciata*. I, J. *Calyptocephala nigricans*. K, L. *Delocerania panamensis*. M. *Dorynota pugnonota*. N. *Imatidium fasciatum*. O, P. *Notosacantha badia*. Q. *Spaethiella* sp. 1. R. *Basipta* sp., proclaws. S. *Ischyrosorynx oblonga*, proclaws. T. *Physonota* sp., proclaws. U. *Basipta* sp., bifid tarsal setae.

and surface texture (Maulik, 1919). Some pectens are discernible under a dissecting scope, but SEM is best for unambiguous state determination. In *Coptocycla* both margins are finely pectinate, with pectens tapering off apically and basally. In *Conchylotenia*, both margins are also pectinate, with pectens reaching about one-third of the claw length.

Claw Appendages. The ventral margins of claws are commonly simple. Hincks (1952) defined Eugenysini and Stolaini as sister taxa on the basis of the single *tooth* on the ventral margin of their claws. Other cassidines may also have a single basal tooth (e.g., *Oocassida cruenta*; Maulik, 1919). *Stoiba* and *Elytrogonia* show taxonomically useful variation in the tooth margin (Chaboo, 2000). *Claw pectens*, being rows of small teeth on the basal margins of claws, have been used taxonomically in Cassidini, Charidotini and Aspidimorphini. These pectens vary in their presence/absence on the inner and outer margins and in the numbers and lengths of individual teeth. Riley (1986) synonymized Charidotini and Cassidini based on pecten evidence. Pecten features are used to identify some Panamanian cassidine genera (Windsor et al., 1992). Some cassidines have pectens on both the inner and outer basal margins of each claw, and their numbers vary between the medial and external edges. Pectens vary in their presence or absence, numbers between mesal and external rows, and in sizes within rows. *Sindia* has claws with simple outer margins and five to six dens of variable sizes on the mesal margin; the dens decrease in size proximally (Maulik, 1919). *Conchylotenia* has four to five pectens mesally and two to three pectens externally. These different sizes of pectens may be described as macropectinate and micropectinate. *Aspidimorpha*, *Sindiola*, and *Laccoptera* have both margins pectinate (Maulik, 1919; Gressitt, 1952).

Trends in Leg Morphology. Compaction of the legs appears to be part of a general syndrome of compaction in the cassidine body. In Notosacanthini, Hemisphaerotini, and Delocraniini, legs are relatively short and the femur-tibial joints do not reach beyond the elytral margin. In other taxa, long legs extend beyond the elytra, even when the latter is strongly explanate. Within the leg,

the loss of tarsomere IV and the tibial notch that receives the tarsus also point to leg compaction.

INTERNAL MORPHOLOGY

Ventral Nerve Cord. Kasap (1979) first described the nerve cord in *Hispa testacea*. In their general review for Chrysomeloidea, Mann and Crowson (1983b) found the number of free abdominal ganglia in Cassidinae varying between three and six.

Midgut. Shrivastava and Verma (1982) and Verma and Shrivastava (1989) studied this aspect in Cassidinae and discussed peritrophic membranes and enzyme functions in *Aspidimorpha miliaris*.

ABDOMEN (fig. 39A; characters 189–210)

Cassidines have five exposed sterna that correspond to abdominal segments III–VII. Sterna III and IV are commonly connate in Cassidinae but they are separated in genera such as *Ceratispa* and *Plesispa*. The sutural line may be apparent (e.g., *Brontispa*) or evanescent (e.g., some *Hispodonta*). Sterna III–VI are usually glabrous or with sparse setation, and they are usually impunctate; *Callistola* has shallow punctation. Pubescence may be concentrated along the posterior section of lateral margins. This lateral pubescence increases slightly posteriorly and sternum VII has dense pubescence along the posterior margin. Sternum III usually has the anterior margin simple, or which may be thickened in a few cases. In *Alurnus*, it is somewhat marginate. Abdominal intercoxal processes are usually similar across Cassidinae, but in *Callispa* the margin is convex and continues across the sternum as a carina to about one-third the length of the sternum. Sterna III–VI have the anterior and posterior margins parallel, and tergum VII has the anterior margin convex and the posterior margin straight. Sternum VII, the propygidium, is more heavily sclerotized than other sterna, and it is hemispherical in shape, with a rounded, distal posterior margin; it is densely pubescent in the posterior half. Sternum VII in the female is slightly indented in the extreme lateral area; this indentation is absent in the male sternum VIII. The terga

are hidden by the elytra except the posterior portion of tergum VIII. All spiracles are present in the pleural fold and gradually decrease in size posteriorly.

REPRODUCTIVE SYSTEM (figs. 74–76; characters 194–210)

Reproductive systems are a traditional source of phylogenetic characters in entomology. It is therefore remarkable that Cassidinae reproductive systems have been generally presumed to be unvarying; they are routinely omitted in species descriptions and are virtually ignored in their systematics. Higher level chrysomelid subfamily distinctions in genitalia have been described (e.g., Chen, 1940), but within Cassidinae, key revisionary works (e.g., Hincks, 1952; Viana, 1964; Würmli, 1975), omit reproductive morphology altogether. Spaeth, the most prolific cassidine worker, never discussed these systems.

Male Reproductive System (fig. 74; chars. 192–196). Cassidine male genitalia have been included in surveys by Sharp and Muir (1912), Powell (1941), Mann (1988a, 1988b), and Mann and Crowson (1981b, 1983a, 1984b). The genitalia comprise the aedeagus, the ejaculatory duct that connects to the testes and to the flagellum at the base of the internal sac, and an incomplete tegmen.

The *aedeagus* is commonly curved and forms an angle of varying sizes with the basal piece. The aedeagal *apex* may be rounded or acute and drawn out into a small hood flanking the *ostium* (or apical orifice). The lower wall of this ostium is differentially sclerotized into single or paired *lateral plates* (Powell, 1941). Lateral lobes are lacking. *Notosacantha* (fig. 74D–E) uniquely has a pair of apicolateral articulated flanges. These have not been described before, probably because they are easily disconnected under KOH treatment and were probably not noticed. The ostium can vary in size, from an opening half the diameter of the aedeagus to as wide as the aedeagus.

Externally, the *basal piece* or tegmen is attached to the ventral or posterior edge of the median foramen, and it consists of a single median *manubrium* and a pair of lateral processes that have been called arms, apopo-

physes, or struts. The latter do not completely enclose the base of the penis, but they are connected by muscles around the latter.

The *internal sac* (fig. 74E, F) is the inverted apical portion of the aedeagus and is continuous with the apical orifice. It is eversible and enters the female's bursa during copulation. The walls may be membranous or lightly sclerotized, and the surface may be armed with spicules and/or pubescence (Mann and Crowson, 1996). The sac appears to have two areas, a simple tubular section and a section where muscles envelop the flagellum (Mann and Crowson, 1996). Cassidines have an *endophallic sclerite* or *ejaculatory guide* (fig. 74F) at the base of the sac (Powell, 1941). This sclerite may be a symmetrical structure or reduced to a single bar. It marks the point of connection between the proximal *ejaculatory duct* and the distal *flagellum*. The sclerite is notched and its surface may be spinose.

With the exception of *Notosacantha*, the aedeagus of most cassidines does not appear to vary greatly except in subtle aspects of the ostium and general angulation. However, the internal sac seems to offer more diversity in its length, internal folding, surface texture, and ejaculatory sclerite. Mann and Crowson (1996) suggested that there was "a polyphyletic development of the internal sac in the Old and New World species of Cassidinae", and they identified variations in symmetry, presence or absence of folds of the internal walls, presence of a dorsal hook, chitinization patterns, setation distribution, spicule presence and arrangement, and position of the ejaculatory guide. My confocal study of two species showed that the morphology of the latter sclerite may be very different (Chaboo, unpubl. data), with discrete variation in the number and arrangement of projections.

The flagellum is a semisclerotized, wire-like tube that is enveloped by hairy folds of the internal sac wall (Barber, 1946; Mann and Crowson, 1996). Its length is highly variable, and Rodriguez (1994a, 1994b, 1995) revealed that once the internal sac is everted into the female, the flagellum enters the spermathecal duct and travels up the duct, and even into the spermatheca, to discharge sperm.

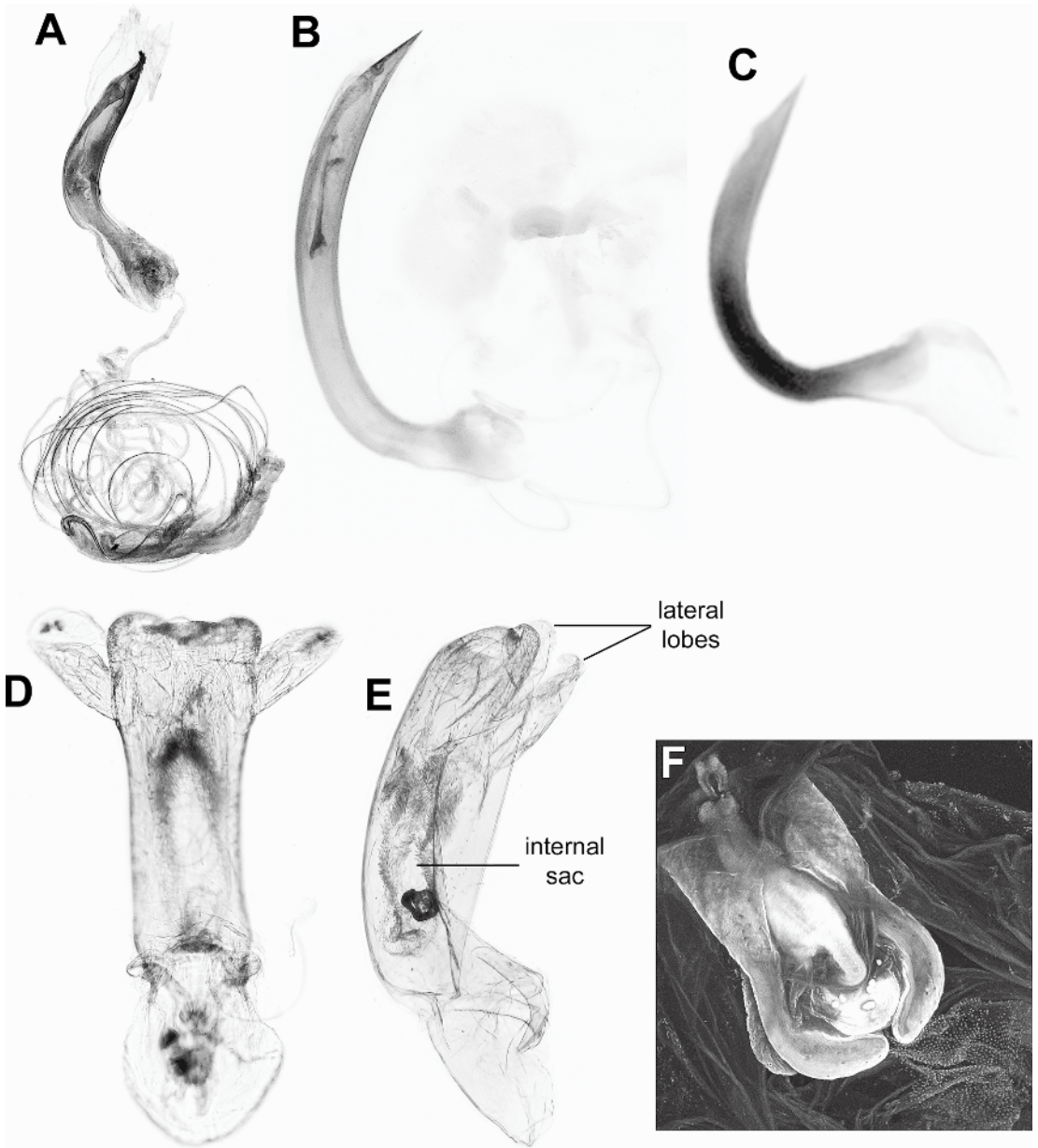


Fig. 74. Aedeagus of Cassidinae. **A.** *Demotispa* sp. **B.** *Palmispa parallela*. **C.** *Stenispis metallica*. **D.** *Notosacantha* sp. **E.** *Notosacantha* sp., lateral view. **F.** *Alurnus bipunctatus*, confocal microscope image of ejaculatory guide.

The *ejaculatory duct* may be short, up to three times longer than the aedeagus, or more commonly it is longer than the total body length. It is especially elongate and coiled in *Eugenysa* species (Chaboo, 2002). The duct consists of a short proximal sclerotized rod

that terminates at the paired testes, and a long flexible distal ejaculatory duct that enters the basal foramen, and connects with the flagellum. Duct length may be correlated with spermathecal duct length (Eberhard, 1996).

Cassidine *testes* may be single or bilobed, with the folliculae distinct or indistinct and varying in number (Virrki, 1957, 1969). An *accessory gland* may be present or absent, single or paired, with varying shapes and number of lobes. Spermatozoa studies along the lines of Virrki and Bruck (1994) will help determine variations within Cassidinae and among other subfamilies.

Apart from Rodriguez' (1994a, 1994b, 1995; Rodriguez et al., 2004) study of the physiology and mechanics of cassidine copulation, the only other functional study has been Verma and Kumar (1972). They described the process of "retournement" in *Aspidimorpha miliaris* where the aedeagus rotates 180° during copulation. This has not been studied further, so it is unclear how widespread is the phenomenon or what is its significance.

Female Reproductive System (figs. 39, 40, 75–76; chars. 198–210). The first study of cassidine female genitalia appeared in Muir and Sharp (1912). Spett and Lewitt (1927, 1928) survey of chrysomelid spermathecae included seven cassidine species. Sanderson (1948) examined four *Physonota* species, while Mann and Crowson (1983) surveyed 20 cassidines. Suzuki (1977a, 1977b, 1983, 1988b, 1997) summarized the literature on chrysomelid reproductive systems, and later discussed genitalic character correlation in Chrysomelidae (Suzuki, 1989b). Leonardi (1972) suggested that spermathecal variation might be useful in taxonomy. Rodriguez' (1994a, 1994b, 1995) study of the reproductive system in *Chelymorpha alternans* revealed the mechanics of the ejaculatory and spermathecal ducts. Borowiec and Skuza (2004) examined spermathecal morphology in 45 species of *Chelymorpha* and subdivided the genus into 10 subgroupings based on variation in the ampulla shape and length and the length and coiling of the spermathecal duct.

The *ovipositor* has the *spiculum* (= sternum IX; Jeannel and Paulian, 1944) lightly sclerotized, and the coxites are generally shorter than tergum VII. *Tergite IX* (= paraproct; Teotia, 1958); = hemitergite (Konstantinov, 1963)) may be a single plate in some cassidines (e.g., *Promecothea*) or two separate plates that connect basally by membrane (e.g., *Miocalaspis*).

Cassidine *spermathecae* (figs. 39, 40, 75, 76) are heavily sclerotized and commonly falcate, with muscles on the inner margin. Two regions, the *pump* and *receptacle*, are identified by their position and differences in diameter. They are usually broadly joined but may be distinguished externally by an indentation between them (figs. 75C, D, 76L) or, more rarely, by an internal wall that may act as a valve (fig. 75G). The pump is commonly longer than the receptacle, curving over the latter. The receptacle is basal and usually inflated, with a larger diameter than that of the pump. *Spermathecal muscles* attach to the mesal surfaces of the pump and receptacle, and their contractions pull the two together and probably control sperm expulsion. The receptacle receives the *spermathecal duct* and *spermathecal gland*. Most cassidine spermathecae have a single receptacle but a few are two or three-chambered, (e.g., *Eugenysa*; Chaboo, 2002), and the gland and duct enter separate chambers.

Cassidines display diverse arrangements in the entries of the spermathecal duct and gland into the spermatheca. In some, the gland and duct connect and enter the spermatheca as a single tube (figs. 39D). In most cases, the insertion is on the surface or is slightly elaborated on a thick section of the duct (fig. 75F); in a few cases the insertion is inverted into the spermatheca (fig. 75C). In most cassidines the gland and duct have separate insertions, and in cases of multiple receptacles, they enter different chambers. The insertions are usually basal and may be proximal or widely separated. *Conchylotenina* has an unusual elongate spermatheca in which the receptacle is inflated and the pump is about five times longer than the latter, greatly narrowed and sinuate. Examination of freshly killed specimens will help determine muscle attachments.

The pump usually has an *apical appendix* (e.g., figs. 75A, 76I), a flap-like projection in a supraapical or subapical position. This appendix may be oriented longitudinally or horizontally to the axis of the spermatheca, and it serves as an attachment for spermathecal muscles. A few cassidines have an additional medial *receptacle appendix* (fig. 75I), which provides additional attachment points and may enable greater development of spermathecal muscles.

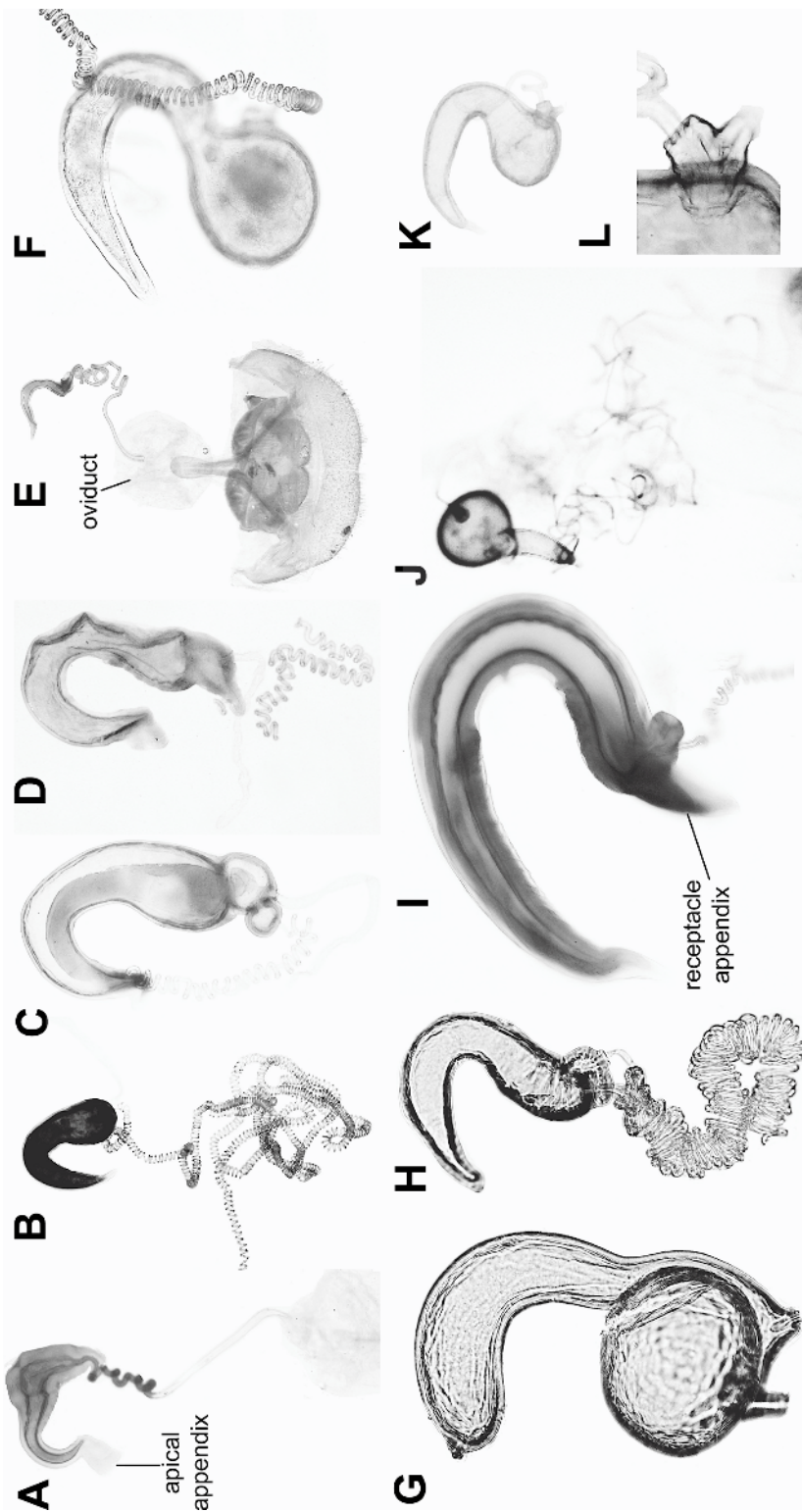


Fig. 75. Spermathecae of Cassidinae. A. *Acromis venosa*. B. *Alurnus bipunctatus*. C. *Amythra reticulata*. D. *Anepsiomorpha deplanata*, distorted. E. *Anisodera guerini*. F. *Arexus* sp. G. *Asamangulia* sp. H. *Baliosus californicus*. I. *Batonota lerouxii*. J. *Botryonopa foveicollis*. K. *Calliaspis rubra*. L. *Calliaspis rubra*, entry of gland and duct.

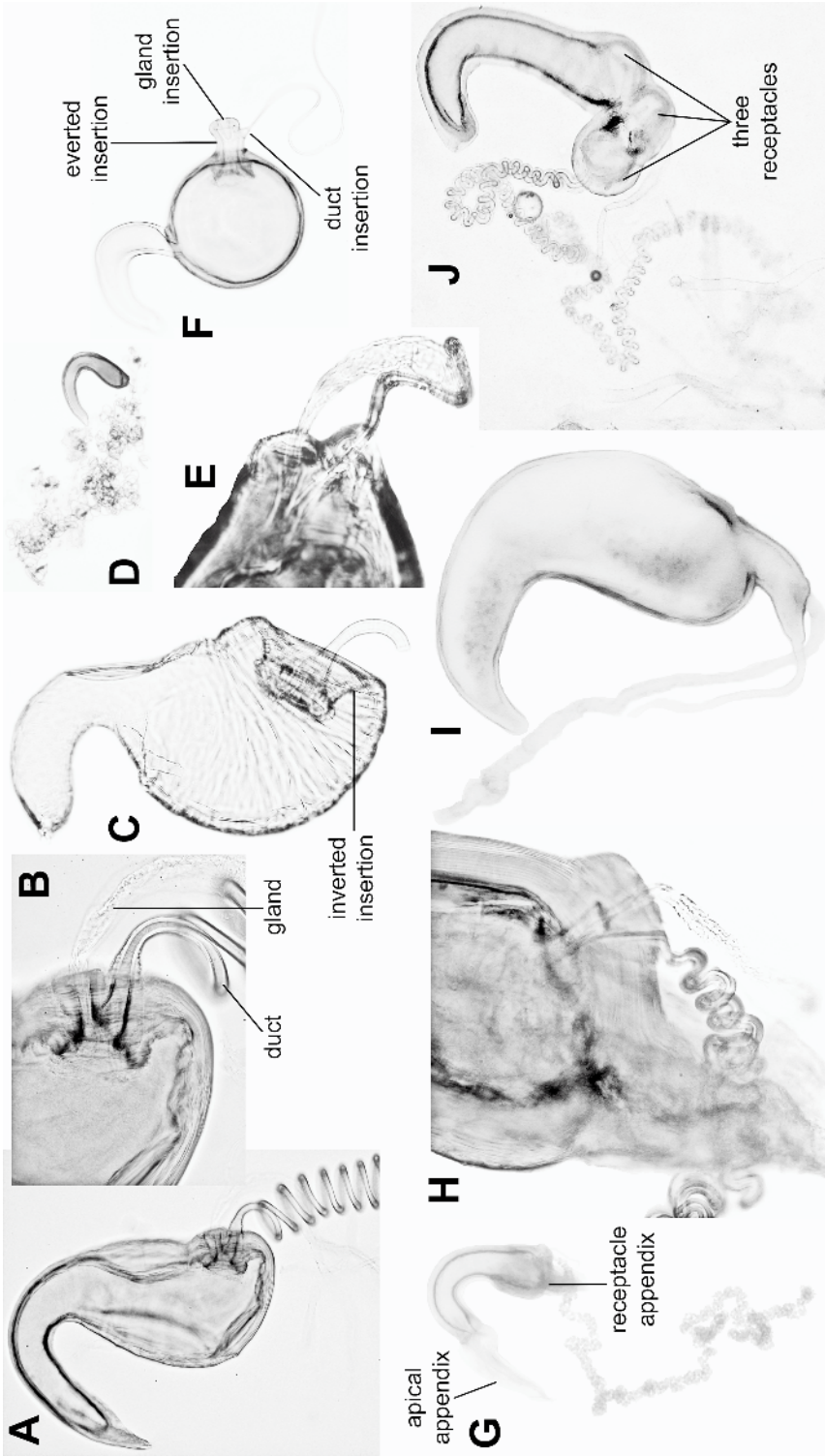


Fig. 76. Spermathecae of Cassidinae. A. *Calyptocephala nigricans*. B. Entry of gland and duct. C. *Calyptocephala nigricans*. D. Entry of gland and duct. D. *Ceratista palmicola*. E. Entry of gland and duct. F. *Dorynota pugionota*, entry of gland and duct. I. *Echona quadristillata*. J. *Eugenysa mariae*.

The *spermathecal* or *accessory gland* of cassidines is a long, flattened ribbon-like gland that is held *in situ* by connective membranes. It is easily torn in routine dissections, making comparative study difficult. The *spermathecal duct* displays much variation in length, pattern of coiling or folding, the presence of sclerotized sacs, and the enlargement of the base before inserting into the spermatheca. The duct is always longer than the length of the spermatheca, but its length can range from 2–5 times longer to >50 times longer than the receptacle. Long ducts are folded in some way, either by spiral coiling (like an old-fashioned telephone cord; e.g., *Omaspides*) or broad looping folds (e.g., *Asteriza*). Folding patterns may be consistent throughout the duct's length. In some cases, the proximate or distal section is folded while the second half is more or less straight. In the spermathecal duct of *Chelymorpha cribaria* (Fabricius), Rodriguez (1994) distinguished a region, the *ampulla*, which he proposed as an entanglement trap; the male flagellum is inserted into the duct and eventually coils on itself within the ampulla. The ampulla is difficult to identify and therefore homologize across Cassidinae. In *Polychalca* and *Eurypepla*, I found a large sclerotized sac along the spermathecal duct, and in cleared specimens it appears that a long section of the duct is tightly packed within this sac.

Rodriguez (1994a, 1994b, 1995) revealed that the male's flagellum travels up the spermathecal duct and sometimes reaches into the spermatheca where it deposits sperm. At the physiological level, it is remarkable that these microscopic tubes are capable of traveling such distances. The mechanism driving the flagellum up the spermathecal duct toward the spermatheca remains unclear. At the behavioral level, the interplay of spermathecal duct length and flagellum length probably influences courtship, mate selection, and sperm selection (Eberhard, 1996).

The *bursa copulatrix* receives the internal sac of the penis during copulation (Lindroth, 1957). It is coated in thick muscle fibers in cassidines. Stammer (1936b) first described the presence of *vaginal pouches* in cassidines, and Mann and Crowson (1983) found

vaginal pouches in all 20 cassidine species they surveyed. These pouches open to the vagina in Cassidinae and Eumolpinae and to the common oviduct in Sagrinae. Cassidine vaginal pouches are paired and open into the lower third of the vagina. They may also be called *mycetomes* as they house bacteria-like microorganisms in Eumolpinae, which are transmitted to the eggshell (Stammer, 1936a, 1936b; Kasap, 1975; Crowson, 1981; Becker 1994; Becker, and Ferronato, 1990). In Eumolpinae, the pouch consists of a sac and a duct, with the duct associated with a pair of accessory glands. In addition to the vaginal pouch, chrysomelid colleterial glands may also house microorganisms that are transmitted to the egg (Becker, 1994; Suzuki, 1988).

Colleterial glands in insects are modified accessory glands that open into the common oviduct (Selman, 1994). They produce a colorless secretion that hardens into distinctive surface sculpturations around the egg, called an *extrachorion* (Hartley, 1961). Such extrachorionic material is produced by several glandular areas in cassidines: ectodermal accessory glands that open adjacent to the vulva; glandular epithelia in the lateral and pedicels of ovarioles in *Gratiana spadicea* (Klug) (Becker and Romanowski, 1986), *Aspidimorpha icterica* Boheman (= *A. puncticosta* Paterson) and *Aspidimorpha tecta* Boheman (Atkins et al., 1966); and the vagina of *A. icterica* (Muir and Sharp, 1904) and *A. tecta* (Hinton, 1981).

In addition to the coating of cassidine eggs with microorganisms and an extrachorion, some species enclose their egg masses in an elaborate oothecal case. The case can comprise up to 200 membrane layers (e.g., *Aspidimorpha puncticosta*; Muir and Sharp, 1904). The production of so many membranes must require a high volume of oothecal secretions. Becker and Romanowski (1986) suggested that secretions must come from the extensive surface of the ovariole pedicels and not from the smaller glandular epithelium that open into the cloaca.

Chrysomelid *ovariole* numbers have been studied (Mann and Singh, 1979; Robertson, 1961; Mann and Singh, 1979; Suzuki, 1974; Suzuki and Hara, 1975; Suzuki and Yamada, 1976). The number of cassidine ovarioles

range from 3 to 21 (Mann and Singh, 1979; Robertson, 1961). In *Gratiana spadicea* there are usually one to two maturing oocytes at any time (Becker and Romanowski, 1986). Bhattacharya and Verma (1982) defined a period of diapause in summer by arrested ovarian development and hypertrophic body fat development in *Aspidimorpha miliaris*. The internal surface of *lateral oviducts* of *Gratiana spadicea* has a cuticular intima lining with spiniform projections that may help in controlling oviposition (Becker and Romanowski, 1986).

PHYLOGENETIC METHODS

A master matrix of 107 taxa and 349 characters was initially assembled in WinClada version 1.00.08 (Nixon, 1999–2000). Behavioral characters were scored on the basis of personal observations and on presumed correlation with characters of specimens examined or descriptions in the literature. Scoring for tarsal setation relied on results of Stork (1980) and my own examination by SEM. Scoring for vaginal pouch presence relied on Mann and Crowson (1981). Scoring of fecal case production and morphological features associated with its production and retention (chars. 6, 7, 13, 19, 192) relied on Erber (1988) and were applied to the Camptostomata subfamilies. Because characters from immature stages were scored by a system of composite taxon coding, some ambiguity may have been introduced into the dataset. Refining some characters created a hierarchy of characters and therefore inapplicable state coding. Ambiguity in the dataset exists as a product of missing information, inapplicable characters, composite taxon coding (for immatures only), and error from my own or published observations.

Matrix Structure. For the final matrix, nine taxa with 80% missing data were filtered using the ambiguity filter. The character ambiguity filter removed 119 characters that had more than 50 missing cells. The mop function removed all uninformative characters, including 11 autapomorphies (although see the debate of Yeates [1992] and Bryant [1995] argument for autapomorphies). The final dataset for analyses consisted of 98 taxa

and 210 characters (table 7; summary statistics are provided at the end of table 7). A second restricted dataset was derived to evaluate the performance of characters of immature stages by removing characters 0–19. Additional information on the matrix structure is provided in the summary statistics provided at the end of table 7. Character numbers in table 7 correspond to character hypotheses listed under the morphology section.

Missing information in the complete dataset accounted for 5% of the matrix (4% in restricted dataset) (table 7). Lack of information was due to several factors: unknown information (larval stages undescribed, or biology unknown), lack of male or female sex in specimen series, or lack of permission to dissect the head and mouthparts. Some cassidines have the head retracted into the prothorax, so the mouth is partially obscured; characters of this region could only be scored from a completely disarticulated specimen. Future effort will be directed at collecting this information.

Cladistic Analysis. Analyses were done using a computer, 2GB RAM, 1 GHz processor. Two sets of analyses were conducted using the same tree search parameters. The first used the complete matrix (98 taxa by 210 characters) and the second set used the restricted matrix (98 taxa by 191 characters) where characters of immature stages were deactivated.

The completed and restricted datasets were analyzed using parsimony. Only heuristic tree searches are possible with datasets of these sizes (tables 8, 9). Large datasets such as the present study can have many local optima of shorter trees, and thus tree searches were done with the Parsimony Ratchet (Nixon, 1999) to expeditiously navigate these optima and locate the likely most globally parsimonious trees. Traditional heuristic searches using tree bisection–reconnection were slower, did not find the same trees when the same search strategies were repeated, and located fewer of the shortest trees than found under the Parsimony Ratchet.

In each set of analyses of the complete and restricted datasets, all characters were treated as unordered (i.e., nonadditive) (Fitch, 1971) and were not weighted a priori (see Wilk-

inson, 1992). Most of the 210 characters in the complete matrix consist of binary states; 30 characters have three states and 3 characters have four states. Some taxa are scored as partially polymorphic for some of these multistate characters. Every effort was made to score characters based on my observations of specimens and to therefore minimize missing entries.

Several rounds of tree searches were done using the same number of iterations (200) and sequential ratchet runs (10) and holding one tree. The numbers of characters sampled were set at 6%, 8%, 10%, 12%, 15%, and 30% (table 8). Samplings of 6% and 8% of the characters were the most effective combinations (i.e., found the largest number of most parsimonious trees) and these were repeated 100 times (i.e., 100 sequential ratchet runs). The same numbers of optimal trees (same statistics) were found under the different search strategies of table 8, indicating that the same tree islands and these are therefore the optimal sets. A total of 79 most parsimonious trees (MPTs) of length 1149, CI of 0.21, and RI of 0.65 were located. The "Nelsen+consensus" function, which collapses unsupported and ambiguous nodes, was used to calculate a strict consensus of each set of MPTs. All tree files with each consensus were saved. Using "keep best," the 40 best trees were retained.

A new consensus was calculated with the "Nelsen + consensus" function and 12 nodes collapsed on this new strict consensus (figs. 77–79, 92) (length = 1147, CI = 0.2, RI = 0.64). This result was selected as the best summary of relationships from this dataset. Character transformations under unambiguous optimizations on this consensus are shown in figures 76–78. Optimizations were considered under both accelerated transformation (ACCTRAN) and delayed transformation (DELTRAN) to understand homoplasy (Farris, 1970; Swofford and Maddison, 1987, 1992; Maddison and Maddison, 1992). No autapomorphies were included in these analyses, and tree statistics were calculated for the phylogenetically informative characters only (Bryant, 1995). Clades are numbered for further discussion (fig. 78). Support for nodes under unweighted characters was compared using Bremer

support values (fig. 79) (Bremer, 1988, 1994). Values were calculated with NONA using the command sequences: h5000; bs 15, 20, and 23. This search yielded progressively longer trees until values were obtained for nodes with greatest support.

To examine the effects of larval characters on resolving relationships, larval characters were deactivated to gain a restricted matrix of adult characters only. This dataset (98 taxa by 191 characters) was subjected to a similar round of tree searches (table 9). Sampling 6% of the characters located the largest set of MPTs and this sampling was therefore repeated 100 times. A total of 139 MPTs were located (length = 1081, CI = 0.2, RI = 0.64). All trees were retained with the "keep best" algorithm, and 29 nodes collapsed on their consensus (fig. 91).

RESULTS

Under equal weighting of the complete matrix, extensive heuristic searches (quantified in table 8) with the parsimony ratchet located 79 most parsimonious trees (MPTs). There were 40 unique arrangements among these. The strict consensus of these arrangements is shown in figures 77–90 and 92. Heuristic searches with the parsimony ratchet on the adults-only dataset yielded 139 MPTs that were all unique and their consensus is shown in figure 91.

The CI, as expected for a dataset of this size, is uninformative (Farris, 1989). The RI indicates that grouping information and homoplasy are reasonable for a dataset of this size (Sanderson and Donoghue, 1989; de Queiroz and Wimberger, 1993; Hauser and Boyajian, 1997). Character state transformations under unambiguous optimizations are shown on the consensus resulting from the complete-matrix analysis in figures 80–90. Character state transformations under accelerated optimization (ACCTRAN) and under delayed optimization (DELTRAN) are given in appendix 5. For discussion purposes, the complete-matrix consensus is also shown with clades numbered (fig. 78) and with tribes demarcated (fig. 92). Clades and their subclades are numbered and named after their first node. These numbers are used in the text when discussing position and relationships. Bremer support values

TABLE 7
Matrix of Characters for Analysis of Cassidinae

Key: ? = missing information; - = inapplicable character. Polymorphisms are denoted as follows: A = 0,1; B = 1,2; C = 1,3, D = 2,3. See page 152 for characters 69-138 and page 154 for characters 139-209. See appendix 4 for character list.

Table with columns for species names and binary character data. Species include Lamprosomatinae sp., Lema trivittata, Ophraella sp., Pachybrachis circumcincta, Plateumaris rufa, Sagra sp., Acromis sparsa, Agenysa caedemadens, Alurnus bipunctatus, Amythra valida, Anepsiomorpha deplanata, Anisodera guerini, Anisostena perspicua, Anoplites inaequalis, Aprotida balyi, Arescus sp.1, Asamangulia cuspidate, Aspidomorpha miliaris, Asteriza flavicornis, Baliosus californicus, Basiprionota chinensis, Botryonopa foveiocollis, Callispa bowringi, Callispa rubra, Callistola sp. fasciata, Calypsocephala nigricans, Canistra plagosa, Cephalodonta sp., Cephaloleia sp., Ceratista palmicola, Chalepus acuticornis, Charidotella bicolor, Chelymorpha cassidea, Conchylotenia hybrida, Cyperista thorachostachyi, Dactylispa sp., Delocrania panamensis, Demotispa sp., Dorcathispa sp., Dorynota pugionota, Echoma marginata, Echoma quadrivittata, Elytrogona quatuordecimaculata, Epistictina viridimaculata, Estigmene chinensis, Eugenysa columbiana, Eugenysa coscaroni, Eurispa vittata, Eurypepla jamaicensis, Exothispa reimeri, Hemisphaerota cyanea, Hilarocassis exclamatonis, Hispodonta chapuisi, Imatidium capense, Ischyrosomyx oblonga, Jonthonota maculata, Klithispa opacicornis, Laccoptera cicatrosa, Lasiochila gestroi, Leptispa denticulate, Metrionella bilimeki, Microrhopala vittata.

TABLE 8
Searches for MPTs from Full Matrix Dataset of Cassidinae
 Consensus of best MPTs located with searches sampling 6% characters shown in figs. 76–79.

No. of iterations	Trees held	% of character sampled	No. of characters sampled	No. of sequential ratchet runs	No. of MPTs	Length	Consistency index	Retention index	No. of collapsed nodes
200	1	6	13	100	79	1149	0.21	0.65	12
200	1	8	17	100	79	1149	0.21	0.65	12
200	1	10	21	10	42	1149	0.21	0.65	18
200	1	12	25	10	38	1149	0.21	0.65	18
200	1	15	32	10	15	1149	0.21	0.65	17
200	1	30	64	100	49	1150	0.21	0.65	28

phyletic clades on all MPTs. *Cassida*, *Charidotella*, *Coptocyla*, and *Stolas* were previously found to be paraphyletic (Hsiao and Windsor, 1999), but this was not tested here. *Acromis* and *Elytrogona* have each been previously defined as monophyletic genera (Chaboo, 2000, 2001). Monophyly of *Alurnus*, *Aproida*, *Arescus*, *Asteriza*, *Botryonopa*, *Calyptocephala*, *Delocrania*, *Eurispa*, *Eurypepla*, *Exothispa*, *Notosacantha*, *Physonota*, and *Spilophora* are strongly supported. The monophyly of all other cassidine genera has not been tested cladistically.

The consensus of the adult dataset analysis (fig. 91) is well resolved but with additional ambiguous nodes. Cassidinae is resolved as monophyletic and comprising one minor basal clade, two well-resolved minor clades, and a large clade that is fully resolved basally and with a large polytomy apically. Resolution among outgroups is similar to the complete-analysis consensus. The most plesiomorphic terminal within Cassidinae is resolved as Arescini on consensuses derived from both restricted and complete analyses. The large crown clade corresponds to clade

54 of the complete-analysis consensus. Basally, classical hispine genera are resolved in very different positions from those on the complete-analysis consensus. Among the tribes whose monophyly is tested, fewer are recovered as monophyletic on the adults-only consensus. Within the large crown clade subtended by *Ischyrosomyx*, both consensuses show a large basal polytomy but with more ingroup resolution on the full-matrix consensus. *Imatidium*, *Hemisphaerota*, *Notosacantha*, and *Spaethiella* are generally placed in similar positions on consensuses of the two analyses, but with different relationships. *Delocrania*, however is placed very differently, among basal cassidines, on the restricted consensus. Characters from immature stages have evidently generally increased the resolution and robustness of clades on the consensus from the complete matrix analysis.

Comparison with Borowiec (1995) (fig. 3). Borowiec's (1995) dataset comprised five uninformative autapomorphies (chars. 4, 5, 13–15), three multi-state characters (chars. 1, 11, and 15) and 11 informative binary characters (chars. 0, 2, 3, 6–9, 10, 12, 16, and

TABLE 9
Searches for MPTs from Adult-Only Dataset of Cassidinae
 Consensus of best MPTs located with searches sampling 6% characters shown in figure 80.

No. of iterations	Trees held	% of characters sampled	No. of characters sampled	No. of sequential ratchet runs	No. of MPTs	Length	Consistency index	Retention index	No. of collapsed nodes
200	1	6	11	100	139	1081	0.2	0.64	29
200	1	8	15	100	119	1081	0.2	0.64	29
200	1	10	19	10	104	1084	0.2	0.64	30
200	1	12	23	10	214	1084	0.2	0.64	30
200	1	15	29	10	192	1084	0.2	0.64	30

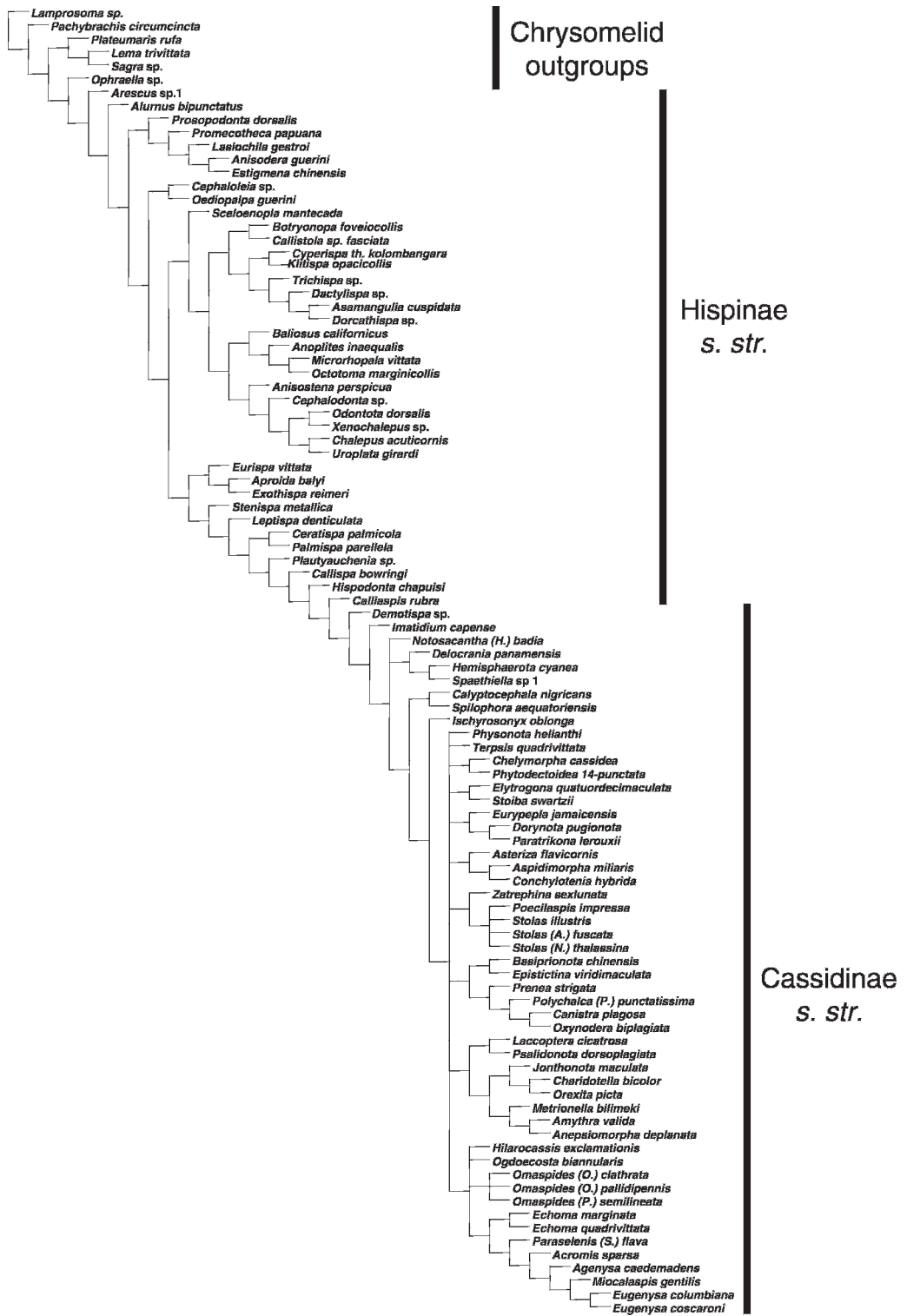


Fig. 77. Strict consensus of 40 most parsimonious trees (1149 steps, CI 0.21, RI 0.64) from the full dataset of Cassidinae. Zero-length branches are collapsed. Vertical bars indicate outgroups, and the classical Hispinae s.str. and Cassidinae s.str.

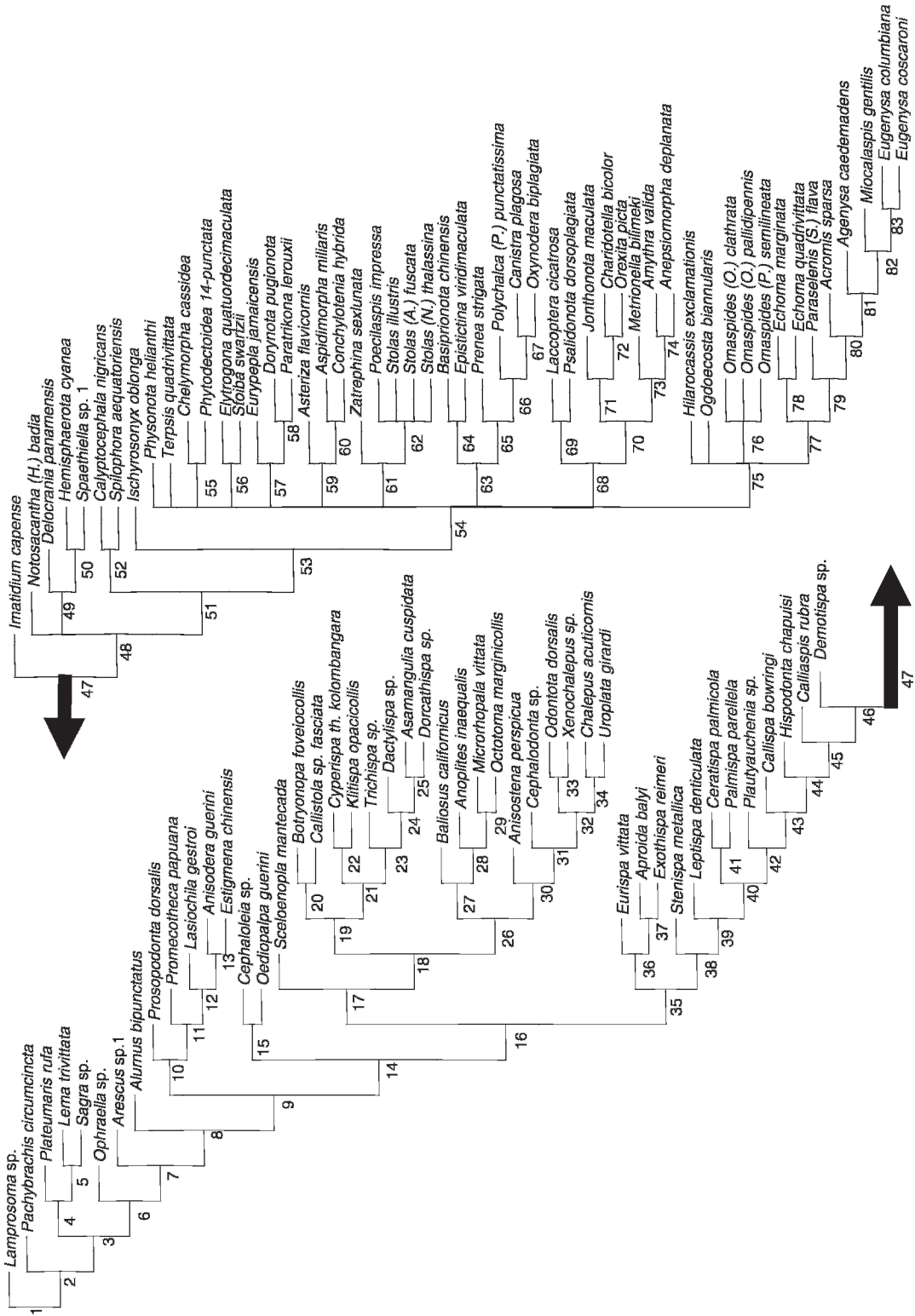


Fig. 78. Strict consensus of Cassidinae showing clade numbers corresponding to those used in the discussion and figures 80-92.

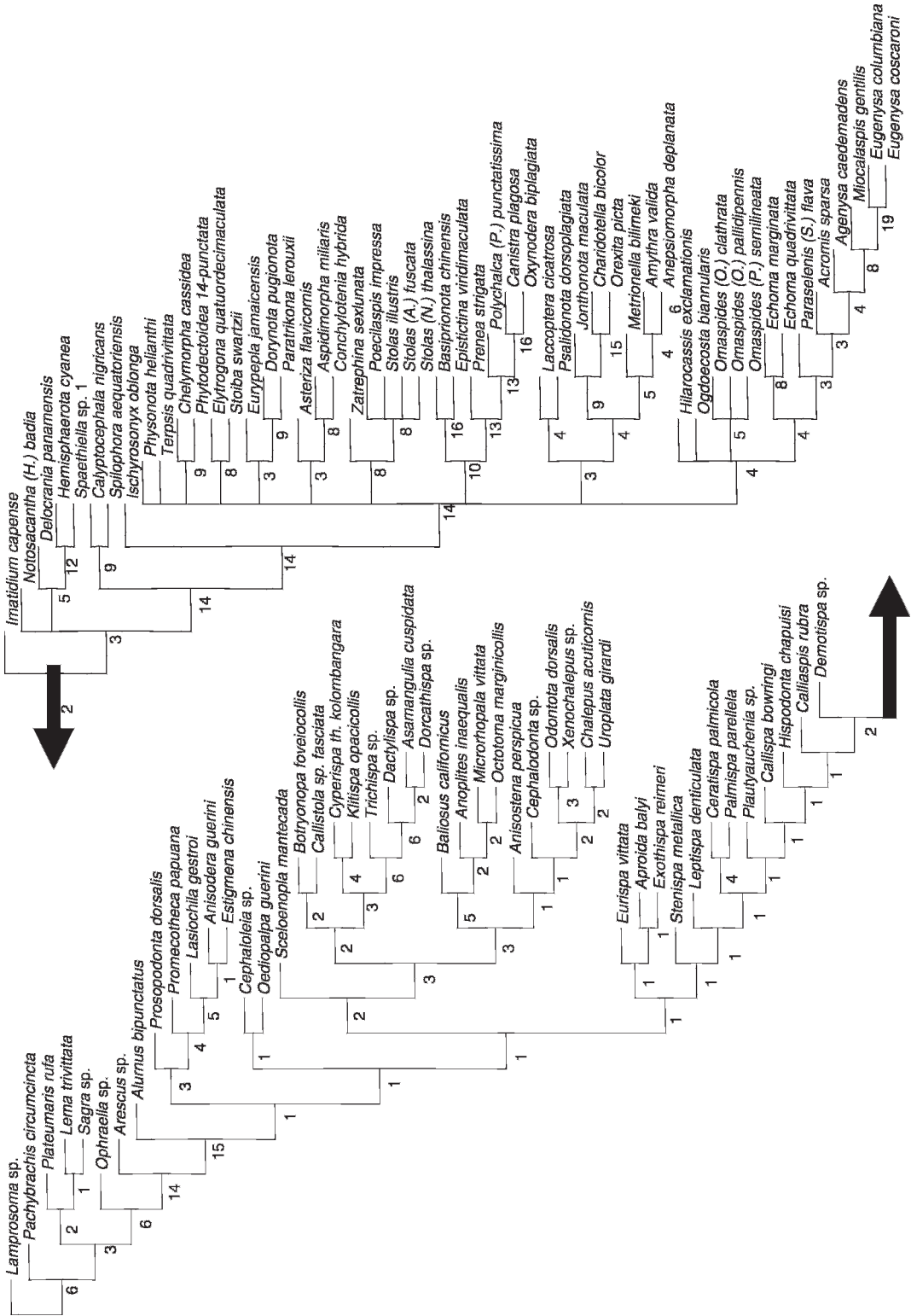


Fig. 79. Strict consensus of Cassidinae showing Bremer support values for each node.

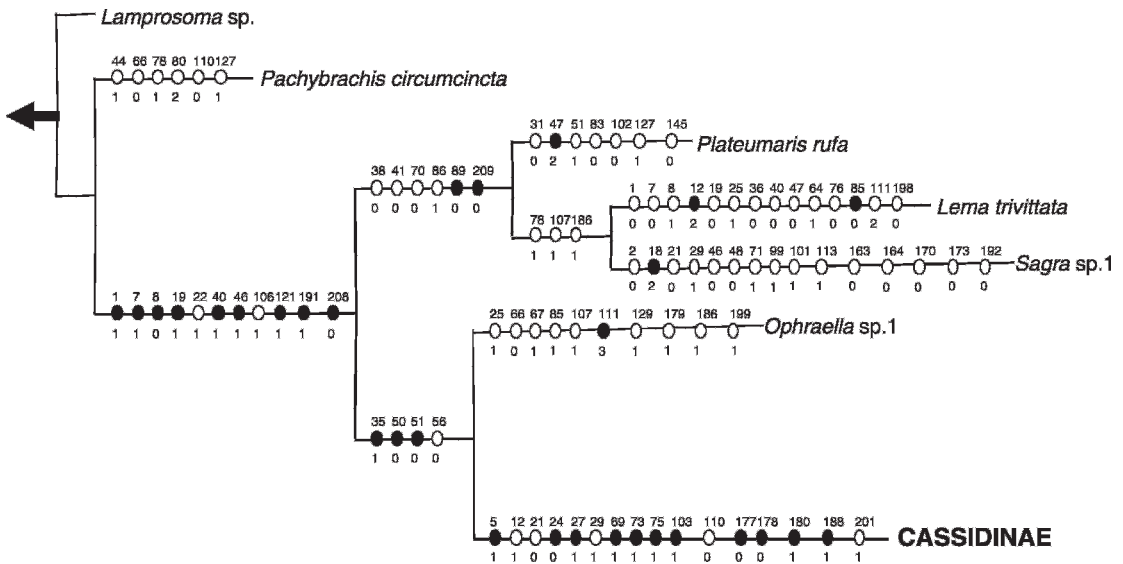


Fig. 80. Outgroup relationships with character (numbers above) and state (numbers below) distributions under unambiguous transformation. Black circles indicate unique characters, white circles indicate homoplasious characters.

17. His character 19, monocot or dicot host plant, can now be refined given the general conclusion by botanical systematics that dicots are paraphyletic (e.g., Chase et al., 1993). His use of a hypothetical all-zero outgroup did not test the position of Cassidinae within Chrysomelidae. The treatment of tribes as terminals did not test their monophyly; however, his sampling of two classical hispine tribes, Callispini and Cephaloleiini, was the first step in testing the relationship between Cassidinae s.str. and Hispinae s.str.

Points of similarity between results of the present study and of Borowiec's (1995) study are the recovery of a close relationship between Delocraniini, Hemisphaerotini, Spiophorini, and Notosacanthini (polytomy at clade 48). These tribal monophylies are each distinguished by many autapomorphies. Another point of similarity is the recovery of Epistictini + Basiprionotini (clade 64) in both studies. Borowiec (1995) synonymized these two tribes under the group name Basiprionotini, but this relationship must be tested with additional species around this node. Eugenysini and Stolaini were synonymized a priori under the group name Mesomphaliini in Borowiec (1995), but they were

recognized as two distinct tribes in Borowiec (1999). Eugenysini is recovered here as a robust monophyletic group (clade 81), and there is no support for a monophyletic Stolaini or Mesomphaliini. Borowiec's (1995) *Cassida* group encompassed 12 tribes and this corresponds coarsely with the crown clade 54 found here.

Comparison with Hsiao and Windsor (1999) (fig. 4). By sampling a larger set of outgroups, the present study can address the question of cassidine placement within Chrysomelidae in a more direct way than did Hsiao and Windsor's (1999) a priori selection of Donaciinae. Taxon sampling in Hsiao and Windsor (1999) was skewed toward Panamanian cassidines (one African species sampled), and this limit is overcome here by sampling greater taxonomic (39 of 43 tribes) and geographic diversity. The consensus of Hsiao and Windsor (1999) is somewhat resolved within certain clades, but the large basal polytomy sheds no light on deep tribal relationships within Cassidinae. A theoretical point also distinguishes their study and the present one; parsimony analysis is preferred here because of problems in neighbor-joining analyses addressed by Farris et al. (1996). Nevertheless, a comparison of their neigh-

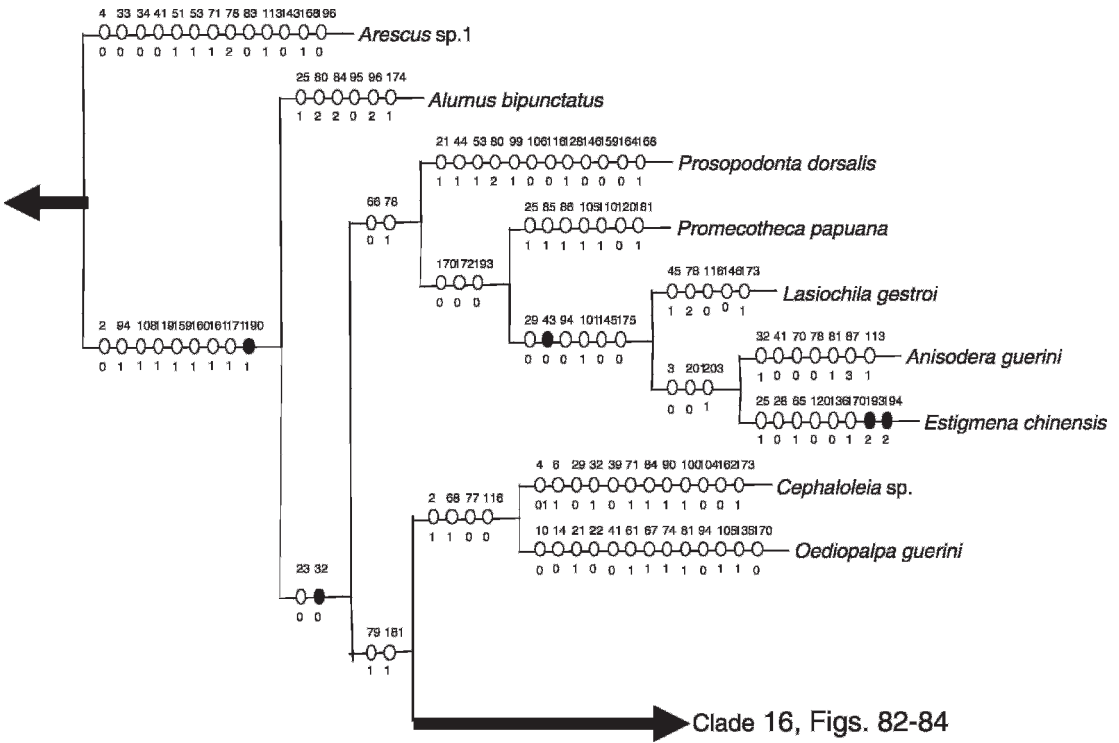


Fig. 81. Clade 7 with character (numbers above) and state (numbers below) distributions under unambiguous transformation. Black circles indicate unique characters, white circles indicate homoplasious characters.

bor-joining topology with the consensus derived here reveals generally similar patterns of a plesiomorphic placement of classical Hispinae s.str. and apomorphic placement of classical Cassidinae s.str. Both studies also locate cephaloleiine genera basally within Cassidinae (only *Cephaloleia* was scored in Hsiao and Windsor, 1999; *Cephaloleia*, *Demotispa*, and *Stenispa* are scored here).

Hsiao and Windsor's (1999) generic sampling permitted testing of monophyly for eight tribes. Five of these—Chalepini, Dorynotini, Eugenysini, Omocerini and Spilophorini—were recovered as monophyletic on their fully resolved neighbor-joining topology. Imatidiini (*Aslamidium*, *Imatidium*, and *Rhodimatidium* were scored) and Cephaloleiini were recovered as a single basal monophyletic clade and synonymized under the group name, Cephaloleiini. No support was found in the present study for that relationship or placement. Instead, the three cephaloleiine genera scored here appear unrelated,

scattered in different areas of the topology: *Cephaloleia* at node 15, *Stenispa* at node 38, and *Demotispa* at node 46. The two imatidiine genera scored here appear in a similar region of the tree, *Calliaspis* at node 45 and *Imatidium* at node 47, and are nested with *Demotispa* (Cephaloleiini). The topological placement of the redefined Cephaloleiini in Hsiao and Windsor's (1999) study is pivotal to the hypothesis, developed in Wilf et al. (2001), of an aquatic donaciine ancestor, terrestrial closed-leaf feeding basal cassidines (in pools formed by rolled leaves), and free-living derived cassidines. Relationships among particular taxa and evolutionary implications of the various phylogenetic hypotheses are taken up further below. Spilophorini (clade 52), Dorynotini (clade 58), Omocerini (clade 65), and Eugenysini (clade 81) are recovered as monophyletic in Hsiao and Windsor (1999) and in the present study, suggesting that both morphological and molecular data support these tribes.

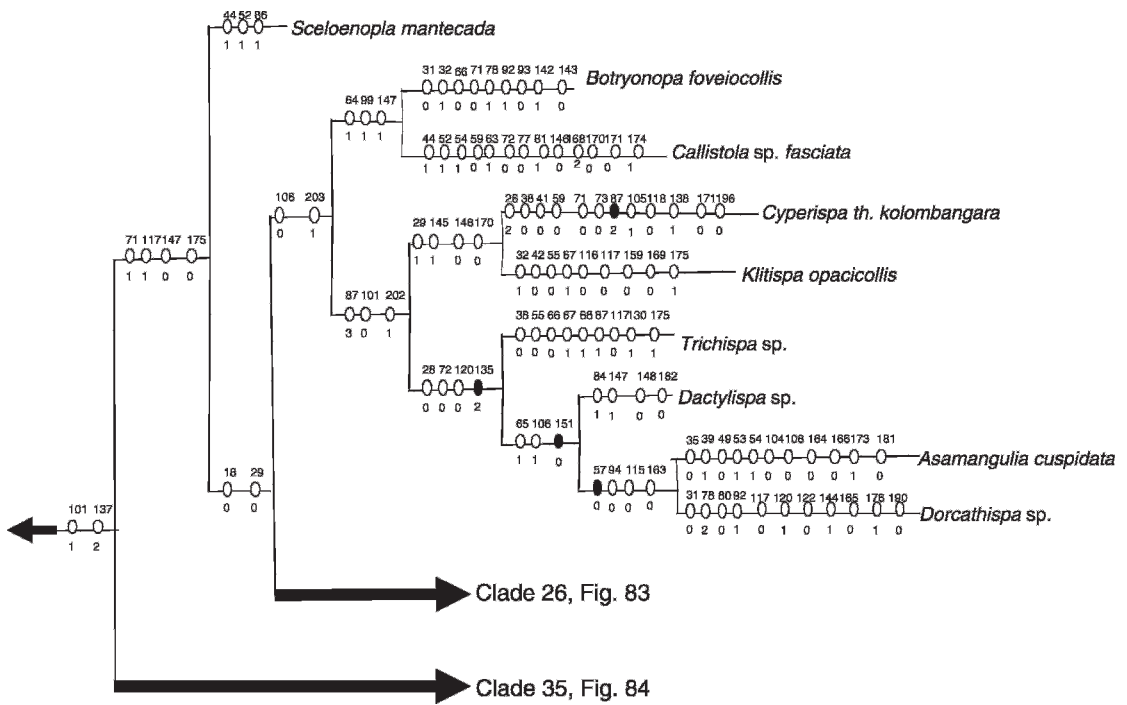


Fig. 82. Clade 16 with character (numbers above) and state (numbers below) distributions under unambiguous transformation. Black circles indicate unique characters, white circles indicate homoplasious characters.

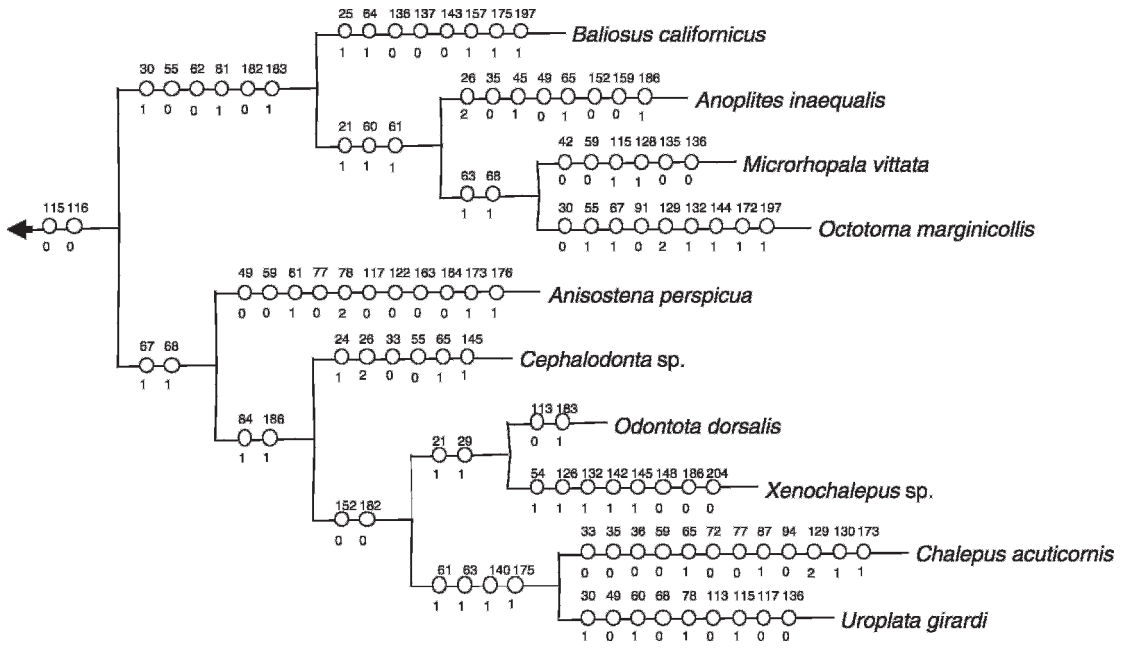


Fig. 83. Clade 26 with character (numbers above) and state (numbers below) distributions under unambiguous transformation. Black circles indicate unique characters, white circles indicate homoplasious characters.

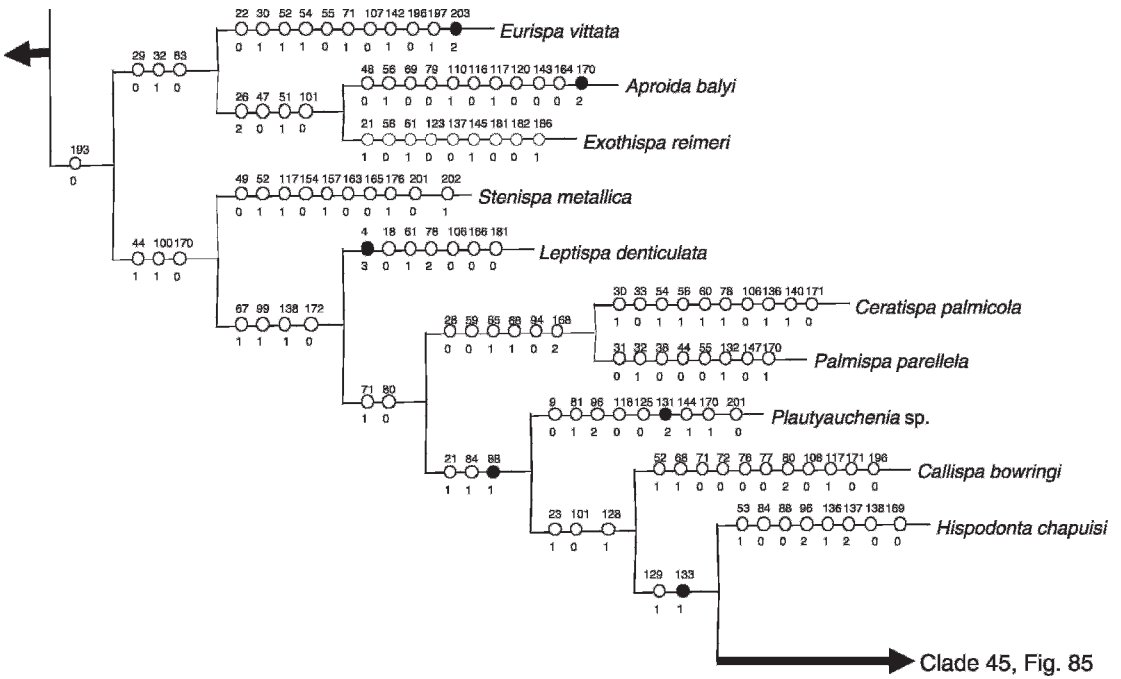


Fig. 84. Clade 35 with character (numbers above) and state (numbers below) distributions under unambiguous transformation. Black circles indicate unique characters, white circles indicate homoplasious characters.

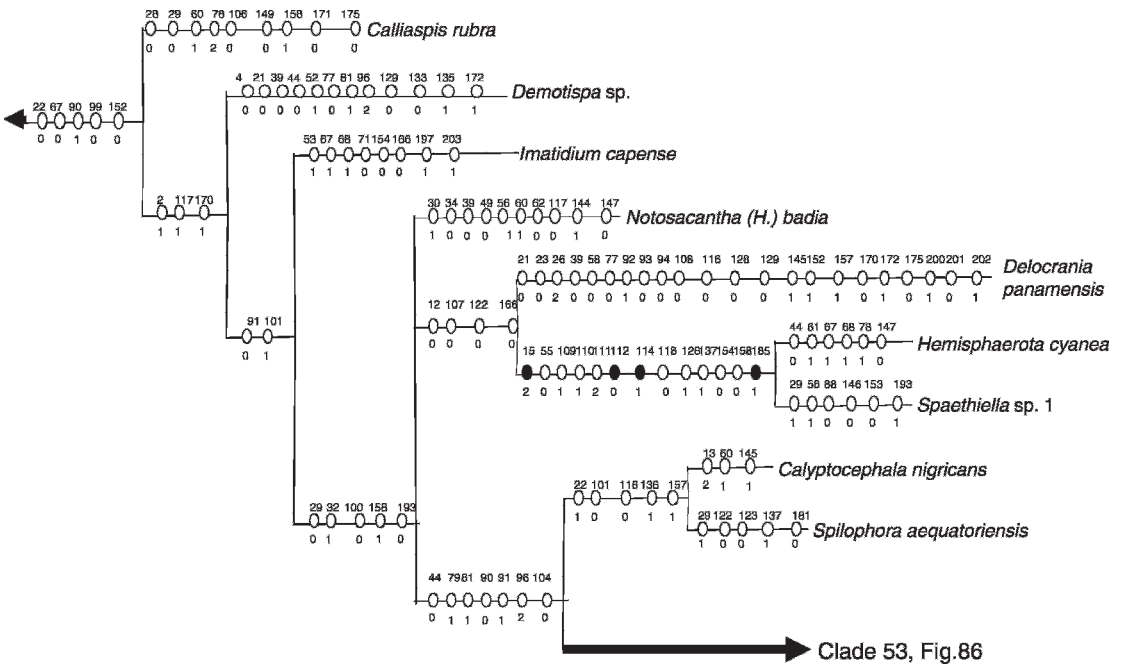


Fig. 85. Clade 45 with character (numbers above) and state (numbers below) distributions under unambiguous transformation. Black circles indicate unique characters, white circles indicate homoplasious characters.

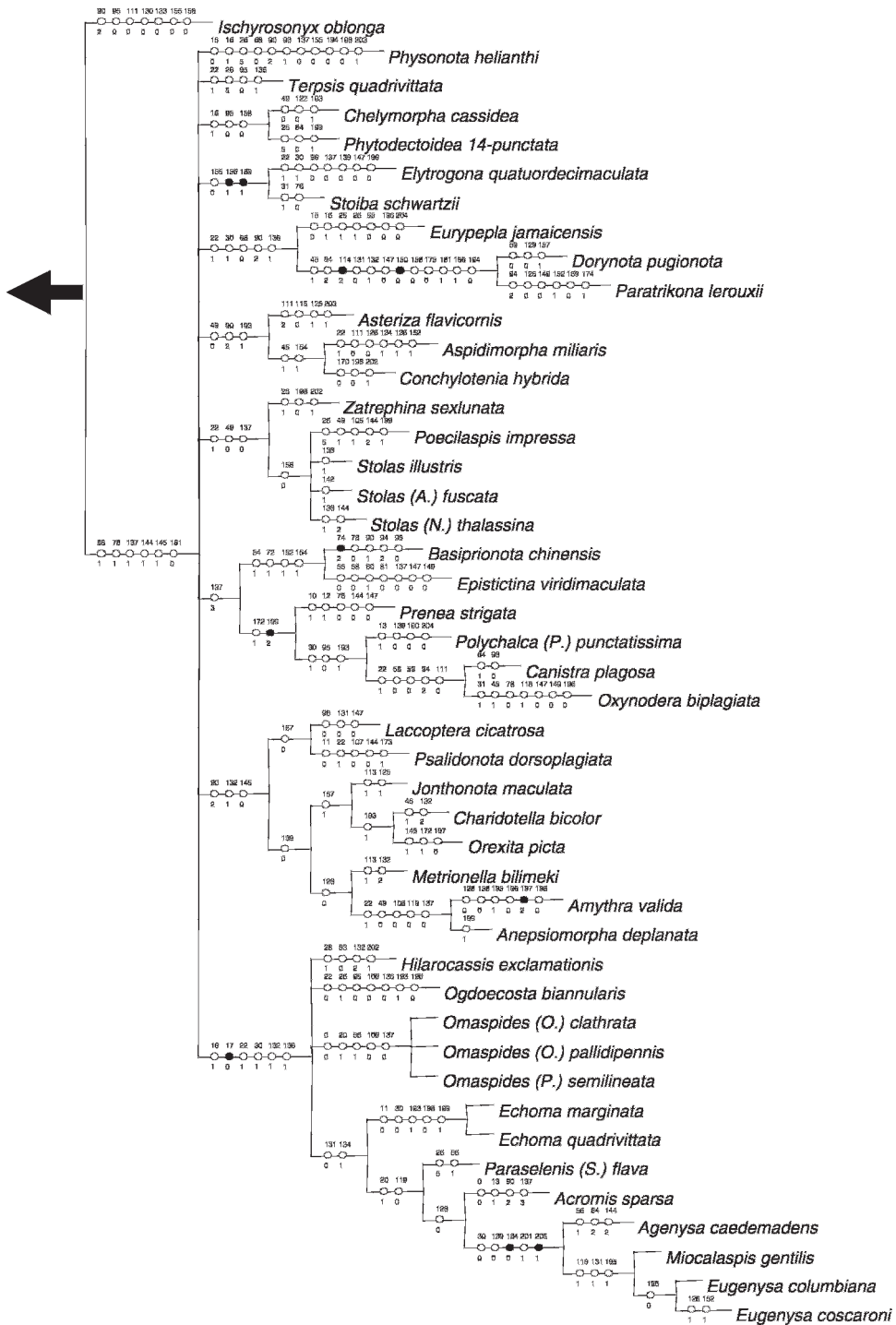


Fig. 86. Clade 53 with character (numbers above) and state (numbers below) distributions under unambiguous transformation. Black circles indicate unique characters, white circles indicate homoplasious characters.

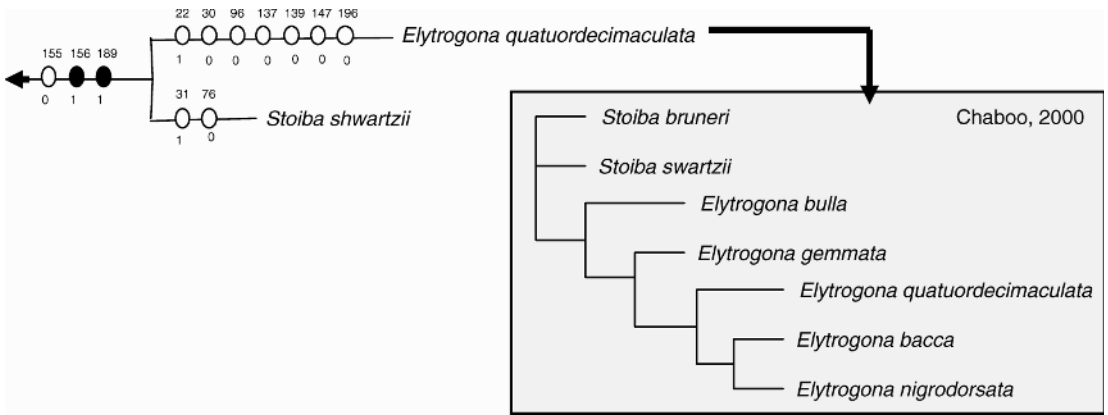


Fig. 87. Clade 56 with character (numbers above) and state (numbers below) distributions under unambiguous transformation. Black circles indicate unique characters, white circles indicate homoplasious characters. The phylogeny proposed for *Elytrogona* (Chaboo, 2000) is shown.

DISCUSSION

OUTGROUP STRUCTURE: POSITION OF CASSIDINAE WITHIN CHRYSOMELIDAE

Eighteen characters from the dataset were inapplicable in outgroups. Relationships among the outgroup taxa were completely resolved in the same way on all 40 MPTs; that is (Lamprosomatinae + (Cryptocephalinae + ((Donaciinae + (Criocerinae + Sagraeinae)) + (Galerucinae s.l. + Cassidinae)))). Galerucinae s.l. is reasonably supported (Bremer support 6) as the sister group on all MPTs (fig. 79, node 6). Under unambiguous optimizations, Galerucinae s.l. + Cassidinae was supported by three unambiguous synapomorphies—the orbital sulcus presence (char. 35), antennal insertion above the frons (char. 50), and proximity of antennal in-

sertion (char. 51)—and by one homoplastic character, relative proportions of antennomeres III and IV (char. 56). Under fast optimization, leaf mining and an incomplete tegmen are treated as unambiguous synapomorphies at node 6, and the level of homoplasious support increased with characters 56, 76, 120, 157, 168, 192, 197, and 202. Under slow optimization, this sister group relationships is supported by additional homoplasies. The placement of Galerucinae s.l. as sister to the cassidine clade is not surprising, as this was suggested previously by larval morphology (Lee, 1993) and by the absence of egg bursters on instar I (shared with Donaciinae) (Cox, 1994). A refined well-supported phylogeny of Chrysomelidae is still lacking because of incongruence among available topological arrangements of subfamily relations.

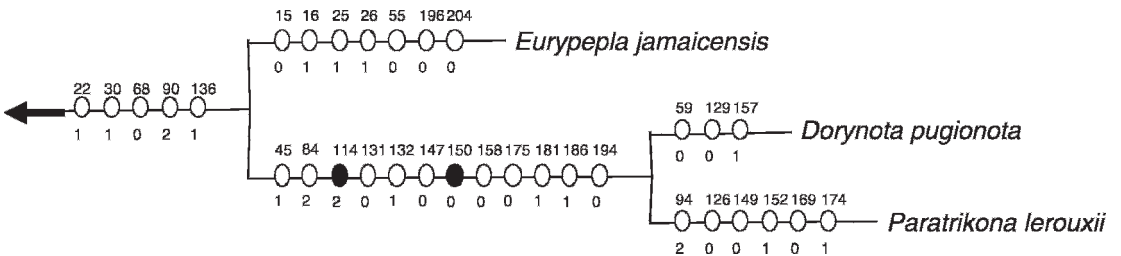


Fig. 88. Clade 57 with character (numbers above) and state (numbers below) distributions under unambiguous transformation. Black circles indicate unique characters, white circles indicate homoplasious characters.

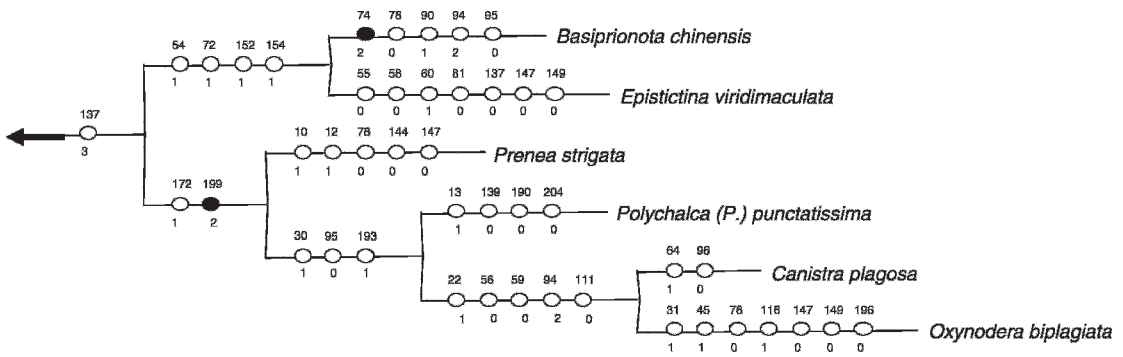


Fig. 89. Clade 63 with character (numbers above) and state (numbers below) distributions under unambiguous transformation. Black circles indicate unique characters, white circles indicate homoplasious characters.

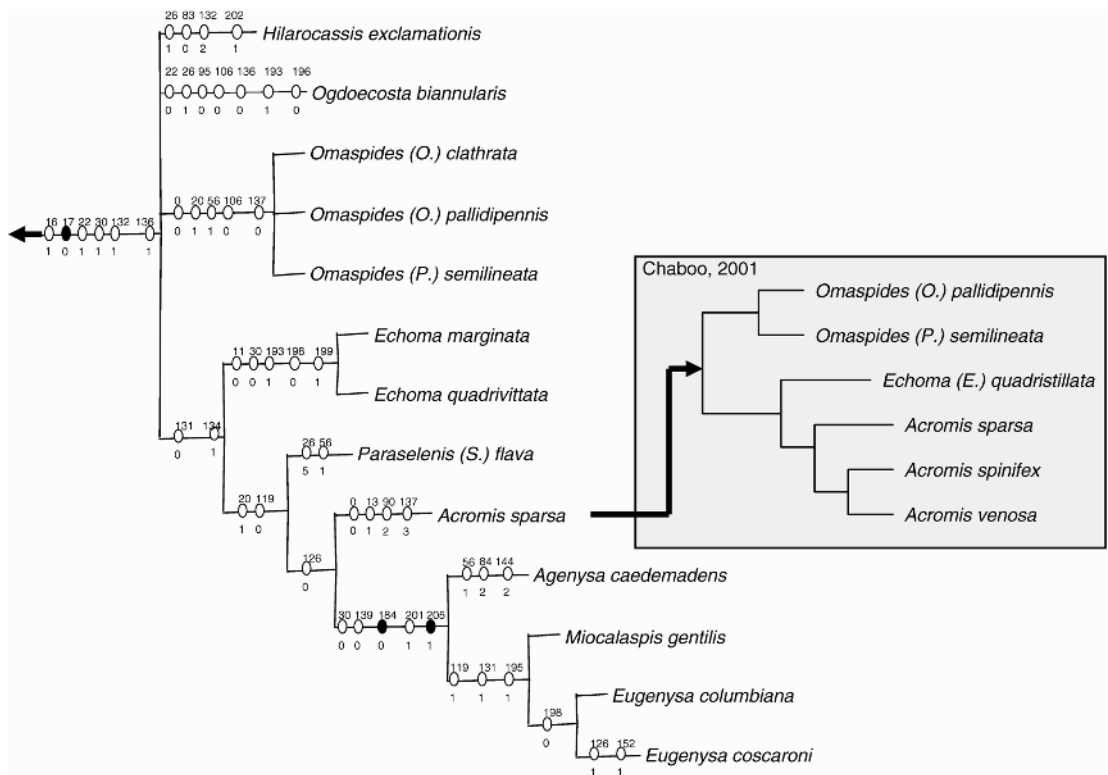


Fig. 90. Clade 75 with character (numbers above) and state (numbers below) distributions under unambiguous transformation. Black circles indicate unique characters, white circles indicate homoplasious characters. The phylogeny proposed for *Acromis* (Chaboo, 2001) is shown.

INGROUP STRUCTURE: MONOPHYLY OF CASSIDINAE

Cassidinae (figs. 77–79, 92; clade 7 on fig. 78) is unequivocally supported under unambiguous optimization by 11 autapomor-

phies (chars. 5, 24, 27, 69, 73, 75, 103, 177, 178, 180, 188) and five plesiomorphies (chars. 12, 21, 29, 110, 201). Autapomorphies comprise one larval character (dorsoventral body compression) and nine adult morphological characters (hypognathy, rounded buc-



Fig. 91. Strict consensus of 139 most parsimonious trees (1147 steps, CI 0.2, RI 0.64) from the restricted analysis of adult characters. Zero-length branches are collapsed.

cal fossa, mouthpart orientation, flattening of the venter of the head, prosternum longer than mesosternum, flattening of the thoracic sterna, bifid setation on tarsomeres I and II, tarsal formula 4-4-4, and flattened appearance of abdomen). Under ACCTTRAN (appendix 5), support for monophyly increases by three homoplasious characters, 26, 29, and 158. Under DELTRAN (appendix 5), characters 206 and 207 appear as unambiguous synapomorphies for monophyly.

Monophyly of Cassidinae is not surprising given such unambiguous evidence as the tarsal formula and mouth position. The general ventral flattening of the head (the “face”), thorax, and abdomen in the adult and the compaction of the thorax (as measured in the relative lengths of prosternum and mesosternum) are novel characters. New synapomorphies include the larval anus position, adult coronal sulcus, prosternal process shape, and spermathecal duct length.

States of tarsal setation were scored by examination of specimens and from literature sources. This character must be tested with more outgroup representatives. Stork (1980) examined tarsi of 20 species, and most subsequent discussions have relied on his findings (Mann and Crowson, 1981; Schmitt 1989; Farrell, 1998; Duckett et al., 2004). I have used a mixture of personal observations and Stork’s (1980) generalizations and refined this feature as three characters (178–180) since states vary among tarsomeres I–III. These characters apply only at the outgroup node.

Crowson (1981) suggested that the loss of tarsomere IV (TIV) was related to the expansion in other tarsomeres. Characters 171 and 172 were defined to capture the latter variation. Expanded tarsomeres I (TI) and II (TII) appear to be convergent within Cassidinae under unambiguous optimization, and monophyletic with multiple independent losses under fast optimization. The loss of TIV and expansion of TI and TII do not appear to be correlated.

Crowson (1981) also suggested that enlarged tarsomeres, and therefore enlargement of the adhesive area in Cucujoidea, Chrysomeloidea, and Curculionoidea, might be related to walking on foliage. The coincidence of bifid tarsal setation and loss of TIV with the possibility of monophyletic origins

of expanded TI and TII may be functionally significant and related to living on leaves. Crowson (1981) predicted the secretion of adhesive oils associated with tarsal setae in chrysomelids and curculionids, and Eisner and collaborators have subsequently demonstrated the production of adhesive oils by bifid tarsal setae in *Hemisphaerota cyanea* (Attygalle et al., 2000; Eisner and Aneshansley, 2000; Eisner and Eisner, 2000). This is a single data point but it supports Crowson’s (1981) hypothesis of special morphological modifications for walking on and attaching to leaves. Duckett et al. (2004) hypothesized that bifid tarsal setae are an adaptation for walking on monocot leaves, and this should be further examined in the context of other tarsal modifications across Carabidae: Lebiini, Cucujoidea, Chrysomeloidea and Curculionoidea (Crowson, 1981).

The consensus topology (figs. 77–79, 92; clades on fig. 78) has two plesiomorphic terminals (nodes 7 and 8), two minor clades (10 and 15; fig. 81), a fully resolved speciose clade (17; figs. 82, 83), a fully resolved transitional area, and a very speciose crown clade (53, fig. 86) comprising 44 terminals in 10 tribes. *Arescus* (Arescini) is resolved at node 7 as sister to all other cassidines (fig. 81). *Alurnus* (Alurnini) at node 8 is the next most plesiomorphic cassidine. Clade 10 comprises (*Prosopodonta* + (*Promecotheca* + Anisoderini)) and clade 15 comprises (*Cephaloleia* + *Oediopalpa*). Clade 17, a major clade of nine tribes, is fully resolved here (figs. 82, 83). All sampled classical hispine tribes were found to be plesiomorphic. There was no support for a monophyletic Hispinae s.str. or a “hispid Hispinae” (Borowiec, 1995; Hsiao and Windsor, 1999). Classic tortoise beetles were found to be monophyletic if rooted between *Demotista* and *Imatidium*.

Thirty-nine of the 43 ingroup tribes were sampled. Single species representatives of Aroidini, Arescini, Asterizini, Basiprionotini, Basiptini, Eurispini, Exothispini, Goniocheniini, and Gonophorini did not permit testing of monophyly of these tribes. For final analyses, the taxon ambiguity filter removed *Pharangispa* so the monophyly of Coelaenomenoderini was also not tested. Delocraniini and Notosacanthini were well supported by many autapomorphies. Of the

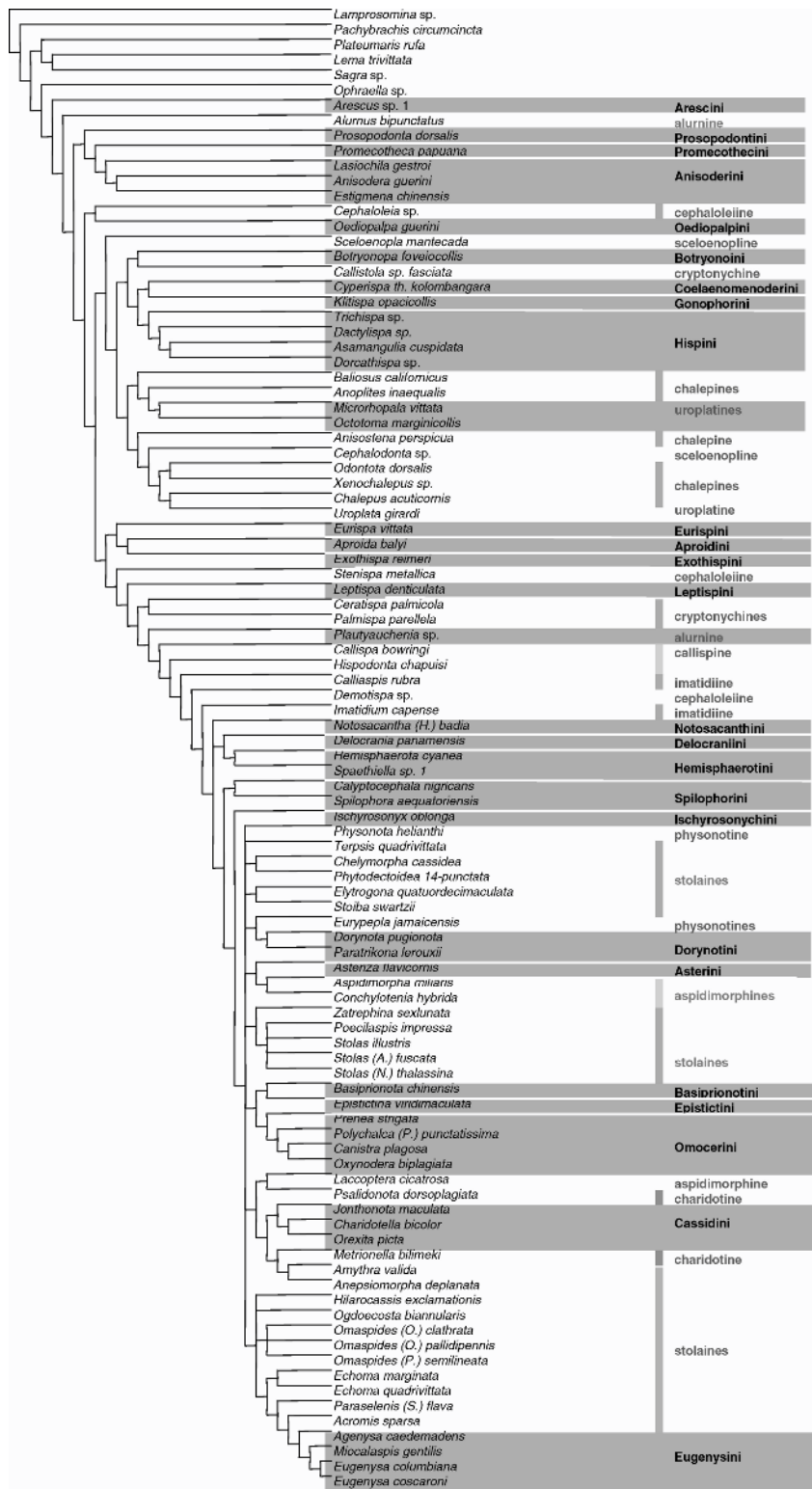


Fig. 92. Tribes of Cassidinae. Group names in boldface text on dark bars are monophyletic. Group names in gray text are paraphyletic.

21 tribes explicitly tested for monophyly, 8 are recovered. Chalepini can be circumscribed as monophyletic if *Cephalodonta* is included, and so can Cryptonychini if *Callistola* is excluded. Tribes resolved here as monophyletic and tribes found to be monophyletic by the default of scoring single exemplars altogether total 24 of the 39 examined tribes. The finding of 7n monophyletic tribes from the 21 tested for monophyly suggests that much of the current internal classification of Cassidinae needs revision before taxonomy can reflect natural groupings.

Systematists are often interested in a clade's most plesiomorphic member because of the unique insight it sheds on character evolution. Within *Hispininae* s.str. Alurnini has been discussed as the most plesiomorphic tribe (Weise, 1910; Fischer, 1935; Monrós and Viana, 1947). Borowiec (1995) did not sample Alurnini, and Hsiao and Windsor (1999) included a single alurnine species resolved in the relationship ((Alurnini + (Hispini + Cryptonychini)) + (Oediopalpini + Spilophorini)). Hsiao and Windsor (1999) proposed Cephaloleiini (including Imatidiini) as the most plesiomorphic tribe. If *Arescus* is indeed the most plesiomorphic cassidine, this finding has significant implications for all evolutionary models in Cassidinae.

Classical tortoise beetles (Cassidinae s.str. including Notosacanthini), form the large monophyletic crown clade 47, rooted between *Demotispia* (Cephaloleiini) and *Imatidium* (Imatidiini). Within Cassidinae s.str., Zaitzev and Medvedev (1982) regarded the Epistictini and Basiprionotini as the most primitive cassidine tribes that "gave rise" to Notosacanthini. Delocraniini, Hemisphaerotini, and Spilophorini have been previously supported as monophyletic, under the section "Hemisphaerotina" (Monrós and Viana, 1951), based on hidden lateral metasternal sclerites. Zaitzev and Medvedev (1982) must have meant the pleural sclerites because the metasternum is always exposed ventrally. My analysis placed these three tribes close together, with the relationship (plesiomorphic cassidines + *Imatidium*) + ((Delocraniini + Hemisphaerotini) + ((Notosacanthini + (Spilophorini + derived cassidines))). Delocraniini, Hemisphaerotini, Notosacanthini

and Spilophorini have been regarded as "transitional taxa" (Maulik, 1919; Hincks, 1952; Borowiec, 1995) because they exhibit a mix of presumed plesiomorphies and autapomorphies in adult and immature morphology and behavior. Their placement here marks a significant evolutionary landmark between plesiomorphic cassidines and apomorphic cassidines. Additionally, each of these tribes exhibits many autapomorphies—perhaps these are long branches within Cassidinae. Monophyly, position, and relationships of each tribe of Cassidinae are discussed below in alphabetic order

SYSTEMATICS OF TRIBES

ALURNINI WEISE (6 genera, 2 sampled; 29 species, 2 sampled)

Alurnines were originally characterized by the large-sized adults, 11-segmented antennae, and pronotal angles with setal tufts (Fisher, 1935; Staines, 2002), but these are homoplasies across Cassidinae. The tribe has been allied with Arescini and Prosopodontini in various catalogs (e.g., Seeno and Wilcox, 1982). Hsiao and Windsor (1999) presented the novel hypothesis (Alurnini + (Cryptonychini + Hispini)) based on molecular support. Duckett et al. (2004) resolved their single alurnine exemplar as derived in the odd relationship (*Coptocyclus* + (*Alurnus* + *Chelymorpha*)). The two alurnines sampled here are recovered separately, with *Alurnus* placed basally at clade 8 (Arescini + (Alurnini + all other cassidines)) (Bremer support 15) and *Platyauchenia* placed in a more derived position at clade 43, (cryptonychines + (*Platyauchenia* + derived cassidines)) (Bremer support 1). The latter finding provides some support for a putative relationship between alurnines and cryptonychines. The lack of support for monophyly of Alurnini is unexpected. Immature stages are known for only a few species in *Alurnus* (Bondar, 1916; Merino and Vasquez, 1963; Villacis Santos, 1968; Strong, 1977), *Coraliomela* (Bruch, 1939), *Mecistomela* (Macêdo et al., 1994), and *Platyauchenia* (Maulik, 1933a); however, they exhibit similar morphology, development and behavior. A comparative morphol-

ogy of known immatures and more characters from immature stages should inform the monophyly, position, and internal relationships of Alurnini.

Alurnines are the largest cassidines and are primarily specialists of palms (Villacis Santos, 1968; Macêdo et al., 1994; Mariau, 2004). The life cycle lasts over 1 year, with up to nine larval instars (Villacis Santos, 1968; table 5). Larvae of Alurnini, Arescini, and Cephaloleiini have been grouped into one ecological guild, rolled-leaf and sheath feeders (Staines, 2004); however, alurnine larval morphology is distinct from the latter tribes. They are heavily sclerotized with bladelike margins that may permit cutting thick fibrous tissues of unopened palm leaves. Both larval morphology and host plants suggest that alurnines are distinct from rolled-leaf feeders.

ANISODERINI WEISE (3 genera, all sampled; 75 species, 3 sampled)

Würlmli (1975a) diagnosed this moderately speciose tribe by the convex eye facets. It was not included in Borowiec (1995) and Hsiao and Windsor (1999). All three anisoderine genera are represented here and are resolved within clade 11 as sister to *Promecotheca*. They are united in the monophyletic subclade 12 by the autapomorphy of having eye facets convex (char. 43) and by homoplasies in characters 23, 94, 101, 145, and 175 under unambiguous transformation. This finding concurs with Würlmli's (1975a) diagnosis of Anisoderini. The tribal phylogeny is resolved as (*Lasiochila* + (*Anisodera* + *Estigmena*)).

Anisoderines are among the largest cassidines, with elongate, heavily sclerotized bodies. *Lasiochila* has leaf-mining larvae (Kimoto and Takizawa, 1997) whereas *Anisodera* and *Estigmena* both have stem-mining larvae (Beeson, 1941). The clade topology indicates that stem mining was a single derivation from a leaf-mining ancestor. The functional significance of the convex eye margins is unclear.

APROIDINI WEISE (1 genus, 3 species; 1 sampled)

Würlmli (1975) considered this monotypic tribe aberrant among Hispinae s.str., with

adults resembling Donaciines more than other hispines. In lateral aspect, the body is rounded ventrally and is slightly upwardly curved at the head and pronotum and at the elytral apex. The mode of pupation is also unique in Cassidinae; the fifth larva becomes affixed by the abdomen to the plant, and as the pupa emerges, the larval exoskeleton is peeled backward, and the tracheoles become distended (Monteith, 1970). The pupa is thus suspended from the leaf by the tracheoles and the larval exuviae (Monteith, 1970). Metasternal distortion in aproidines suggests flightlessness (Samuelson, 1989).

Aproidini was not considered in previous cladistic assessments of Cassidinae. The single exemplar, supported by several autapomorphies from the adults and immatures, here is placed in clade 36 (Bremer support 1) with the relationship (*Eurispia* + (*Aproidea* + *Exothispia*)) based on homoplasious support. Previous hypotheses of a relationship with *Eurispia* (Chapuis, 1875; Chen, 1973; Würlmli, 1975) are somewhat supported here. Other suggested relationships with Anisoderini (Weise, 1911; Würlmli, 1975; Samuelson, 1989) and an intermediate placement between Hispinae s.str. and Cassidinae s.str. (Lawrence and Britton, 1994) are not supported.

ARESCINI WEISE (4 genera, 17 species; 1 sampled)

Staines (2002) diagnosed Arescini by the lack of the head keel and the enlarged pro- and mesocoxae. The latter feature is redefined here as characters 160 and 161. Arescini was not included in Borowiec (1995) and Hsiao and Windsor (1999). Wilf et al. (2002) inserted Arescini as sister to Cephaloleiini *a posteriori* on the topology of Hsiao and Windsor (1999). *Arescus* appears to form a distinct terminal within Cassidinae, and its branch is robustly supported here on all located MPTs as sister to all other Cassidinae (clade 7, Bremer support 14), with the latter supported by two autapomorphies: larval mining and adult abdominal sterna I and II fused. This is a novel hypothesis for Cassidinae and for the position of this tribe. Variation in cassidine thorax morphology appears to arise from compaction in the longitudinal line and to changes in the coxal articulation; characters

160 and 161 may be correlated with each other and also with changes in the surrounding segments and muscles.

If *Arescini* is indeed the most plesiomorphic cassidine, this has significant implications for our understanding of evolutionary patterns in Cassidinae. *Arescines* are considered rolled-leaf feeders (char. 4, state 0), and this behavior appears as convergent within Cassidinae.

ASPIDIMORPHINI HINCKS (7 genera, 3 sampled; 281 species, 3 sampled)

Hincks (1952) diagnosed this Old World tribe by its pectinate claws (char. 187), but this feature is widespread among Cassidini, Charidotini, and Aspidimorphini. Consequently, Cassidini and Charidotini were synonymized by Riley (1986) and then amalgamated with Aspidimorphini by Borowiec (1995). A single aspidimorphine exemplar, *Laccoptera*, was sampled by Hsiao and Windsor (1999) and was resolved among genera of Cassidini. Of the three aspidimorphine genera sampled here, two are united as clade 60, *Aspidimorpha* + *Conchylotenina*, while the third falls out in clade 69 as *Laccoptera* + *Psalidonota*. No apomorphic characters support either clade. Pectinate claws (char. 187, state 0) have two origins under all optimizations. These results support the previous synonymies (Riley, 1986; Borowiec, 1995). Aspidimorphini was poorly diagnosed from its inception, and its boundaries collapse within the context of derived cassidines. Some sampled genera of Aspidimorphini, Cassidini, and Charidotini are united in the monophyletic clade 68 (Bremer support 3). Further investigation of the *Aspidimorpha* + *Conchylotenina* clade will determine if they form a reliable monophyletic clade. Borowiec's (1994, 1997b) and Świętojańska's (2001) treatment of taxonomic aspects of aspidimorphines provide steps for their exploring systematics and biology.

ASTERIZINI HINCKS (1 genus, 2 species; 1 sampled)

Hincks (1952) diagnosed this small monotypic Neotropical tribe by its narrowed and thickened lateral elytral margins, but this

feature is homoplasious across Cassidinae. Borowiec (1995) hypothesized a close relationship among the genera of Asterizini, Ischyrosonychini and Physonotini and synonymized these three tribes under the group name Ischyrosonychini. The diagnostic features listed by Borowiec (1995) are also homoplasious across Cassidinae. *Asteriza* is recovered here as sister to Aspidimorphini in clade 59. This relationship has not been considered previously and is weakly supported here (Bremer support 3) by three characters (49, 90, and 193) under unambiguous and delayed optimizations, as well as by characters 56, 68, 155, 175, 187 under accelerated optimization. The Asterizini lineage (node 59, fig. 78) is not supported by any apomorphies. New data on immature stages and host plants collected recently by H. Matsuzawa (personal commun.) should help resolve this tribe's status.

BASIPRIONOTINI HINCKS (7 genera, 81 species; 1 sampled)

Tribal monophyly has been argued on the basis of the almost-completely hidden mouth and the triangular shape of the clypeus (Hincks, 1952). A close relationship with Epistictini was argued on the basis of antennal striations (Hincks, 1952). Borowiec (1995) united Basiprionotini and Epistictini under the older group name, Basiprionotini, and resolved this as a plesiomorphic branch in one of his two major subclades. Zaitzev and Medvedev (1982) also regarded Basiprionotini and Epistictini as closely related and probably the most primitive of cassidine tribes. Hsiao and Windsor (1999) did not sample Basiprionotini or Epistictini. The single basiprionotine sampled here does not test tribal monophyly; however, previous hypotheses could be examined. Basiprionotini and Epistictini are recovered here as sister taxa in a robustly supported clade 64 (Bremer support 16) (fig. 89). This finding supports hypotheses of Hincks (1952), Zaitzev and Medvedev (1982), and Borowiec (1999). The classical autapomorphy, striate antennae, is found to have three origins in Cassidinae and is not unique to clade 65. Synapomorphies of clade 64 include antennomere I punctate, mouth anterior margin

between eyes, elytra lacking both a transverse internal ridge, and the longitudinal internal carina under unambiguous and fast optimizations, and additionally by the partial exposure of the head under slow optimizations. None of these character states is unique to the Basiprionotini + Epistictini clade; however, the strong Bremer support suggests that this is a distinct clade among the derived Cassidinae. The almost completely hidden mouth provides an autapomorphy for the branch Basiprionotini.

The clade Basiprionotini + Epistictini comprises eight genera and ca. 100 species and forms a well-circumscribed focus taxon for future study. Basiprionotines are found in parts of Asia and Madagascar, and only four host plant species of Verbenaceae are known (Shultze, 1908; Gressitt, 1952; Medvedev and Eroshkina, 1988; Borowiec, 1999). The pest status of *Craspedonta leayana* was summarized from Garthwaite (1939) and Beeson (1941) under Biology above. Immature stages are described for *Basiprionota* (Schultze, 1908; Gressitt, 1952; Gressitt and Kimoto, 1963; Zaitsev and Medvedev, 1982; Chen et al., 1986) and *Craspedonta* (Weise, 1901; Garthwaite, 1939; Beeson, 1941; Zaitsev and Medvedev, 1982; Cox, 1988; Zaitsev, 1992; Świętojańska and Ghate, 2003), collected but undescribed for *Megapyga* (appendix 2), and are unknown for the remaining basiprionotine genera, *Androya* Spaeth, *Cassidopsis* Fairmaire, *Metriopepla* (Waterhouse), and *Pseudoandroya* Spaeth. Borowiec's (1994) review of afrotropical basiprionotines provides a firm basis for further systematic work on this group.

BASIPTINI HINCKS (1 genus, 5 species; 1 sampled)

Hincks (1952) diagnosed this monotypic African tribe by the metepisternal inflation and a trapezoidal clypeus. Borowiec (1995) hypothesized a close relationship with genera of Cassidini and synonymized it under this name. The single *Basipta* species sampled here does indeed appear among derived cassidines of clade 54 in initial tree searches, but it was subsequently filtered from analyses due to high levels of missing information. Diagnostic characters proposed by Hincks

(1952) are homoplasious in the context of Cassidinae. However, the independent findings of a paraphyletic Cassidini by Hsiao and Windsor (1999) and in the present study suggest that Borowiec's (1995) synonymy may be premature.

Recent collection of the life cycle of one *Basipta* species revealed a complex ootheca, five instars with exuvio-fecal shields, solitary pupation, and no parental care (Chaboo et al., unpublished data).

BOTRYONOPINI WEISE (2 genera, 40 species; 1 sampled)

Würmli (1975a) circumscribed botryonopines by the absence of pronotal punctation and the absence of pronotal sensory tufts. This particular character combination is not unusual among cassidines. Furthermore, the first character is incorrect since *Botryonopa* has pronotal punctation and the second feature applies to many cassidines. Gressitt's (1950) character of the proximity of the mouth cavity to the antennal insertions in *Botryonopa* will require a major comparison across Cassidinae to demarcate unambiguous states.

The single exemplar included in my analysis is resolved in clade 19 as ((*Botryonopa* + *Callistola*) + ((Coelaenomenoderini + Gonophorini) + Hispini)) and is supported by characters 106 and 203. Subclade 20, *Botryonopa* + *Callistola*, is weakly supported (Bremer value 2) by the synapomorphic characters 106 and 203 under unambiguous transformation, by characters 9, 64, 99, 147, and 152 under fast optimization, and by characters 64, 99, 107, 137, and 146 under slow optimization. Brief descriptions by Gressitt (1950) suggest that a thorough analysis of head morphology may reveal mouth character support for this obscure tribe. Maulik (1949b) described the larvae and pupa of *Botryonopa sanguinea* Guérin that were collected from the unopened buds of the palm, *Metroxylon*; Mariau (2004) indicated a coconut palm host for *B. sanguinea* Guérin.

CALLISPINI WEISE (6 genera, 2 sampled; 173 species, 2 sampled)

Würmli (1975) circumscribed this tribe by the first five puncture rows curving outward

basally, a feature that is difficult to distinguish across Cassidinae. Borowiec (1995) placed Callispini within a large subclade of Cassidinae. *Callispa* and *Hispodonta* were sampled here and appear at clades 44 and 45 (fig. 84) respectively, indicating nonmonophyly of Callispini and under all optimizations.

Callispines occur in the Old World and specialize on Areaceae, Musaceae, Orchidaceae, Poaceae, and Zingiberaceae (Gressitt, 1960a, 1960b, 1963b; Gressitt and Kimoto 1963; Jolivet and Hawkwood, 1995). Immature stages are known in the genera *Hispodonta* (Gressitt, 1960a, 1960b, 1963a; Gressitt and Kimoto, 1963) and *Callispa* (Uhmann, 1949b; Kalshoven, 1951; Gressitt and Kimoto, 1963; Chen et al., 1986; Zaitsev, 2001) but are unknown for *Amblispa* Baly, *Pseudocallispa* Uhmann, and *Spilispa* Chapuis. The extremely thin and flattened larval body appears to resemble Imatidiine and Cephaloleiine larvae, as well as those in the coleopteran families Psephenidae (water pennies) and Colydiidae (W. Shepard, personal commun.), but detailed comparative study is needed.

CASSIDINI HINCKS (76 genera, 3 sampled; 964 species, 3 sampled)

This is the largest cassidine tribe, accounting for 16% of subfamily diversity (fig. 2). Members include the quintessential cassidines with well-developed pronotal and elytral extensions, disc-like profiles in dorsal view, and metallic golden colors. Many species are relatively well studied. Cassidini have been difficult to circumscribe in a satisfactory manner. Hincks' (1952) diagnosis was based on negative characters (his couplet 42): absence of inflation of the metepisternum, and metepisternum not projected beyond metepimeron. Seeno and Wilcox (1982) recognized Cassidini, Aspidimorphini, and Charidotini as three separate tribes. Riley (1986) conducted a detailed study of the pectinate claws and concluded that charidotines belong in Cassidini. Borowiec (1994a) agreed with this synonymy and redefined Cassidini to include aspidimorphines. Hsiao and Windsor (1999) treated Cassidini + Charidotini and Aspidimorphini as two

distinct groups, and they found a polyphyletic Cassidini with genera resolving in five different locations on their topologies.

Three Cassidini genera (*Charidotella*, *Jonthonota* and *Orexita*) are sampled here, along with all three aspidimorphine genera (*Aspidimorpha*, *Conchylotenina* and *Laccoptera*) and two charidotine genera (*Metrionella* and *Psalidonota*). Altogether 15 genera of Cassidini were examined, but this sample does not represent an inadequate grasp of diversity and cannot circumscribe tribal boundaries. Nevertheless, the current sampling regime allows some testing of previous hypotheses of monophyly and relationships among these three problematic tribes. Most of these genera are placed in clade 68 (Bremer support 3) and are fully resolved in subclade 70 (fig. 86). Also placed in clade 68 are two stolaine genera, *Amythra* and *Anepsiomorpha*. These placements support the previous synonymies of Riley (1986) and Borowiec (1994a) but contrast with the chaotic polyphyly of Cassidini found by Hsiao and Windsor (1999).

Clade 68 is monophyletic and characters 90, 132, and 145 provide synapomorphies under unambiguous and slow character optimizations. Characters 59 and 201 also support this node under accelerated transformation. There are no unambiguous autapomorphies within this clade, and its subclades have reasonable support (Bremer values range from 4 to 15). Synonymies with Charidotini (Riley, 1986), Aspidimorphini (Borowiec, 1996), and Basiptini (Borowiec, 1999) have resulted in the tribe Cassidini comprising more than 1500 species.

An extensive literature has accumulated on the biology of many Cassidini species. These immatures are the most commonly represented in specimen collections. Detailed comparative study of these species and genera is feasible and should promote resolution of relationships.

CEPHALOLEIINI WEISE (9 genera, 3 sampled; 311 species, 3 sampled)

Three features have been used to distinguish Cephaloleiini: finely punctate elytra, elytra lacking costae, ridges and tubercles, and presence of the anterior pronotal seta

(Sanderson, 1967). These are all homoplasies. Borowiec (1995) treated *Cephaloleiini* as monophyletic and sister to *Callispini*. Hsiao and Windsor (1995) sampled a single species of *Cephaloleiini* and three species of *Imatidiini*, which were placed within a single monophyletic clade. In their densely sampled molecular phylogeny of *Cephaloleia* species (98 ingroup taxa and 7 outgroups [six other cassidines and one criocerine]), McKenna and Farrell (2005) found the relationship (*Cephaloleia* + (*Cephaloleia* + *Imatidiini*) + ((*Alurnini* + *Prosopodontini*) + *Arescini*)) + *Criocerinae*. Although the taxon sampling at the outgroup node was not a focus of their research, the placement of *imatidiini* within the *Cephaloleia* clade is intriguing and concurs with the finding of Hsiao and Windsor (1995).

Cephaloleiini have been considered synonymous with *Imatidiini* (Borowiec, 1995). The known *cephaloleiine* larvae are highly flattened and, like *arescines*, live uniquely in rolled leaves ("rolled-leaf cassidines"). The only two known *imatidiine* larvae, *Imatidium neivai* Bondar (Bondar, 1940) and *Imatidium* sp. (Chaboo, unpubl. data) also have similar morphology.

My sampling of *Cephaloleiini*, *Arescini*, and *Imatidiini* includes one *arescine* species, three species in three *cephaloleiine* genera that appear in three different locations on the consensus, and the *imatidiines* *Calliaspis* and *Imatidium* that are resolved as (plesiomorphic cassidines + *Calliaspis* + (*Demotisca* + (*Imatidium* + derived cassidines))).

Character transitions on my topology suggest a correlation between extreme flattened larval morphology and rolled-leaf feeding. Rolled-leaf feeding occurs in several unrelated clades of cassidines, suggesting convergent evolution. The correlation of extremely flattened larval and pupal forms with rolled-leaf feeding is not a surprise. Such morphology probably aids or is constrained by movement in the restricted spaces between layers of a rolled leaf.

CHALEPINI WEISE (25 genera, 6 sampled; 342 species, 6 sampled)

Chalepini ranks as the fifth largest cassidine tribe (fig. 2). It was circumscribed by

Staines (2002) by adults with a long clypeus and reduced labrum, a tubercle and trichobothrium at the anterolateral pronotal angles, and by denticulate lateral elytral margins. Hsiao and Windsor (1999) sampled the *chalepines* *Anisostena* and *Sumitrosis*, and resolved these in a monophyletic clade and sister to a monophyletic *Uroplatini* (*Microrhopala* and *Probaenia* were sampled). Under the wider generic sample considered here, *Chalepini* was recovered as paraphyletic (clade 26); *Baliosus* and *Anoplites* grouped with the *uroplatines*, *Microrhopala* and *Odontota* (clades 27 and 28), and *Odontota*, *Xenochalepus* and *Chalepus* grouped with another *uroplatine*, *Uroplata* (clades 32–34). This finding suggests that both *chalepine* and *uroplatine* taxa may share a close relationship, as proposed earlier by Hsiao and Windsor (1999). However, neither tribe forms natural groups here.

Biological data include some 17 plant family records (table 3) and immature stage reports in 9 genera, *Anisostena*, *Baliosus*, *Chalepus*, *Craspedonisca*, *Odontota*, *Sternostena*, *Stethispa*, *Sumitrosis*, and *Xenochalepus* (appendix 2). However, these offer an inadequate account of the biology of this moderately speciose clade.

CHARIDOTINI HINCKS (6 genera, 2 sampled; 312 species, 2 sampled)

Charidotine adults are medium sized and rounded, and have metallic golden colors. Their historical treatment has been indicated in the above discussion of *Cassidini*. Riley's (1986) synonymy of *charidotines* with *Cassidini*, on the basis of pectinate claws in adults of both tribes, has been accepted (Borowiec, 1994a; Hsiao and Windsor, 1999). The single *charidotine* sampled by Hsiao and Windsor (1999) was resolved among genera of *Cassidini*. *Metriionella* and *Psolidonota* are sampled here and are resolved separately within clade 68, subclade 69 with (*Psolidonota* + *Laccoptera*) (*Aspidimorphini*) (Bremer support 4), and in subclade 73 with (*Metriionella* + (*Amythra* + *Anepsimorpha*)) (*Stolaini*) (Bremer support 5). These relationships are not robustly supported, and the lack of resolution among the 10 tribes situated in

clade 54 is a complex problem for further investigation.

Despite their moderate diversity, charidotines are known from a few families of host plants (e.g., compare to Chalepini) (table 3). Immatures are superficially known in three genera (appendix 2).

COELAENOMENODERINI WEISE (8 genera, 2 sampled; 73 species, 2 sampled)

Würmli (1975a) diagnosed the tribe on the basis of large domed eyes and an elongate body with widened posterior in adults. The eye feature was not scored here due to the wide variation in eye shape. The other two characters, body elongation and posterior wideness, are homoplasious in the context of Cassidinae.

Pharangispa was filtered due to high levels of missing data. *Cyperispa*, the only coelaenomenoderine genus included in the analysis, is united with Gonophorini by four homoplasious characters 29, 144, 147, and 171 (clade 22, fig. 82). Further investigations must be directed at capturing more of coelaenomenoderine diversity (as suggested by recognition of eight genera) and must encompass more biological information. Hosts are known in four plant families (table 3), and immature stages are known for species of *Balyana*, *Cyperispa*, *Coelaenomenodera*, and *Enischnispa* (appendix 2).

CRYPTONYCHINI WEISE (24 genera, 3 sampled; 136 species, 3 sampled)

Uhmann (1958) diagnosed this large Old World tribe by the rostrum shape; however, Würmli (1975) indicated that tribal circumscription was problematic due to sexual dimorphism and wide variability in morphology. Cryptonychini was treated as related to Eurispini and Callohispani (Seeno and Wilcox, 1982). Mariau (2004) treated *Callispa* (Callispini) as a member of Cryptonychini. The two cryptonychines sampled here are resolved in clade 20 (*Callistola* + *Botryonopa*) and clade 41 (*Ceratista* + *Palmispa*). The "rostrum" is morphologically an extension of the vertex of the head beyond the eye margin; it is sexually dimorphic but the functions are unknown. This feature is treated as character

33 and originates four times on the consensus topology. Lack of monophyly is not unexpected given previous doubts about the tribal circumscription. The 24 cryptonychine genera encompass about 134 species (compare to the six charidotine genera encompassing more than 300 species) perhaps reflecting great intratribal morphological diversity or exuberant taxonomy.

Data on immature stages are known in 10 genera: *Aulostyrax* (Gressitt, 1960a), *Bronthispa* (Böving and Craighead, 1931; Maulik, 1938; Lange, 1950; Kalshoven, 1951; Gressitt, 1955, 1960a, 1960b, 1963b; Gressitt and Kimoto, 1963; Cox, 1988; Kimoto and Takizawa, 1994, 1997); *Caledonispa* (Gressitt, 1960b, 1963); *Callistola* (Gressitt, 1960a, 1963b; Gressitt and Kimoto, 1963a); *Cryptonychus* (Maulik, 1932); *Enischnispa* (Gressitt, 1963b; Gressitt and Kimoto, 1963); *Isope-dispa* (Gressitt, 1960b); *Octodonta* (Gressitt, 1960a, 1963b; Gressitt and Kimoto, 1963; Kogan and Kogan, 1979); *Oxycephala* (Gressitt, 1960a, 1955); and *Stephanispa* Gressitt (Gressitt, 1960b). Most of these were collected, reared, and described by J.L. Gressitt, a remarkable feat. Mariau (2004) summarized cryptonychine biology indicating that larvae are mostly sheath feeders between unopened spears of palms. Some also mine stems and leaves (Maulik, 1932; Lepesme, 1947). Eleven plant families have been recorded as hosts (table 3).

DELOCRANIINI HINCKS (1 genus, 3 species; 1 sampled, all examined)

Delocraniini is distinct for morphology, membership as a "transitional" group (Maulik, 1919), and is allied with Notosacanthini and Spilophorini (Hincks, 1952; Borowiec, 1995). Several autapomorphies support Delocraniini: a longitudinally grooved frontoclypeus, an arrangement of cells on the elytral explanate margin, and the occurrence of single trichobothria at regular intervals along the elytral edge and that correspond with carina between cells on the explanate margin.

Hsiao and Windsor (1999) did not sample Delocraniini. In the present study, the three known species and two putative new species (Chaboo, unpubl. data) are scored the same. Delocraniine autapomorphies were pruned

from the dataset prior to analysis. The single terminal on cladograms represents the entire tribe. Delocraniini falls out in clade 49 (Bremer support 3) at the root of the polytomy Notosacanthini + (Delocraniini + Hemisphaerotini) + ((Spilophorini + Cassidinae s.str.)). Maulik's (1919) hypothesis of Delocraniini positioned between Hispinae s.str. and Cassidinae s.str. is supported here. Immature stages of *Delocrania cossyphoides* are known (Bondar, 1940; Zenner, 1968; Genty et al., 1978; Buzzi, 1988; Mariau, 2004) and a generic revision with its descriptions is under way (Chaboo, unpubl. data).

DORYNOTINI HINCKS (6 genera, 4 sampled; 47 species, 4 sampled)

The relatively small Neotropical tribe was defined on the basis of parallel claws (Hincks, 1952), but this feature is widespread across Cassidinae. Borowiec (1995) resolved Dorynotini as a member of a derived polytomy with Cassidini and Ischyrosonychini. The single species considered by Hsiao and Windsor (1999) was placed among genera of Cassidini. The four genera sampled here are dispersed among various cassidines, and tribal monophyly is not recovered. Two genera, *Dorynota* and *Paratrikona*, are resolved here as sister taxa (Clade 58). The other two genera, *Polychalca* and *Oxynodera*, form clade 66 with *Canistra* (Omocerini) (fig. 89).

Only Bignoniaceae hosts are known (Jolivet and Hawkeswood, 1995; Borowiec and Świętojańska, 2005). Exophagous immatures have been described in *Dorynota* and *Paranota* (appendix 2) and are collected and await description in *Paratrikona* (Chaboo, unpubl. data).

EPISTICTINI HINCKS (3 genera, 11 species; 1 sampled)

Hincks (1952) diagnosed Epistictini by its free mouthparts and short clypeus but these are neither unique to the tribe nor do they represent a unique combination. Monophyly was not tested here but the single exemplar is recovered among derived cassidines in clade 64, *Epistictina* + *Basiprionota*, supporting previous hypotheses (Hincks, 1952; Zaitzev and Medvedev, 1982; Borowiec, 1995). This

finding is discussed above under Basiprionotini. The placement of (*Epistictina* + *Basiprionota*) as sister to the omocerine clade 65 (*Prenea* + (*Polychalca* + (*Canistra* + *Oxynodera*))) is identical in all MPTs and is supported by the situation of the elytral basal margin (fig. 89). Borowiec's (1994) account of afro-tropical epistictines is a starting point for further research. Few immatures are known for these Asian species: in *Epistictia* (Gressitt, 1952; Takizawa, 1983) and in *Epistictina* (Zaitzev and Medvedev, 1982; Chen et al., 1986; Ghate and Rane, 2002). Their hosts are in Bignoniaceae and Meliaceae.

EUGENYSINI HINCKS (3 genera, all sampled; 35 species, 4 sampled)

Eugenysines are considered a natural group within Cassidini based on the apical expansion of tarsomere V (which hides the base of the claws) (Hincks, 1952). Eugenysines and stolaines have been regarded as each other's closest relatives on the basis of a single ventral process of the claw (Hincks, 1952). Borowiec (1995) amalgamated Eugenysini, Omocerini and Stolaini under the group name Mesomphaliini and recovered this terminal in the relationship (Basiprionotini + (Omocerini + (Mesomphaliini + (Dorynotini + Cassidini + Ischyrosonychini)))). Hsiao and Windsor (1999) sampled a single species that was recovered in the most derived cassidine clade as (*Eugenysa* + (*Stolas* + *Echoma*)).

In the present study, multiple species in the three eugenysine genera were examined. Monophyly is supported by two synapomorphies: the apical expansion of tarsomere V (char. 185) (which hides the base of the claws) (supporting Hinck's [1952] character hypothesis); and the very long, tightly coiled ejaculatory duct (char. 206) (defined in Chaboo, 2002). Another diagnostic character, the single basal tooth of the claws, also appears in all Stolaini and some Cassidini. Generic relationships are resolved in clade 81 (fig. 90), (*Agenysa* + (*Miocalaspis* + *Eugenysa*)), with the sister group relationship of *Miocalaspis* + *Eugenysa* supported by a three-chambered spermathecal receptacle (described in Chaboo, 2002).

The crown placement of Eugenysini is germane to discussions of maternal care in cassidines. The two sampled *Eugenysa* species exhibit maternal care (Windsor and Choe, 1994; Chaboo, 2002; table 6). These relationships suggest that maternal care originated once within the tribe. Eugenysines are so little known that new records of care should be expected.

EURISPINI WEISE (3 genera, 14 species;
1 sampled)

As presently circumscribed, this Indo-Australian tribe comprises the genera *Eurispia*, *Leucispia*, and *Squamispia* (Würmli, 1975a; Seeno and Wilcox, 1982). The tribe was previously allied with Leptispini and Cryptonychini (Weise, 1911; Würmli, 1975a; Seeno and Wilcox, 1982). Samuelson (1968) suggested that Aproidini and Anisoderini were more closely related, especially because of the granular eye facets. Neither Borowiec (1995) nor Hsiao and Windsor (1999) investigated this tribe. A single exemplar, *Eurispia vittata*, is scored here and is resolved in clade 36 as (Eurispini + (Aproidini + Exothispini)) (fig. 84; Bremer support 1) and is supported by three synapomorphies, characters 29, 32 and 83 under unambiguous optimization. A sinuous spermathecal duct (char. 203 state 2) may be an autapomorphy for *Eurispia*. Results here appear to support Samuelson's (1968) hypothesis of eurispine affiliations with Aproidini.

Adult eurispines have a very distinct narrowly elongate body form, cylindrical pronotum with posterior sensory tufts, relatively short legs, and body with deep punctures that contain erect scales (Würmli, 1975a). The body form and punctures with scales appear to be autapomorphies that will support tribal monophyly when more eurispines are sampled. Adult eurispines are free-living while larvae are sheath feeders (e.g., of the Cyperaceae *Gahnia*). Both adults and larvae can overwinter in the tight basal axils of their hosts (Chaboo, personal obs.).

EXOTHISPINI WEISE (1 genus, 1 species;
sampled)

Exothispini was previously considered as related to Callohispiini and Coelaenomeno-

derini (Würmli, 1975a), but this is not supported here with its placement in clade 37, *Aproida* + *Exothispia* (Bremer support 1). This sister group relationship is supported by characters 26, 47, 51 and 101 under unambiguous (clade 37, fig. 84) and slow optimizations (appendix 5), and additionally by character 136 under fast optimization (appendix 5). Tarsomere V has a ventral projection positioned between the claws (char. 182, state 0) (Würmli, 1975a), but this appears to be homoplastic. The biology of *Exothispia reimeri* Kolbe is unknown and this impedes a decisive resolution of its position.

GONIOCHENIINI HINCKS (5 genera, 13 species;
1 sampled)

This Neotropical tribe was defined on the basis of changes in antennal pubescence (Spaeth, 1942; Viana, 1964b), partial coverage of the head by the pronotum, and prosternal process shape (Hincks, 1952). It was not included in Borowiec (1995) and was represented by a single species in Hsiao and Windsor (1999), where it was resolved as sister to some stolaine genera. This tribal concept and its placement were not tested here since the single exemplar of *Batonota* was pruned from the final analysis due to ambiguity.

The sole detailed description of immature stages of Goniocheniini is that of a fifth instar of *Chlamydocassis cribripennis* (Boheman) (Buzzi, 1988; Świątojańska et al., 2005). Fiebrig (1910) provided limited description of immatures of two other *Chlamydocassis* species. Immatures of a *Polychalma* species have been collected and will be described (Riley, unpubl. data). Adults and larvae are exophagous leaf feeders of hosts in Ehretiaceae, Lamiaceae, and Sterculiaceae (table 3). Larvae carry a large shield mass with exuviae deeply embedded within the fecal matrix.

GONOPHORINI WEISE (10 genera, 290 species;
1 sampled)

Würmli (1975) circumscribed this Old World tribe by a suite of features; however, he acknowledged that this was a difficult group to define. Monophyly is still very much questionable. A single genus, *Klitispia*, was

sampled here and is resolved in clade 22 (fig. 82; Bremer support 4) with the relationship (Coelaenomenoderini + Gonophorini). This sister relationship is moderately supported by secondary loss of the midcranial suture, presence of the parascutellary striole, presence of fenestrate elytral punctures, and expanded tarsomere I. Gonophorine larvae are leaf miners of Araceae, Arecaceae, Costaceae, Marantaceae, Musaceae, Orchidaceae, Pandanaceae, Poaceae, and Zingiberaceae (Kalshoven, 1951; Gressitt, 1963; Jolivet and Hawkeswood, 1995).

HEMISPHAEROTINI HINCKS (2 genera, all sampled; 42 species, 2 sampled)

Borowiec (1995) located this tribe as derived within Cassidinae and sister to Hispinae s.str. Hsiao and Windsor (1999) sampled a single species that was united as sister to Prosopodontini. In the present study, Hemisphaerotini is recovered by all analyses with unambiguous support (clade 50, fig. 85) based on the membranous egg mass covering (autapomorphy), larvae with four caudal processes (autapomorphy), basket-like (or bird's nest) exuvio-fecal shield architecture (autapomorphy), immobile shield (autapomorphy), elongate prothoracic spiracles (autapomorphy), adults with broad angular prosternal processes, and a scutellum that overlaps the pronotal posterior angle (autapomorphy). Pupal caudal processes and retention of the exuvio-fecal shield is shared with other derived cassidines. Hemisphaerotine biology and aspects of immature morphology and shields were recently reviewed (Chaboo and Nguyen, 2004).

HISPINI WEISE (23 genera, 4 sampled; 611 species, 4 sampled)

This is the second largest tribe of Cassidinae, accounting for 10% of cassidine diversity (fig. 2). Members are found worldwide and adults typically have the dorsum spinose. This spininess has been considerably valued, so much so that Würmli (1975a) spent little time covering the morphology since the tribe appeared to be so well supported. The single exemplar sampled by Hsiao and Windsor (1999) did not test tribal monophyly, but it

was placed in the relationship (Alurnini + (Hispini + Cryptonychini)). Four genera are sampled here and are recovered as the resolved monophyletic clade 23 (fig. 82) with subclades 24 and 25, in the relationship (*Trichispa* + (*Dactylispa* + (*Asamangulia* + *Dorcathispa*))). Four synapomorphies (i.e., chars. 28, 70, 113 and 134; Bremer support 6) support tribal monophyly. The spinose lateral elytral edges (char. 134) are an exclusive feature of Hispini, and this supports Würmli's (1975a) view.

The function of dorsal spininess has been historically attributed as a defensive mechanism. Although untested, this is a reasonable hypothesis, as adults are conspicuous on host plants and are slow flyers. The well-circumscribed tribal boundaries of Hispini provide a firm context for investigating its biology and systematics.

Given their rank as the second most speciose clade in Cassidinae, it is not a surprise that Hispini use the highest number of hosts—30 families of monocots and eudicots (table 3). What is surprising is how little known are immature stages, which are unrecorded for *Acymenychnus* Weise, *Callanispa* Uhmman, *Cassidispa* Gestro, *Chrysispa* Weise, *Dorcathispa* Weise, *Jambhala* Würmli, *Phidodontina* Uhmman, *Pleurispa* Weise, *Polyconia* Weise, *Pseudispella* Kraatz, *Rhadinosa* Weise, *Sinispa* Uhmman, *Thomispa* Würmli, *Thoracispa* Chapuis, *Trichispa* Chapuis, and *Unguispa* Uhmman.

HISPOLEPTINI UHMANN (1 genus, 4 species; not sampled)

This small South American tribe has been diagnosed by a combination of adult features that appear throughout Cassidinae. Its placement near Sceloenoplini and Chalepini (Seeno and Wilcox, 1982) remains untested because it has not been represented in any systematic studies to date. Individuals are rarely collected, and few specimens exist in collections.

Mariau (2004) summarized what little is known of hispoleptine biology and indicated that some species have four instars and a prolonged developmental period from egg to adult. Immatures are undescribed.

IMATIDIINI HINCKS (8 genera, 2 sampled; 78 species, 2 sampled)

The monophyly, relationships and inclusions of Imatidiini have always been ambiguous, often discussed but with little resolution. As early as 1910, Weise suggested that it was allied with Cephaloleiini and should be classified in Hispinae s.str. because of life-history features. Bondar (1940a, 1940b) also considered Imatidiini and Cephaloleiini closely related and transferred Imatidiini to Hispinae s.str., a move supported by hispine researchers (Monrós and Viana, 1947, 1951; Papp, 1953). However, cassidine researchers usually placed Imatidiini in Cassidinae s.str. (Spaeth, 1914, 1938; Blackwelder, 1946; Aslam, 1965; Windsor et al., 1992) where it has been allied with Hemisphaerotini and Spilophorini (Seeno and Wilcox, 1982).

Borowiec's (1995) synonymy of Imatidiini under the name Cephaloleiini has been supported (Borowiec, 1999; Hsiao and Windsor, 1999). However, Borowiec (2000) later considered Imatidiini valid, including *Demotispia* Baly, one of nine cephaloleine genera. Staines (2002) again synonymized Imatidiini with Cephaloleiini.

Bondar's (1940a, 1940b) illustrations of the larva of *Imatidium nevei* Bondar are poor, but they clearly show an extremely flattened form similar to described cephaloleine, arescine and callispine larvae. Immatures of another *Imatidium* species studied here were similarly flattened. Imatidiine larval biology is of extreme interest since some species are known to be open external leaf feeders (Bondar, 1940a, 1940b, 1941, 1942, 1943). At least two species have adults that construct leaf shelters in which they feed cryptically (Gilbert et al., 2001).

Hsiao and Windsor (1999) found Cephaloleiini (including Imatidiini) as the sister clade to all other Cassidinae. Wilf et al. (2000) inserted a terminal to represent Arescini, although it was not originally analyzed in Hsiao and Windsor (1999). Duckett et al. (2004) sampled a single *Imatidium* exemplar, which was resolved in the relationship *Imatidium* + (Cryptocephalinae + other cassidines). Farrell and Sequeira (2004) also found *Imatidium* falling out separately from other cassidines. The results of Duckett

et al. (2004) and Farrell and Sequeira (2004) are real surprises and may be due to the different evolutionary histories of the sampled genes.

Remarkably, although Imatidiini appears to have enjoyed much attention relative to other cassidine tribes, there has been little discussion of actual morphological data to support various opinions and hypotheses of imatidiine monophyly, affiliations, or various synonymies. Synonymy with Cephaloleiini may be necessary because of the similar scale-like larvae (L. Borowiec, personal commun.) and similar adult morphology (C. Staines, personal commun.), but detailed comparative morphology is lacking.

In the present study, Imatidiini is represented by two generic exemplars, *Calliaspis* and *Imatidium*. These are recovered closely together at nodes 45 and 47, in a completely resolved area of topologies but with poor support (Bremer support 1). Imatidiine and cephaloleine monophyly and sister relationships are not supported. Arescini is recovered as sister to remaining cassidines, in contrast to Wilf et al. (2000). However no one (Borowiec, 1995; Hsiao and Windsor, 1995; McKenna and Farrell, 2005; present study) has examined imatidiine relationships adequately (i.e., taxon sampling).

ISCHYROSONYCHINI HINCKS (2 genera, 18 species; 1 sampled)

This New World tribe was diagnosed by the free mouthparts and short clypeus of the adult head. It was allied with Basiprionotini based on the longitudinally striate antennomeres (Hincks, 1952). In catalog classifications, it appears close to Asterizini and Stolaini (Seeno and Wilcox, 1982). These three tribes have been synonymized under two different group names, Physonotini by Borowiec (1999) and Ischyrosonychini by Riley et al. (2002); however, no unambiguous diagnostic characters have been proposed for this group concept. Hsiao and Windsor (1999) found support for the sister relationship Ischyrosonychini + Physonotini, nested among derived cassidines. They did not sample Asterizini. My sample of *Asteriza* (Asterizini), *Ischyrosonyx* (Ischyrosonychini),

and *Eurypepla* and *Physonota* (Physonotini) tests these previous hypotheses. No support is found for a close relationship between Ischyrosonychini with Asterizini or Physonotini. Ischyrosonychini is resolved at node 53 as sister to all other derived cassidines (Bremer support 14). Synapomorphies supporting node 54 include larvae with anus in a terminal position (char. 12, state 0), partial coverage of the head by the pronotum (an autapomorphy) (char. 26, state 0), adult head with midfrontal sulcus extended to frons (char. 31, state 0), mesosternum notched and receiving the prosternal process (char. 118, state 0), the elytral basal margin crenulate (an autapomorphy) (char. 139, state 1), elytral epipleura with an internal longitudinal carina (char. 154, state 0), and spermathecal gland and duct entries separated but closely positioned (char. 197, state 1). The quality and quantity of characters and the robustness of support for clade 53 are powerful arguments favoring this grouping of derived cassidines.

LEPTISPINI WEISE (1 genus, 67 species;
1 sampled)

This tribe was previously defined by its triangular hairy clypeus (Würmli, 1975a). The single exemplar here is recovered between *Stenispa* (Cephaloleiini) and *Ceratispa* (Cryptonychini) based on characters 67, 98, 137, and 173 (clade 38). It is distinguished here by the unique cryptic feeding of larvae within a leaf shelter. *Stenispa* larvae are exophagous (Riley and Enns, 1979; Ford and Cavey, 1985) whereas *Ceratispa* larvae are miners (Gressitt, 1960a, 1963).

The unusual leaf-shelter building behavior of *Leptispa* larvae (Maulik, 1919) is complex and needs further study. The pubescent venter of adults described by Maulik (1919) and their ability to withstand periods of submersion suggest additional characters. The single long caudal process of larvae is a source of missing information since the available simple line illustrations do not show sclerite attachment. Homologizing this process with other caudal processes of cassidine immatures is difficult without examination of specimens.

NOTOSACANTHINI HINCKS (2 genera, 254
species; 1 sampled)

This well-defined tribe has been problematic for separating classical cassidines and hispines. It has historically been treated within Cassidinae s.str. (Zaitzev and Medvedev, 1982; Borowiec, 1999; Borowiec and Świętojańska, 2004) or within Hispinae s.str. When classified in Cassidinae s.str., Notosacanthini has been variously allied with Epistictini and Basiprionotini (Zaitzev and Medvedev, 1982), with *Aspidimorpha* (Aspidimorphini) (Hawkeswood, 1989; Monteith, 1991), and even with Oncocephalini (Medvedev and Eroshkina, 1988). Borowiec (1995) resolved Notosacanthini as sister to one cassidine subclade where other members included so-called transitional tribes, Delocraniini, Spilophorini, Hemisphaerotini, Cephaloleiini, and Callispini.

Notosacanthine monophyly is strongly supported by several autapomorphies that were removed prior to analysis. Putative affiliations with Aspidimorphini, Epistictini and Basiprionotini are rejected here. Oncocephalini was not included here so this hypothesis remains to be tested. Notosacanthines are firmly ensconced in an intermediate area between Cassidinae s.str. and Hispinae s.str., along with Delocraniini, Hemisphaerotini, Imatidiini and Spilophorini (clade 47). These tribes all have exophagous larvae; however, known *Notosacantha* larvae are leaf miners (Medvedev and Eroshkina, 1988; Reid, 1995; H. Ghate, personal commun.; M. de Baar and G. Monteith, personal commun.; Chaboo, personal obs.).

OEDIOPALPINI MONRÓS AND VIANA (1 genus,
37 species; 1 sampled)

This monogeneric tribe was previously allied with Cephaloleiini (Seeno and Wilcox, 1982). The single species sampled by Hsiao and Windsor (1999) was resolved as sister to Spilophorini. Staines (2002) synonymized Oediopalpini with Spilophorini. Wilf et al. (2000) revised the topology of Hsiao and Windsor (1999), relocating *Oediopalpa* as sister to Delocraniini, although no additional analyses were performed. The present study recognizes a sister relationship between oediopalpines and *Cephaloleia* (clade 15).

The placement of *Oediopalpa* suggests that cassidine larval shields and the attendant morphological apparatus (telescoped anus, urogomphi) originated twice, with *Oediopalpa* and with Cassidinae s.str.

OMOCERINI HINCKS (7 genera, 4 sampled; 139 species, 4 sampled)

Goniocheniini and Omocerini were separated on the basis of an antennal feature, the demarcation of the distal section of the antenna beginning with antennomeres IV and V in goniocheniines and with VI and VII in omocerines (Spaeth, 1942; Viana, 1964a). Hincks (1952) noted that a change in pubescence demarcated distal and proximal antennal sections. Viana (1968) viewed this as a weak character since the pubescence feature is not easily defined. Seenó and Wilcox (1982) treated omocerines with Spilophorini and Goniocheniini. Borowiec (1995) synonymized Omocerini with Eugenyini and Stolaini under Mesomphaliini on the basis of unclear morphological distinctions. Two genera, *Omocera* and *Discomorpha*, were sampled by Hsiao and Windsor (1999) and were recovered as sister taxa, and sister to derived cassidines. Four genera, *Canistra*, *Oxynoderia*, *Prenea*, and *Polychalca*, including many species, were sampled in the present study and these are recovered in the monophyletic clade 65 (fig. 89) based on three synapomorphies: epipleural brace and internal carina connected (char. 155), straight or slightly sinuate apical margin of tarsomere III (char. 172), and duct and gland insertions located on an expanded section of the proximal spermathecal duct (an autapomorphy) (char. 199). However, the original character diagnosis based on distributions of proximal and distal antennomeres fails when compared among a wider sample of cassidines. The identification of a genitalic novelty is not surprising, as genitalia were ignored in cassidine systematics until recently.

ONCOCEPHALINI WEISE (3 genera, 72 species)

Oncocephalines were previously allied with Gonophorini and Hispini (Seenó and Wilcox, 1982). This Old World tribe has not been represented in any systematic studies to date,

and little is known about their biology and morphology. A few species are known to be leaf miners of Convolvulaceae, Dioscoraceae, Orchidaceae, Poaceae, and Zingiberaceae (table 3).

PHYSONOTINI HINCKS (6 genera, 2 sampled; 46 species, 2 sampled)

Physonotini was diagnosed by narrowed elytral lateral margins, thickened elytral margins, a broad prosternum that is expanded posteriorly, and dorsum lacking opalescence (Hincks, 1952). Borowiec (1995) synonymized this tribe with Ischyrosomychni and Asterizini because of ambiguous boundaries, and he resolved this terminal in the subclade of derived cassidines as (Basiprionotini + (Omocerini + (Mesomphaliini) + (Dorynotini + Cassidini + Ischyrosomychni))). Head visibility separated (Omocerini + derived cassidines) from Basiprionotini. Hsiao and Windsor (1999) sampled a single species of *Physonota* that was resolved as Physyonotini + Ischyrosomychni. Borowiec (1999) synonymized these two tribes plus Asterizini, under the name Physyonotini; however, Riley et al. (2002) called the same group Ischyrosomychni because it is the oldest available name.

Physonotine systematics has been touched on in the above treatments of Asterizini and Ischyrosomychni. Six physyonotine species in four genera were examined here, and characters were scored for *Eurypepla* and *Physonota*. These are resolved separately in clade 54 with *Eurypepla* in clade 57 as sister to Dorynotini (fig. 86). *Ischyrosomyx* (Ischyrosomychni) and *Asteriza* (Asterizini) also appear separated, with the former at clade 54 as sister to derived cassidines and the latter ensconced with aspidimorphine genera. The general lack of resolution at node 54 restricts discussion of these tribal relationships.

Physonotines have several unusual features: gregarious larvae that range widely in shield behavior (naked, wet, or hard shields) (Chaboo and Gómez, unpubl. data); petalophagous larvae (Chaboo, 2004); a fixed quiescent fifth instar (pre-pupa) (Gómez, 2004), and adult color polymorphism in *Physonota* (Caulfield, 1887; Sanderson, 1948; Kirk, 1971; Britten et al., 2003) and *Eurypepla* (Chaboo, 2004).

Petalophagy by *Eurypepla* larvae (Chaboo, 2004) is a flexible behavior, in contrast to that reported in two stolaine *Echoma* species (Windsor et al., 1995). This rare feeding pattern has two independent origins among crown cassidines.

PROMECOTHECININI WEISE (2 genera, 34 species; 1 sampled)

Würmli (1975) circumscribed this small Indo-Australian tribe on the basis of a short adult head retracted into the prothorax and a long, toothed hindfemur. The head shortening and retraction may have appeared distinct when considered only among Hispinae s.str. but these appear to be common across Cassidinae. Promecothecinini were previously allied with Colaenomenoderini and Gonophorini (Seeno and Wilcox, 1982). The single sampled species is recovered as sister to Anisoderini (fig. 81) based on characters on 107, 170, 172, and 193 under unambiguous and slow optimizations, and 170, 172 and 193 under fast optimizations. This sister group relationship is a novel hypothesis. Promecothecines are found in Asia, Australia, and Madagascar where they feed on Arecaceae, Flagellariaceae, Heliconiaceae, Pandanaceae, Poaceae, Musaceae, and Zingiberaceae (Jolivet and Hawkeswood, 1995; Staines, 2004; Mariau, 2004).

PROSOPODONTINI WEISE (1 genus, 26 species; 1 sampled)

Staines (2002) diagnosed Prosopodontini by the small head, clypeus extended to antennal bases, setae on posterior pronotal angles, scutellum shape, and elytra with 10 puncture rows and a parascutellary striole. None of these features is unique to this tribe. The single species sampled by Hsiao and Windsor (1999) was recovered as sister to Hemisphaerotini. In contrast, the single species sampled by McKenna and Farrell (2005) was resolved as sister to *Alurnus*. Neither hypothesis is supported here.

Prosopodonta was recovered here in a weakly supported basal branch (clade 10, Bremer support 3; fig. 81) with the relationship (Prosopodontini + (Promecothecini + Anisoderini)). Support for this group included

discrete clypeus (char. 66) under unambiguous and fast optimizations, distal medial emargination of the labrum (char. 78), shovel-shaped terminal segments of larvae (char. 9), and spermathecal gland separated but closely situated, (under slow optimization; char. 197). All of these are homoplasious.

Prosopodonta larvae have been reported as miners (Jolivet and Hawkeswood, 1995) and external leaf feeders (McCoy, 1984, 1985) of Neotropical *Heliconia* (Jolivet and Hawkeswood, 1995) and Arecaceae (Staines, 2004). There is some ambiguity about larval identification (Staines, 2004); nevertheless, if *Prosopodonta* species do range from mining to exophagy, this diversity has implications for understanding transitions in larval feeding and microhabitat.

SCELOENOPLINI UHMANN (5 genera, 2 sampled; 219 species, 2 sampled)

Seeno and Wilcox (1982) previously placed this moderately large Neotropical tribe near Prosopodontini and Hispoleptini. Staines (2002) diagnosed Sceloenoplinae by proximal and distal sections of antenna distinguished at antennomeres IV, anterior pronotal seta, presence of parascutellary stria, and number of elytral puncture rows (Staines, 2002). All of these characters are plesiomorphic when compared across Cassidinae. Sceloenoplinae was not included in previous cladistic analyses and is investigated here by sampling two genera, *Cephalodonta* and *Sceloenopla*. Sceloenopline monophyly is not supported; instead, *Sceloenopla* is resolved basally in clade 17 as sister to seven other tribes (fig. 82), and *Cephalodonta* is placed among chalepines in clade 30 (fig. 83). The lack of monophyly is not unexpected given historically problematic tribal circumscription.

Members have been recorded on six plant families (table 3), and some species have larvae that are scrapers (Mantovani et al., 2005)

SPILOPHORINI UHMANN (2 genera, both sampled; 30 species, 2 sampled)

Spilophorini was defined on the basis of presence of the anterior and posterior trichobothria and carinate labrum (Hincks, 1952).

These are symplesiomorphies in the context of all Cassidinae. Borowiec (1995) presumed monophyly of Spilophorini and recovered it in a clade with Delocraniini, Hemisphaerotini, Notosacanthini, Cephaloleiini, and Callispini. Hsiao and Windsor (1999) sampled the two recognized genera and supported tribal monophyly and a sister group relationship with Oediopalpini. Wilf et al. (2000) used the results of Hsiao and Windsor (1999); however, Spilophorini was omitted without explanation on their figure 2. The inclusion of this taxon would have conflicted with their evolutionary hypothesis.

The present study recovered a reasonably supported (Bremer support 9) spilophorine branch (clade 52), *Calyptocephala* + *Spilophora*, within the transitional zone between Cassidinae s.str. and Hispinae s.str., close to Delocraniini, Hemisphaerotini, and Notosacanthini. Under unambiguous character optimization (fig. 85), support comprises the following five homoplasious states: discontinuous dorsal body profile (char. 22), posterior pronotal trichobothria present (char. 101), posterior margin of mesoscutellum truncate (char. 116), elytral basal margin wider than pronotal posterior margin (char. 136), and CuA cell 1 open in hindwings (char. 157). Under slow optimization, this character list included the presence of antennal ventromarginal grooves (char. 59). Under fast optimization, characters 22, 72, 77, 82, 99, 101, 116, 136, 157 and 200 provided additional support.

Spilophorines form a small Neotropical tribe. The known larvae (Moura, 1985; Buzzi and Miyazaki, 1992; Windsor et al., 1992) make an exuviae-only shield, with the exuviae longitudinally compressed and the thick paired caudal processes prominently displaced. This design is very similar to the shield constructed by the larva of *Oediopalpa guerini* (Chaboo, unpubl. data). These particular shields are different from other exuviae-only shields in their pattern of exuvial compression.

STOLAINI HINCKS (16 genera, all sampled; 528 species, 20 sampled)

This Neotropical tribe accounts for 9% of cassidine diversity (fig. 2) and was originally diagnosed on the basis of a single basal tooth

on the claws and confused elytral punctation (Hincks, 1952). This tooth feature also occurs in Eugenysini and in some cassidine genera. The elytral character is widespread across Cassidinae. Morphology of Stolaini was previously treated in Michalski (1995).

In previous cladistic analyses, Borowiec (1995) synonymized Eugenysini, Omocerini and Stolaini under the group name Mesomphaliini and presumed this terminal monophyletic prior to analysis. Hsiao and Windsor (1999) failed to find monophyly of Stolaini, with genera appearing among derived cassidines with the relationship—(((Stolaini + Eugenysini) + Stolaini) + (Cassidini + (Goniocheniini + Ischyrosynychini))) + Stolaini).

All 16 stolaine genera are sampled here to test tribal monophyly and the tribe was not recovered as monophyletic. Stolaine genera were grouped in a large derived polytomy along with genera of Aspidimorphini, Asterizini, Basiprionotini, Cassidini, Charidotini, Dorynotini, Epistictini, Eugenysini, Omocerini, and Physonotini. A few stolaine genera are united as sister taxa; for example, clade 75 *Amythra* + *Anepsiomorpha*; clade 56 *Elytrogona* + *Stoiba*; clade 55 *Chelymorpha* + *Phytodectoidea*; clade 61 *Zatrephina* + (*Poecilaspis* + *Stolas*), and finally, clade 75 is a polytomy involving the remaining genera grouped with a monophyletic Eugenysini. This finding is not a surprise given the previous ambiguous support. Clearly presence or absence of a claw tooth is a weak phylogenetic signal.

Monophyly of *Echoma*, *Eugenysa*, and *Omaspides* is supported, but not of *Stolas*. *Stolas* was also previously found to be paraphyletic (Hsiao and Windsor, 1999). The boundaries of *Acromis* (fig. 90) and *Elytrogona* (fig. 87) were previously redefined (Chaboo, 2000, 2001) and hold up under the present analysis. The position of Eugenysini among Stolaine genera is discussed above under Eugenysini. Maternal care in these tribes (fig. 19, table 6) is discussed below.

The sister group relationship *Elytrogona* + *Stoiba* is not surprising since this was proposed before based on their shared development of a suite of morphological modifications related to flightlessness (Chaboo, 2000). They occur only in the Greater Antillean Caribbean islands.

Stolaine larvae are typically exophagous leaf feeders, but petalophagy has been reported as obligate in two species of *Echoma* (Windsor et al., 1995). This rare feeding pattern has two origins, in *Echoma* and in *Eurypepla* (Physonotini) among derived cassidines.

UROPLATINI WEISE (32 genera, 3 sampled; 396 species, 3 sampled)

Uroplatines form the fourth largest cassidine tribe, accounting for 7% of known species diversity (fig. 2). Uroplatini and Chalepini were differentiated by fusion of their terminal antennomeres (Maulik, 1932) and a close relationship between them has been proposed in various catalogs. Riley et al. (2001) argued that the antennal feature is continuous among these genera and synonymized Uroplatini under Chalepini. Hsiao and Windsor (1999) sampled two uroplatines and these were resolved in a basal monophyletic clade along with the sampled chalepine taxa. Uroplatines and chalepines sampled here appear in the fully resolved monophyletic clade 26 that also includes the exemplar sceloenopline, *Cephalodonta*. This clade is recovered on all MPTs, and appears in the consensus of both complete (fig. 77) and restricted matrix analyses (fig. 91). Two homoplasious characters support clade 26, depression of the scutellum and a truncate posterior shape of the scutellum. The placement of the uroplatines approximates to previous hypotheses, as follows (fig. 83): clade 27 as (chalepines + (*Microrhopala* + *Octotoma*)). *Microrhopala* + *Octotoma* is supported by two synapomorphies: fusion of distal antennomeres and frontoclypeus distinctly protuberant from antennal bases. Characters 152 and 182 support clade 32 (chalepines + *Uroplata*). Uroplatine monophyly is not supported but there is clearly some relationship between Uroplatini and Chalepini.

The character, number of antennomeres, was removed in the final analyses due to scoring difficulties (missing or incomplete antennae). Determining the exact number of antennomeres is difficult because fusion of sections can be complete or partial; sutures may be developed, reduced or absent. Be-

cause this feature has been fundamental in diagnosing Uroplatini and Chalepini, it must be investigated in additional taxa and in more detail.

EMERGENT EVOLUTIONARY PATTERNS

A strongly formulated phylogenetic hypothesis should have great predictive powers. Phylogenies not only bring a historical context to familiar biological patterns, they also permit novel ones to emerge. The Cassidine phylogenetic hypothesis and the integrated biology proposed here are not final, but they offer a reasonable evolutionary model for discussing the origin, radiation and prediction of recognized and novel biological phenomena.

I. Adult Head Morphology. My phylogenetic results suggest that several distinct processes have altered the landscape of the cassidine head: (1) progressive retraction of the head into the prothorax (2) head shortening, (3) "flattening" of the venter and (4) an increasingly posterior position of the mouth. The relationship between head shortening and head retraction with clypeal reduction, fusion, and loss and gular size is unclear. Cassidine head morphology is diverse and the functional significance of such distinct changes is unclear.

A detailed study of cassidine mouthparts should increase our understanding of their trophic specializations and should help define additional characters. These transforming processes of the head are separate from prothoracic changes that affect dorsal head exposure (pronotal anterior extension) and mouth exposure (prosternal anterior extension).

II. Adult Thorax Morphology. The phylogeny proposed here suggests that the adult thorax has become shortened and compacted across the clade. The pleuron has been transformed from a lateral position in plesiomorphic cassidines to a ventral position in derived cassidines. The relative length of the prothorax to the meso- and metathorax has also altered with the former becoming shortened relative to the length of the hypomeron. At the same time, these three thoracic segments increasingly overlap, interlock and even fuse. For example, grooves

appear in the anterior margin of the meso- and metasternum for retention of processes from the preceding segment. The result is an increasingly shortened, rigid thoracic box with tightly fitted elytra, elytral clasps and locks. These changes must certainly affect flight mechanics.

III. Adult Leg Morphology. Adult legs apparently became shorter and the relative proportions of the femur and tibia have been altered. Femoral and tibial grooves, for folding the tibiae and tarsi, and corresponding thoracic depressions support a pattern of compaction in the adult bodies of derived cassidines. Variations in the tarsomere (inflation, flattening ventral pubescence, and setation types) and claw development should be explored further.

IV. Trophic Specialization of Larvae. Seven ecological guilds are diagnosed here for Cassidinae based on feeding mode and microhabitat. The natural history of leaf miners, stem miners, leaf-shelter constructors, open-leaf feeders, rolled-leaf dwellers, flower-bract grazers and petalophagous larvae are summarized under Biology. Stem mining, bract grazing, petalophagy and feeding within a leaf-shelter occur as small generic and intra-generic specializations. My proposed phylogeny suggests two major radiations of leaf miners and open-leaf chewers, a minor radiation of cryptic rolled-leaf scrapers, and several small clades of stem-mining, floral-scraping (a single origin within *Cephaloleia*), flower-chewing (two origins within *Echoma* and *Eurypepla*) and leaf-shelter chewing (a single origin within Leptispini; clade 39).

The biological data are not detailed enough to indicate how plastic some of these feeding patterns are. Guild concepts have heavily influenced historical taxonomic concepts. Precise terms must distinguish taxonomic and ecological groupings and should be refined by additional parameters as immature stages become better known.

V. Larval Morphology. Although morphology of immature stages was not treated in detail, there are clearly many questions to explore in immature stages of Cassidinae. Morphology appears to be intimately tied to ecological diversity; for example, my phylogenetic hypothesis suggests convergent evo-

lution of the grossly similar platyform water-penny larvae in Cephaloleini, Callispini, and Imatidiini. Developmental mechanisms underlying that morphology, including particular structures such as the elongate spiracles, scoli, caudal process, and telescoped anus, warrant attention. Comparative morphological and ecological analysis may reveal the influences of habitat and ecological constraints.

VI. Convergence of Leaf Shelter Constructions. Leaf shelters are built in two tribes, in Leptispini (Froggatt, 1914; Fletcher, 1914; Maulik, 1919; Voronova and Zaitsev, 1982; Chen et al., 1986) and in Imatidiini (Gilbert et al., 2001). *Leptispa* larvae bend leaves of rice and coconut to make the construction in which they feed and pupate. In *Imatidium rufiventre*, adults overlap and glue two leaves of *Inga* together and feed while hidden within the shelter. Larvae are free-living and pupation is on exposed leaf surfaces. The host plants, building stages, and construction behaviors appear to be completely different in Leptispini and Imatidiini.

VII. Origin and Radiation of Maternal Care. Maternal care has originated in the most derived clade of cassidines, clade 54 (Bremer support 14), which is a polytomy basally but fully resolved in the relevant subclade 75 (Bremer support 4). The behavior is currently known in 17 species of five genera in two tribes (fig. 19, table 6). Four of these genera were sampled here. Given the root polytomy of clade 76, it appears that maternal care has two possible origins, in one clade 76 (Bremer support 5) and in another clade 79 (Bremer support 3) under both unambiguous and delayed optimizations. The biologies of *Agenysa* and *Miocalaspis* are not known; however, both are likely to exhibit maternal care. Both *Hilarocassis* and *Ogdoecosta* may have maternal care. Such a finding would support a single origin of maternal care and may help resolve the polytomy at clade 75.

Windsor and Choe (1994) previously hypothesized two host-mediated origins of maternal care in Cassidinae, one on *Ipomoea* (Convolvulaceae) and the other on *Mikania* (Asteraceae). *Omaspides* (*O.*) *pallidipennis* (Boheman) also shows care on its hostplant, *Passiflora*. The use of *Mikania* as a host appears as a secondary derivation within

clade 79, indicating this host selection is unrelated to the origin of care.

Most cassidine maternal care records were described in the last 15 years. Extrapolating from known species diversity of these genera, it is possible that about 100 species exhibit care. Clustering of eggs, larvae and pupae appears to have preceded the origin of maternal care. Studies of both care providing and related non-care providing species will contribute additional phylogenetic characters and will help elucidate the evolutionary history of this complex behavior.

VIII. Origin and Radiation of Shields. Based on available information, my results indicate two origins of shield retention by larvae. One origin is in *Oediopalpa* (in clade 15) and the other is at the base of clade 48, traditional tortoise beetles. Ambiguity presented in other characters for Notosacanthini and Spilophorini results in a polytomy on the consensus; however shields appear to have originated once in derived cassidines, clade 48. These two origins at clades 15 and 48 also coincide with origins of the telescoped anus and the caudal processes. Both nodes 15 and 48 mark transitions between leaf mining to exophagous feeding. Shield retention may have influenced the evolution of exophagy in cassidines.

My field observations indicate that the caudal processes and telescoped anus are functionally correlated in shield retention and repair. Caudal processes hold the shield and provide an interlocking device for the internal scaffold of the shield. The telescoped anus is long, extensible, and mobile and is used to attach feces with precision; even when sections are broken off, individuals can precisely replace lost fecal filaments. It is unclear whether these functionally correlated traits are also morphologically integrated, that is, inherited together.

Clade 15. Immatures for only a single species of *Oediopalpa* (36 species) have been described (Maulik, 1932). Examination of dried pinned specimens clearly shows an exuvial shield and paired caudal processes, which appear to resemble those of *Calyptcephala* (Spilophorini). The status of the anus was not ascertained from the dried, shriveled specimen. *Oediopalpa* is placed here as sister to *Cephaloleia*, a rolled-leaf dweller.

Clade 48. The second origin of shield retention is at the base of a large speciose clade of ca. 3000 species. With the exception of Notosacanthini, most known larvae in this clade retain shields. In the tribe Physonotini, some *Physonota* species may be naked (carry no shield) or may have a wet fecal coat (K. Olmstead, personal commun.), similar to *Eurypepla* (Chaboo, 2004). Soft shields and the lack of shields appear to be secondary derivations.

Immatures of *Asteriza* and *Elytrogona* have been collected and await description; both genera have larvae with shield retention (H. Matsuzawa, personal commun.). Immatures of *Agenysa* and *Miocolaspis* are still unknown but their placement within a large clade of external-feeding, shield-retaining larvae and the appearance of these features in related genera suggest that species in these two genera also have these features.

Shield behavior and the morphological apparatus necessary for building and retaining could have been significant innovations driving cassidine speciation. In *Oediopalpa* (clade 15), its origin was followed by minor diversification, that is, 37 species (Papp, 1975); in comparison clade 48 represents a radiation of ca. 3000 species. The repeated origin of such seemingly complex features is not unlikely given other remarkable evidence of convergent evolution, for example the arthropod eye (Oakely and Cunningham, 2002).

Life on open leaves might pose a particular evolutionary challenge in presenting greater exposure to abiotic and biotic dangers that are not part of the landscape of internal or closed-leaf feeding. Fecal shield retention could have influenced the entry of cassidine larvae into this new landscape. A variety of hypotheses seek to explain the functional significance of shield retention (Olmstead, 1994, 1996; Olmstead and Denno, 1992, 1993; Müller and Hilker, 1999, 2001, 2003), and these have been variously tested. Investigations of shield functions have been directed at predator effects. When shields are removed, predators quickly ate all naked larvae (Olmstead 1994, 1996). However, shields may have had a different function originally, perhaps for protection from insolation or desiccation. We may not be able

to unravel the original function. Vencl et al. (2004) have hypothesized that shields may be correlated with switching to chemically complex, derived dicotyledonous host plants. The position of *Oediopalpa* under this scenario is interesting as its members are grass-feeders.

CONCLUSIONS

The main goals of the present research, testing the monophyly of and developing a hypothesis of cassidine tribal relationships, have been achieved. A biological synthesis for classical hispine leaf miners and tortoise beetles was a secondary goal but was essential to defining novel biological characters (e.g., larval morphology) and detecting previously unrecognized evolutionary trends (e.g., adult thoracic compaction) and patterns (duration and numbers of larval instars; diversification in association with ecological guilds). The functional significance of shields is being tested, and the historical insights revealed by the present study can help to refine experimental research.

The finding of support for the relationship Galerucinae s.l. + Cassidinae is not surprising. They share similar proximity and position of antennal insertions. Evidently, all chrysomelid subfamilies must be sampled in an expanded study to stabilize the outgroup node. Within Cassidinae, the paraphyly of classical Hispinae s.str. and classical Cassidinae s.str. is not unexpected. The placements of *Demotispa*, *Imatidium*, *Notosacantha*, *Delocrania* and Hemisphaerotini are crucial to the distinction of the classical cassidines and hispines, and these groups are placed medially on the consensus. Within this nexus of taxa, there are a series of dramatic transitions in the morphology and life history of Cassidinae. Dense sampling around particular internal nodes is needed to stabilize internal relationships. Few characters have been defined in the past, and many have been demonstrated as homoplasious in my study (e.g., the single basal claw of *Stolaini* and *Eugenysini*).

This study demonstrates that Cassidine morphology is a rich pool of character information. Character hypotheses proposed here may be discarded in future studies, but novel ones will be defined. Additional data

types (ecological, behavioral, protein, and sequence data) are needed to improve the phylogenetic hypothesis presented here. Including cassidine fossils in analyses will help calibrate and date these patterns in geological time.

Although the present study suggests that many currently recognized tribes are not monophyletic, it is premature to propose a new classification and new tribal diagnoses without sampling Callohispani, Hispoleptini, Hybosispini, and Oncocephalini, and additional genera. The current availability of several alternative higher level phylogenetic hypotheses indicates the vitality of systematic research in Cassidinae. Competing hypotheses at all hierarchic levels (tribal and generic trees) will permit evaluation of character quality and ideas regarding ingroup relationships.

Future efforts in Cassidine systematics should focus on unknown biology information. Fieldwork that emphasizes the collection of ecological and behavioral data and immature stages will fill this gap. Adult mouthparts and internal anatomy and immature stages are also promising avenues for morphological research. Data for Aproidini, Arescini, and Exothispini may improve our understanding of the evolution of early cassidines and of hypognathy. Studies of Delocraniini, Hemisphaerotini, Imatidiini, and Notosacanthini are critical to understanding larval feeding transitions from mining to exophagy. Current hypotheses of relationships among derived cassidines are not stable. Phylogenetic studies should move away from single gene trees (Doyle, 1992) and focus on truly integrated phylogenies using all data types. The evolution of Cassidinae involved many interesting trends and was punctuated by complex innovations, and deeper knowledge will add resolution to this history.

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APPENDIX 1

TAXON LIST FOR ADULT MORPHOLOGY AND
PHYLOGENETIC ANALYSIS OF CASSIDINAE

Taxa are arranged alphabetically by subfamily, tribe, and genus. Species for which states are coded in the matrix are listed first. Species examined to assess variation within genera are indicated second under "Additional species". Depositions of specimens are indicated in brackets and are listed in appendix 3.

OUTGROUPS

Galerucinae s.l.

Ophraella Wilcox species 1. Country: Trinidad.
Sample = 6 [AMNH].

Cryptocephalinae

Pachybrachis circumcincta Sahlberg. Country: U.S.:
California. Sample = 6 [AMNH].

Donaciinae

Plateumaris rufa (Say). Country: U.S.: New Jersey,
Massachusetts. Sample = 10 [AMNH].

Lamprosomatinae

Lamprosoma Kirby species 1. Country: Trinidad and
Colombia. Sample = 5 [AMNH].

Sagrinae

Sagra Fabricius species 1. Country: Cameroon.
Sample = 4 [AMNH].

Criocerinae

Lema trivittata Say. Country: Mexico. Sample = 12
[AMNH].

INGROUP

Alurnini Weise

Alurnus bipunctatus Olivier. Country: Peru. Sample =
3 [AMNH].

Plautyauchenia deyrollei Riley. Country: Brazil. Sam-
ple = 3 [BMNH].

Anisoderini Weise

Anisoderina guerinii Baly. Country: Thailand; Laos.
Sample = 7 [BPBM].

Estigmene chinensis Hope. Country: Laos. Sample =
8 [BPBM].

Lasiochila gestroi (Baly). Country: Laos. Sample = 7
[BPBM].

Aproidini Weise

Aproida balyi Pascoe. Country: Australia. Sample = 6
adults, 1 pupa, 1 larva [BPBM].

Arescini Weise

Arescus Perty species 1. Country: Brazil. Sample = 4
[AMNH].

Aspidimorphini Hincks

Aspidimorpha miliaris Fabricius. Country: Philippines;
Vietnam. Sample = 5 [CUIC].

Conchylotenaria hybrida Boheman. Country: South
Africa. Sample = 2 [CUIC].

Laccoptera cicatrosa (Boheman). Country: Senegal.
Sample = 7 [AMNH; BMNH].

Additional species examined but not coded:

Aspidimorpha furcata (Thunberg). Country: China.
Sample = 2 [AMNH].

Aspidimorpha quadrinodosa Boheman. Country:
Congo. Sample = 8 [MMUE].

Asterizini Hincks

Asteriza flavicornis Olivier. Country: Guyana. Sample
= 11 [CUIC; MMUE].

Basiprionotini Hincks

Basiprionota chinensis (Fabricius). Country: China.
Sample = 3 [AMNH].

Additional species examined but not coded:

Basiprionota quadriimpressa (Boheman). Country:
Java. Sample = 10 [MMUE].

Prioptera sinuata (Olivier). Country: Brazil. Sample =
1 [CUIC].

Basiptini Hincks

Basipta stolidia Boheman. Country: South Africa.
Sample = 10 [BMNH].

Additional species examined but not coded:

Basipta glauca Chevrolat. Country: South Africa.
Sample = 6 [MMUE].

Botryonopini Weise

Botryonopa foveicollis Baly. Country: Philippines.
Sample = 2 [BPBM].

Callispini Weise

Callispa bowringi Baly. Country: Thailand. Sample =
9 [BPBM].

Hispodonta chapuisi Gestro. Country: New Guinea.
Sample = 8 [BPBM].

Additional species examined but not coded:

Callispa fraudulenta Würmli. Country: Philippines.
Sample: 47 [AMNH, paratypes].

Cassidini Hincks

Charidotella bicolor Fabricius. Country: U.S.: New
York. Sample = 2 [AMNH].

Jonthonota maculata Mann. Country: U.S.: Oregon.
Sample = 4 [AMNH].

Orexita picta Boheman. Country: Brazil. Sample = 24
[AMNH].

Additional species examined but not coded:

Agroiconota bivittata Say. Country: U.S.: Mississippi.
Sample = 1 [CUIC].

Cassida rubiginosa Muller. Country: U.S.: New York.
Sample = 10 [CSCC; CUIC].

Charidotella (Philaspis) bivulnerata (Boheman).
Country: Mexico. Sample = 4 [AMNH; CUIC].

Charidotis punctatostrata Boheman. Country: Brazil.
Sample = 5 [AMNH].

Chirida guttata Olivier (= *Deloyala* Chevrolat).
Country: Mexico; U.S.: Texas. Sample = 14
[CSCC; CUIC].

Deloyala clavata Barber [= *Helocassis clavata* (Fab-
ricius)]. Country: U.S.: Arizona. Sample = 1
[CUIC].

Gratiana pallidula (Boheman). Country: U.S.: Ar-
izona, California, Texas. Sample = 1 [AMNH].

Microtenochira hebraea Spaeth (= *Microtenochira*
reticularis (Degeer)). Country: Trinidad. Sample =
1 [CSCC].

- Orectis rugosa* Boheman. Country: Guatemala. Sample = 3 [AMNH].
- Oxylepus deflexicollis* (Boheman). Country: Oran. Sample = 10 [MMUE].
- Plagiometriona clavata* Blackwelder (= *Helocassis clavata* (Fabricius)). Country: Panama. Sample = 3 [CSCC].
- Syngambria bisinuata* (Boheman). Country: Brazil. Sample = 3 [AMNH].
- Cephaloleiini** Weise
- Cephaloleia* Chevrolat species 1. Country: Brazil. Sample = 3 [AMNH].
- Demotispa* Baly species 1. Country: Brazil, Peru. Sample = 10 [AMNH].
- Stenispa metallica* Fabricius. Country: U.S.: New Jersey. Sample = 8 [AMNH].
- Chalepini** Weise
- Anisostena perspicua* Horn. Country: U.S.: Maine. Sample = 10 [AMNH; CUIC].
- Anoplitis inaequalis* Weber (= *Chalepus* Thunberg). Country: U.S.: North Carolina. Sample = 6 [AMNH].
- Baliosus californicus* (Horn). Country: U.S.: Oregon. Sample = 4 [AMNH].
- Chalepus acuticornis* Chapman. Country: Guatemala, Mexico. Sample = 10 [AMNH].
- Odontota dorsalis* Thunberg. Country: U.S.: New Jersey. Sample = >200 [AMNH].
- Xenochalepus* species 1. Country: Mexico. Sample = 3 [AMNH].
- Charidotini** Hincks
- Metrionella bilimeki* Spaeth. Country: Mexico. Sample = 18 [AMNH].
- Psalidonota dorsoplagiata* Champion (= *Coptocycla* (P.) *dorsoplagiata* Champion). Country: U.S. Sample = 25 [AMNH].
- Additional species examined but not coded:
- Charidotis punctatostrigata* Boheman. Country: Brazil. Sample = 6 [AMNH; CUIC]
- Coelaenomenoderini** Weise
- Cyperispa thorachostachyi kolombangana* Gressitt. Country: Solomon Islands. Sample = 8 [BPBM].
- Pharangispa alpiniae marginata* Samuelson. Country: Solomon Islands. Sample = 2 adults, 3 larvae [BPBM].
- Cryptonychini** Weise
- Callistola speciosa fasciata* Weise. Country: Brazil. Sample = 21 [AMNH].
- Ceratispa palmicola* Gressitt. Country: New Guinea. Sample = 8 [BPBM].
- Palmispa parallela* Gressitt. Country: New Guinea. Sample = 4 [BPBM].
- Delocraniini** Hincks
- Delocrania panamensis* Champion. Country: Costa Rica; Panama. Sample = 14 [AMNH; EGRG; INBIO; SEMC].
- Additional species examined but not coded:
- Delocrania cossyphoides* Guérin. Country: Brazil; Guyana; Surinam. Sample = 7 [USNM; IRSNB].
- Delocrania latipennis* Champion. Country: Ecuador. Sample = 1 [KSEM].
- Dorynotini** Hincks
- Dorynota pugionata* (Germar). Country: Brazil. Sample = 6 [MMUE].
- Paratrikona lerouxi* Boheman. Country: Cuba. Sample = 8 [MMUE; AMNH].
- Polychalca* (*Polychalca*) *punctatissima* (Wolf) (= *Desmonota variolosa* Boheman). Country: Venezuela. Sample = 5 [AMNH].
- Oxynodera biplagiata* Guérin. Country: Venezuela. Sample = 1 [CUIC].
- Additional species examined but not coded:
- Akantaka insidiosa* Boheman. Country: Colombia; Costa Rica. Sample = 3 [MMUE].
- Batonota* Hope species 1. Country: Mexico. Sample = >100 [AMNH].
- Epistictini** Hincks
- Epistictina viridimaculata* (Boheman). Country: Sumatra. Sample = 9 [CUIC; MMUE].
- Eugenysini** Hincks
- Eugenysa caedemadens* (Lichstenstein). Country: Brazil, French Guiana; Surinam. Sample = 15 [CUIC; MCZ].
- Eugenysa columbiana* Boheman. Country: Colombia; Costa Rica. Sample = 18, >100 larvae, >20 pupae [CSCC; MCZ; MMUE].
- Eugenysa coscaroni* Viana. Country: Panama. Sample = 8 [CSCC; CUIC; KSEM; MMUE].
- Miocalaspis gentilis* (Erichson). Country: Colombia. Sample = 2 [MMUE].
- Additional species examined but not coded:
- Eugenysa connectens* Spaeth. Country: Bolivia. Sample = 11 [MCZ].
- Eugenysa guianensis* (Boheman). Country: French Guiana; Peru, Venezuela. Sample = 10 [AMNH].
- Eugenysa grossa* (Linnaeus). Country: Sample = 13 [MCZ].
- Eurispini** Weise
- Eurispa vittata* Baly. Country: Australia. Sample = 6 [BPBM].
- Exothispini** Weise
- Exothispa reimeri* Kolbe. Country: Mozambique. Sample = 1 [RMCA].
- Gonicheniini** Hincks
- Batonota lerouxii* Spaeth (= *Paratrikona lerouxii* (Boheman)). Country: Cuba. Sample = 6 [MMUE].
- Additional species examined but not coded:
- Zeugonota quadrinodosa* Boheman. Country: Brazil. Sample = 1 [AMNH].
- Gonophorini** Weise
- Klititspa opacicollis* Gestro. Country: Philippines. Sample = 4 [AMNH].
- Hemisphaerotini** Hincks
- Hemisphaerota cyanea* Say. Country: U.S.: North Carolina; Florida. Sample = 12 adults; 2 larvae [AMNH; CUIC; MCZ].
- Spaethiella circumdata* Boheman. Country: Costa Rica. Sample = 5 [MMUE].
- Additional species examined but not coded:
- Hemisphaerota gundlachi* (Boheman). Country: Cuba. Sample = 11 adults, 1 larva [MCZ; MMUE].

- Hemisphaerota palmarum* Boheman. Country: Dominican Republic. Sample = >100 (all stages) [CSCC].
- Spaethiella* Barber and Bridwell species 1 and 2. Country: Costa Rica; Venezuela. Sample = >100 [INBIO; CUIC].
- Hispidini** Weise
- Asamangulia cuspidata* Maulik. Country: India. Sample = 22 [AMNH].
- Dactylispa angusta* Gestro. Country: Philippines. Sample = >100 [AMNH].
- Dorcatthispa* Weise species 1. Country: South Africa. Sample = 7 [SANC].
- Trichispa* Chapuis species 1. Country: South Africa. Sample = 7 [PPRI].
- Hispoleptini** Weise
- Not sampled.
- Imatidiini** Hincks
- Calliaspis rubra* Olivier. Country: Brazil. Sample = 2 [AMNH].
- Imatidium capense* Herbst. Country: Venezuela. Sample = 2 [CUIC].
- Additional species examined but not coded:
- Imatidium fasciatum* Gestro. Country: Colombia. Sample = 4 [AMNH].
- Ischyrosomychni** Hincks
- Ischyrosomyx oblonga* Sturm. Country: Argentina. Sample = 7 [CUIC; MMUE].
- Additional species examined but not coded:
- Cistudinella obducta* (Boheman). Country: Brazil. Sample = 1 [AMNH].
- Leptispini** Weise
- Leptispa denticulata* Achard. Country: Congo. Sample = 5 [IRSNB].
- Notosacanthini** Hincks
- Notosacantha (Hoplionota) badia* (Boheman). Country: Philippines. Sample = 8 [AMNH; MMUE].
- Oediopalpini** Monrós and Viana
- Oediopalpa guerini* (Baly). Country: Panama. Sample = 8 [AMNH].
- Omocerini** Hincks
- Canistra plagosa* Erichson. Country: Colombia. Sample = 6 [AMNH; MMUE].
- Oxynoderma biplagiata* (Guérin) (= *Discomorpha* Chevrolat). Country: Venezuela. Sample = 3 [CUIC].
- Prenea strigata* Panzer. Country: Brazil. Sample = 5 [AMNH; CUIC].
- Additional species examined but not coded:
- Discomorpha (Discomorpha) biplagiata* Guérin. Country: Colombia. Sample = 6 [MMUE].
- Dolichotoma aenea* Germar. Country: Brazil. Sample = 1 [AMNH].
- Polychalca cribipennis* Boheman. Country: Brazil. Sample = 3 [AMNH].
- Polychalca (Desmonota) platynota* Germar. Country: Brazil. Sample = 4 [AMNH; MMUE].
- Tauroma* Hope species 1 (= *Omocerus* Chevrolat). Country: Brazil. Sample = 4 [AMNH; CSCC].
- Oncoccephalini** Weise
- Not sampled.
- Physonotini** Hincks
- Eurypepla jamaicensis* Linnaeus. Country: U.S.: Puerto Rico. Sample = 4 [AMNH].
- Physonota* Boheman species 1. Country: U.S.: Puerto Rico. Sample = 4 [AMNH].
- Additional species examined but not coded:
- Cistudinella* Champion species near *apiata*. Country: Brazil. Sample = 10 [MMUE].
- Eurypepla calochroma* Boheman. Country: U.S. Sample = >50 [CSCC].
- Eurypedus nigrolineata* Boheman. Country: Panama. Sample = >100 [CSCC].
- Physonota alutacea* Boheman. Country: Trinidad; Mexico. Sample = 15 [AMNH; MMUE].
- Promecothecini** Weise
- Promecotheca papuana* Csikii. Country: New Britain. Sample = 8 adults, 15 larvae, 1 pupa [BPBM].
- Prosopodontini** Weise
- Prosopodonta dorsata* Baly. Country: Costa Rica. Sample = 34 [INBIO].
- Sceloenoplini** Uhmann
- Cephalodonta* Chevrolat species 1. Country: Guyana. Sample = 4 [AMNH].
- Sceloenopla mantecada* Sanderson. Country: Puerto Rico. Sample = 3 [CUIC].
- Spilophorini** Hincks
- Calyptocephala nigricans* Germar. Country: Brazil. Sample = 7 [AMNH; MMUE].
- Spilophora aequatoriensis* Spaeth. Country: Ecuador. Sample = 3 [MMUE].
- Additional species examined but not coded:
- Spilophora peruana* (Erichson). Country: Peru. Sample = 1 [AMNH].
- Stolaini** Hincks
- Acromis sparsa* Boheman. Chaboo (2002) listed all localities, specimen numbers and deposits.
- Amythra valida* (Boheman) (= *reticulata*). Country: Brazil. Sample = 4 [USNM].
- Anepsiomorpha deplanata* (Boheman). Country: Argentina. Sample = 25 [USNM].
- Chelymorpha cassidea* Fabricius. Country: U.S.: New York. Sample = 10 [CUIC].
- Echoma marginata* (Kirsch). Country: Brazil. Sample = 6 [FMNH].
- Elytrogona quatuordecimaculata* (Latreille). Chaboo (2001) listed localities, specimens and deposits.
- Hilarocassis exclamationis* (Linnaeus). Country: Costa Rica; Mexico; Panama. Sample = 22 [CAS; CMN; FMNH].
- Ogdoecosta biannularis* (Boheman). Country: Mexico. Sample = 55 [CAS; CISC].
- Omaspides (Omaspides) clathrata* (Linnaeus). Country: Brazil; Surinam. Sample = 5 [USNM].
- Omaspides (Omaspides) pallidipennis* (Boheman). Country: Brazil, Peru. Sample = 7 [CUIC; FMNH; USNM].
- Omaspides (Parechoma) semilineata* (Boheman). Country: Brazil. Sample = 9 [AMNH; FMNH].
- Paraselenis (Spaethiechoma) flava* (Linnaeus). Country: Brazil. Sample = 8 [FMNH].

- Poecilaspis impressa* Panzer (= *Botanochara* Dejean). Country: Brazil. Sample = 5 [AMNH].
- Phytodectoidea quatuordecimpunctata* (Boheman). Country: Mexico. Sample = 4 [CSCC; CISC].
- Stoiba swartzii* (Schönherr). Country: Jamaica. Sample = 40 [AMNH; BMNH; CMNH; LBC; USNM].
- Stolas (Anacassis) fuscata* Klug. Country: Brazil; Paraguay. Sample = 5 [FMNH].
- Stolas illustris* Chevrolat. Country: Mexico; Guatemala. Sample = 4 [CMN; CISC; FSCA].
- Terpsis quadrivittata* (Champion). Country: Panama. Sample = 5 [USNM].
- Zatrephina sexlunata* (Klug). Country: Brazil. Sample = 11 [AMNH; CAS].
- Additional species examined but not coded:
- Acromis spinifex* (Linnaeus). Chaboo (2002) listed localities, specimen numbers and deposits.
- Acromis venosa* Erichson. Chaboo (2002) listed localities, specimen numbers and deposits.
- Hilarocassis albida* Germar. Country: Brazil. Sample = 4 [USNM].
- Ogdoecosta flavomaculata* (Champion). Country: Honduras, Mexico. Sample = 5 [USNM].
- Stoiba angusticollis* (Suffrian). Country: Cuba. Sample = 9 [AMNH; LBC; MZC].
- Stoiba flavicollis* (Klug). Country: Cuba. Sample = 104 [BMNH; KSEM; NHRS; MCZ MMUE; MNHUB; MZHF].
- Stolas sexmaculata* Boheman (= *Mesomphalia* Hope). Country: Brazil. Sample = 2 [AMNH].
- Stolas lebasii* (Boheman). Country: Costa Rica. Sample = 5 [CSCC].
- Zatrephina imperialis* Spaeth (= *sexlunata* (Klug)). Country: Argentina. Sample = 4 [AMNH].
- Uroplatini Weise
- Microrhopala vittata* (Fabricius). Country: U.S.: New Jersey, New York, Washington, Wyoming. Sample = >200 [AMNH].
- Octotoma marginicollis* Horn. Country: Mexico; U.S.: Arizona. Sample = 3 [AMNH].
- Uroplata girardi* Pic. Country: Tonga Islands. Sample = 3 [AMNH].

APPENDIX 2

INFORMATION SOURCES FOR MORPHOLOGY AND BIOLOGY OF IMMATURES IN 170 GENERA OF CASSIDINAE

Taxa are arranged alphabetically by subfamily and genus. Literature sources are indicated first, followed by species examined where specimens were available. Specimen numbers and codens of repositories are indicated in parentheses. Identifications were based on adult associations (numbers of adults examined are not indicated because a single adult specimen was borrowed from each collection series). Localities are stated as on original data labels. Full names of repositories are listed in appendix 3.

OUTGROUPS

Criocerinae: Böving and Craighead, 1930; Hennig, 1938; Sailsbury, 1943; Steinhausen, 1966; Schmitt,

1985a, 1985b, 1988; Lawrence, 1991; Lawrence and Britton, 1994; Cox, 2006; *Crioceris* Muller (Sailsbury, 1943; Peterson, 1951; Lawrence, 1991); *Lema* Fabricius (Riley, 1869; Knab, 1915; Sailsbury, 1943; Kaufman, 1967; Lawrence, 1991); *Lilioceris* Reitter (Medvedev and Zaitsev, 1979); *Oulema* Gozis (Lawrence, 1991).

Cryptocephalinae: Selman, 1988; Lawrence, 1991; Lawrence and Britton, 1994; *Cryptocephalus* Geoffroy (Beeson, 1941; Mohr, 1966; LeSage, 1986; Lawrence, 1991); *Griburius* Haldeman (Beamer, 1926); *Lexiphanes* Gistel (LeSage, 1984b); *Neochlamisus* Karren (Brown and Funk, 1995; Chaboo et al., in press); *Pachybrachis* Chevrolat (Fall, 1915; Lawson, 1976; LeSage, 1984a, 1984b, 1985a, 1985b; Lawrence, 1991).

Donaciinae: Sanderson, 1900; Böving, 1910; Böving and Craighead, 1930; Varley, 1939; Hoffman, 1940; Lawrence, 1991; Lee, 1991c; Bieńkowski, 1992, 1996; Bieńkowski and Orlova-Bieńkowskaja, 2004; Jolivet and Verma, 2002; Jolivet, 2003; *Donacia* (Sanderson, 1900; Peterson, 1951; Narita, 1989, 2003); *Plateumaris* (Narita, 2003).

Galerucinae s. l.: *Acalymna* Barber (Balduf, 1922; Böving, 1927; Gould, 1944; Peterson, 1951; Lawson, 1991); *Altica* Geoffroy (Woods, 1918; Peterson, 1951; Barstow and Gittens, 1971, 1973; DeSwarte and Balsbaugh, 1973; Lawson, 1991); *Blepharida* Chevrolat (Böving and Craighead, 1931; Peterson, 1951; Lawson, 1991; Frost, 1972, 1973); *Cerotoma* Chevrolat (Böving, 1931; Peterson, 1951); *Chaetocnema* Stephens (Anderson, 1938); *Crepidodera* Chevrolat (Balduf, 1926; Parry, 1986); *Diabrotica* Chevrolat (Lawrence, 1991); *Diamphidia* Gerstaecker (Chaboo et al., 2007); *Dibolia* Latreille (Peterson, 1951; Lawson 1991); *Disonycha* Chevrolat (Chittenden, 1899; Peterson, 1951; Lawson, 1991); *Eptirix* Foudras (Chamberlain et al., 1924; Peterson, 1951; Lawson, 1991); *Kuschelina* Bechyně (Böving in Blake, 1927); *Mantura* Stephens (Böving and Craighead, 1931; Lawson, 1991); *Longitarsus* Latreille (Böving and Craighead, 1931); *Phyllobrotica* Chevrolat (Böving, 1927); *Phyllotreta* Chevrolat (Chittenden, 1917; Peterson, 1951); *Polyclada* Chevrolat (Chaboo et al., in press b); *Pseudolampis* Horn (Casari and Duckett, 1998); *Psylliodes* Latreille (Böving and Craighead, 1931); *Pyrrhalta* Joannis (Lawrence, 1991); *Scelopypyrus* Crotch (Wilcox, 1965).

Lamprosomatinae: Fiebrig, 1910; *Oomorphoides* (Lee and Morimoto, 1991); *Oomorphus* Curtis (Kasap and Crowson, 1976).

Sagrinae: Bowring, 1856; Van Vollenhoven, 1862; Lucas, 1886; Crowson, 1948; Monrós, 1959; Tayade, 1978.

INGROUP

Acentroptera Baly: Mantovani et al., 2005.

Acrocassis Spaeth. **Specimens examined:** *Acrocassis* Boheman prob. *gibbipennis* (Boheman). Locality: South Africa, coll. Catherine Duckett, 2000 (CNDC).

Acrocassis Chevrolat: Fiebrig, 1910; Buzzi, 1980, 1988; Windsor, 1987; Preston-Mafham and Preston-

- Mafham, 1993; Upton, 1996; Chadwick, 1998; Chaboo, 2001; Vencl et al., 2005; A. Trillo, personal. comm. **Specimens examined:** All three *Acromis* species. Localities and repositories are listed in Chaboo (2001).
- Aethiopocassis* Spaeth: Świętojańska, 2004a.
- Agroiconota* Spaeth: Marques, 1932; Windsor et al., 1992. **Specimens examined:** *Agroiconota bivittata* (Say). Locality: U.S.: 1 mi. E Noberly No., Randolph Co., no data, no collector (6; UMRM); U.S.: Kansas, Hays, 26.VII.1945, coll. N.L.H. Krauss (1 egg mass, 5 larvae; USNM).
- Akantaka* Maulik: Windsor et al., 1992.
- Alurnus* Fabricius: Bondar, 1915; Merino and Vasquez, 1963; Villacis Santos, 1968; Strong, 1977a, 1977b. **Specimens examined:** *Alurnus humeralis* Rosenberg. Locality: Ecuador, Santo Domingo de los Colorado, from African palm (*Elaeis guianensis*), coll. Gualberto Marino (2 larvae, 1 adult; USNM).
- Anacassis* Spaeth: Buzzi, 1975a, 1975b, 1983, 1996; Morelli and Ponce de Leon, 1990. **Specimens examined:** *Anacassis prolixa* Boheman. Locality: Argentina: Misiones Lett., 4.II.1942, coll. H.L. Parker (1 egg mass; USNM).
- Anisodera* Chevrolat: Beeson, 1941. **Specimens examined:** Undetermined species. Locality: U.S.: San Francisco, ex *Zingiber* roots from Indonesia, 12.X.1990; det. Vogt (1 larva; USNM).
- Anisostena* Weise: Ford and Cavey, 1982, 1985; Staines, 2006.
- Anoplites* Kirby: Uhmman, 1949a.
- Aporocassida* Spaeth: Frers, 1922.
- Aproida* Pascoe: Monteith, 1970; Lawrence and Britton, 1994. **Specimens examined:** *Aproida balyi* Pascoe. Locality: Australia: S.E. Queensland, Cunningham's Gap, 24.III.1963, coll. G. Monteith (2 larvae, MCZ).
- Arescus* Perty: Böving and Craighead, 1931; Maulik, 1937; Wang, 1977; Seifert and Seifert, 1979a, 1979b; Strong, 1977a, 1977b; 1981, 1982a, 1982b; Strong and Wang, 1977; Morrison and Strong, 1981; McCoy, 1984, 1985; Staines, 1996; Wilf et al., 2000. **Specimens examined:** *Arescus labiatus* Perty. Locality: Brazil: Agua Preta, Bahia, 19.VI.1944, folded leaves of bananeirinha de mato (*Heliconia*), coll. P. Silva (1 larva; USNM). Undetermined species 1. Locality: Panama: 2.X.1933, ex bananas, no collector (1 larva; USNM). Undetermined species 2. Locality: Suriname, ex bird-of-paradise flower, colls. A.M. Potter and T.H. Russell (3 larvae; USNM).
- Asamangulia* Maulik: Kalshoven, 1951.
- Aspidimorpha* Hope: Sharp, 1899; Muir and Sharp, 1904; Maxwell-Lefroy, 1906; Kershaw and Muir, 1907; Schultze, 1908; Maulik, 1919; Taylor, 1930; Beeson, 1941; Paterson, 1941; Kalshoven, 1951; Gressitt, 1952; Skaife, 1953; Gressitt and Kimoto, 1963; Simon Thomas 1964; Taylor, 1965; Katiyar and Gargav, 1975; Takizawa, 1980; Hinton, 1981; Lawrence and Britton, 1981; Hawkeswood, 1982, 1987; Verma and Shrivasta, 1985; Cox, 1988, 1994a; Chen et al., 1986; Nakamura, 1989; Nakamura and Abbas, 1987, 1989; Buzzi, 1988; Miah et al., 1992; Zaitsev, 1992; Hilker, 1994; Kimoto and Takizawa, 1994, 1997; Jolivet and Verma, 2002; Heron, in press. **Specimens examined:** *Aspidimorpha furcata* (Thunberg). Locality: India: Goa, Mormugao, ex *Ipomoea*, XII.1924, coll. J.C. Bridwell (3 egg masses, 10 larvae; USNM). *Aspidimorpha miliaris* (Fabricius). Locality: Philippines, Negros, Victorias IV.1929, coll. F. Pierce (1 egg mass, 5 pupae; USNM). *Aspidimorpha sanctaerucis* (Fabricius). Locality: Java: Bogor, 12.II.1954 (1 pupa; USNM). *Aspidimorpha Hope* sp. Locality: Hollandia, V.1945, coll. B. Malkin (2 pupae; USNM).
- Aspidispa* Baly: Gressitt, 1960a, 1963b; Gressitt and Kimoto, 1963. **Specimens examined:** *Aspidispa kortalsiae* Gressitt. Locality: New Guinea: Baimy Lake, 21.VI.1961, coll. J.L. Gressitt (1 larva, MCZ).
- Asteriza* Chevrolat: H. Matsumara (personal commun.).
- Aulostyrax* Maulik: Gressitt, 1960a.
- Baliosus* Weise: Harris, 1835; Bondar, 1938; Chittenden, 1904; Needham et al., 1928; Ford and Cavey, 1985; Staines, 2006. **Specimens examined:** *Baliosus nervosus* (Panzer) (= *Baliosus rubra* Weber). Locality: U.S.: Michigan, South Haven, 6.X.1894 (2 larvae, 1 pupa, 1 adult; USNM).
- Balyana* Peringuey: Mariau, 1975.
- Basiprionota* Chevrolat: Schultze, 1908; Gressitt, 1952; Gressitt and Kimoto, 1963; Zaitsev and Medvedev, 1982; Chen et al., 1986. **Specimens examined:** *Basiprionota cerata* (Spaeth). Locality: Vietnam: Buon boi, 6.VI.1985, coll. L.N. Medvedev (1 larva; 1 pupa; CCCC, gift of collector).
- Basipta* Chevrolat: Maulik, 1919. **Specimens examined:** *Basipta glauca* Chevrolat. Locality: South Africa: Kwa-Zulu-Natal, Durban, I.2006, ex *Brachylaena discolor*, colls. C.S. Chaboo, H. Heron and E. Grobbelaar (long series of all life stages; AMNH, PPRI).
- Batonota* Hope. **Specimens examined:** Undetermined species. Locality: Brazil: Minas Gerais, ex *Tabebuia ochracea* (Bignoniaceae), coll. D. Yanega, (3 larvae; UCRC).
- Botanochara* Dejean: Frers, 1922; Buzzi, 1977; Costa et al., 1988.
- Botryonopa* Blanchard: Maulik, 1949a; Kalshoven, 1951; Chen et al., 1986. **Specimens examined:** Undetermined species. Locality: Palau Group, Pelelus, coastal native forest, ex *Pandanus tectorius*, 23.VIII.1946, coll. H.K. Townes (1 larva, 1 adult; USNM).
- Brachycornyna* Guérin-Méneville: Staines, 2006.
- Brontispa* Sharp: Böving and Craighead, 1931; Maulik, 1938; Lange, 1950; Kalshoven, 1951; Gressitt, 1955, 1960a, 1960b, 1963b; Gressitt and Kimoto, 1963; Cox, 1988, 1994a; Kimoto and Takizawa, 1994, 1997. **Specimens examined:** *Brontispa mariana* Spaeth. Locality: Udot Truk Atoll, 7-27.I.1949, coll. D. Langford (7 larvae; USNM).
- Caledonispa* Uhmman: Gressitt, 1960b, 1963. **Specimens examined:** *Caledonispa* sp. Locality: New Caledonia: 20°34'S 164°46'E, Mt. Panie refuge, 1300m, 16-18.IX.2000, colls. Bouchard, Burwell and Monteith (1 larva, 26 adults; QM).

- Callispa* Baly: Uhmman, 1949b; Kalshoven, 1951; Gressitt and Kimoto, 1963; Chen et al., 1986; Zaitsev, 2001. **Specimens examined:** *Callispa bowringi* Baly. Locality: Vietnam, coll. L.N. Medvedev (1 egg mass, 3 larvae, 1 adult; CCCC, gift of collector).
- Callistola* Dejean: Gressitt, 1960a, 1963b; Gressitt and Kimoto, 1963a.
- Calyptocephala* Chevrolat: Moura, 1985; Buzzi and Miyazaki, 1992; Windsor et al., 1992.
- Canistra* Erichson: Fiebrig, 1910.
- Carinispa* Uhmman: Uhmman, 1949a, 1949b.
- Cassida* Linnaeus: Suffrian, 1844; Guérin, 1846; Chapuis and Candèze, 1855; Riley, 1868; 1870a; Weise, 1893; Fyles, 1902; Muir and Sharp, 1904; Kershaw and Muir, 1907; Fiebrig, 1910; Blatchley, 1910; Rabaud, 1915a, 1915b, 1915c; Paterson, 1931; Böving and Craighead, 1931; Yeung, 1934; Engel, 1935; Nietzsche, 1939; Méquignon, 1941; Maulik, 1949b; Peterson, 1951; Varma, 1955; Gressitt, 1952, 1955; van Emden, 1962; Gressitt and Kimoto, 1963; Taylor, 1965; Mohr, 1966; Eisner et al., 1967; Steinhausen, 1969; Matis, 1970; Sankaran and Krishnaswamy, 1974; Kosior, 1975; Medvedev and Matys, 1975; Dubeshko and Medvedev, 1975; Maw, 1976; Ward and Pienkowski, 1978a, 1978b; Takizawa, 1980; Hinton, 1981; Medvedev, 1982; Brovdii, 1983; Singh et al., 1985; Chen et al., 1986; George and Venkatamaram, 1986; Cox, 1988, 1994a; Zaitsev, 1988, 1992; Nakamura et al., 1994; Kimoto and Takizawa, 1994; Lee, 1994; Leonardi and Sassi, 1997; Kimoto and Takizawa, 1994, 1997; Lee, 1994; Zwölfer, 1996; Müller and Hilker, 1999; Müller, 2002; Mathews and Reid, 2002; Borowiec and Świętojańska, 2003; Świętojańska, 2004b, 2005a, 2005b, 2005c. **Specimens examined:** *Cassida rubiginosa* Müller. Locality: U.S.: New York, Tompkins Co., Ithaca, Cornell University, Beebe Lake, ex *Arctium* sp. (burdock), 22.6.2003, coll. C.S. Chaboo (10 larvae, 5 adults; CCCC). Undetermined species 1. Locality: U.S.: Indiana: Vermillion Co., VI.20, coll. L. Luth (2 larvae; UMRM). Undetermined species 2. Locality: U.S.: Massachusetts, Chicopee, 16.VII.1900, coll. Dimmock (1 larva, 1 adult; USNM). Undetermined species 3. Locality: U.S.: Massachusetts, Boston Harbor, Great Brewster Island, 28.VI.1975, coll. A. Harkins (5 pupae, 5 adults; USNM).
- Cassidinoma* Hincks: Fiebrig, 1910; Buzzi, 1988.
- Cephalodonta* Chevrolat: Bondar, 1937.
- Cephaloleia* Blanchard: Maulik, 1932, 1933b; Bondar, 1938; Bruch, 1939b; Seifert and Seifert, 1976b; Strong and Wang, 1977; Seifert, 1982; Morrison and Strong, 1981; Staines, 1996; Johnson, 2004. **Specimens examined:** *Cephaloleia variabilis* Staines. Locality: Panama: Darien Province, along road near Rio Chucumaque, W. of Yaviza, X.2002, coll. D.D. McKenna (20 larvae, MCZ).
- Ceratispa* Gestro: Gressitt, 1960a, 1963b; Gressitt and Kimoto, 1963.
- Chalepus* Thunberg: Chittenden, 1904; Bruch, 1904, 1933; Needham et al., 1928; Bondar, 1938; Böving and Craighead, 1931; Uhmman, 1934; Peterson, 1951; Ford and Cavey, 1985; Staines, 2006. **Specimens examined:** *Chalepus omogerus* Crotch. Locality: U.S.: Virginia, near Chain Bridge, reared from *Phaseolus polystachus*, colls. Snyder and Barber (3 larvae, 4 pupae; USNM). Undetermined species. Locality: U.S.: Massachusetts, Springfield, 3.VIII.1902, coll. Dimmock (1 larva, 1 adult; USNM).
- Charidotella* Weise: Dugès, 1887; LeBlanc, 1986; Buzzi, 1988; Windsor et al., 1992; K. Olmstead, personal commun. **Specimens examined:** *Charidotella bifossulata* (Boheman). Locality: not available (1 pupa; USNM). *Charidotella bisbinota* (Boheman). Locality: Cuba, Camaguey, 15.VII.1923, coll. J. Acuna (1 pupa, 1 adult; USNM). *Charidotella emarginata* (Boheman). Locality: U.S.: Arizona, Patagonia, Santa Cruz, 17.VIII.1958, C. O'Brien (4 larvae; USNM). *Charidotella sexpunctata* (Fabricius). Locality: U.S.: Mass, Chicopee, 26.VII.1909, coll. F. Knab (13 larvae; USNM).
- Charidotis* Boheman: Fiebrig, 1910; Windsor et al., 1992; Medeiros et al., 2005. **Specimens examined:** Undetermined species. Locality: Brazil, Sao Paulo, no date, coll. Parker (2 egg masses, 16 larvae; USNM).
- Chelobasis* Gray: Maulik, 1932; Wang, 1977; Strong, 1977; Strong and Wang, 1977.
- Chelymorpha* Chevrolat: Riley, 1870a; Frers, 1922a, 1922b; Chittenden, 1924; Peterson, 1951; Takizawa, 1980; Buzzi, 1988; Vasconcelos-Neto and Jolivet, 1989, 1994; Lawson, 1991; Windsor et al., 1992; Fáveri et al., 1994; Medeiros et al., 2005; Vencl et al., 2005; K. Olmstead, personal commun. **Specimens examined:** *Chelymorpha cassidea* (Fabricius). Locality: U.S., Massachusetts, Springfield, no date, no collector (11 egg masses, 2 larvae, 8 pupae; USNM). *Chelymorpha phytophagica* Crotch. Locality: U.S.: Texas, El Paso, ex sweet potato vine, 8.VIII.1942, coll. W.K. Clore (1 larva, 1 pupa, 1 adult; USNM). Undetermined species 1. Locality: Cuba: Santiago de las Vegas, 7.IV.1905, no collector (1 larva, 1 adult; USNM). Undetermined species 2. Locality: Panama: Soberania National Park, near Gamboa, Pipeline Rd., 21.VI.1995, coll. C. Chaboo (2 larvae, 1 adult; CCCC).
- Chersinella* Champion: Windsor et al., 1992.
- Chiridopsis* Spaeth: Takizawa, 1980; Zaitsev, 1988; Kalaichelvan and Verma, 2000; Borowiec et al., 2001; Ghate et al., 2004.
- Chlamydocassis* Spaeth: Fiebrig, 1910; Buzzi, 1988; Świętojańska et al., 2005.
- Choeridiona* Baly: H. Ghate, personal commun.
- Cistudinella* Champion: Buzzi, 1988; Windsor et al., 1992; Medeiros et al., 2005; Gómez, unpublished data. **Specimens examined:** Undetermined species. Locality: Brazil: Minas Gerais, coll. D. Yanega (larvae, pupae, adults; UCRC).
- Cladophora* Dejean: Staines, 2002.
- Coelaenomenodera* Blanchard: Cotterell, 1925; Maulik, 1920, 1931; Cachan, 1957; Morin and Mariau, 1970; Mariau and Morin, 1971, 1972, 1974; Mariau, 1975; Chen et al., 1986; Cox, 1988, 1994a.
- Conchylotenia* Spaeth: Muir and Sharp, 1904; Olckers and Hulley, 1989; Heron, 1999. **Specimens examined:** Undetermined species. Locality: South Africa:

- coll. C.N. Duckett, site number 2000-071 (1 larva; CNCDC).
- Coptocycla* Chevrolat: Paterson, 1931; Windsor et al., 1992; Chaboo, in review; Yanega, personal commun. **Specimens examined:** *Coptocycla leprosa* Boheman. Locality: Panama: Taboga Island 12.VI.1911, coll. A. Busck (1 pupa; USNM); Mexico: Tehuantepec, coll. F. Knab (4 pupae; USNM). *Coptocycla texana* (Schaeffer). Locality: U.S.: Texas, Brownsville, ex Anacuna, 5.IV.1935, coll. Reagan (3 larvae, 1 pupa; USNM). Undetermined species 1. Locality: Costa Rica: Flor Sur, Catje Tiba, 21.VI.1970, coll. Loren B. Ford, ex *Cordia alliodora* (1 larva; USNM). Undetermined species 2. Locality: Costa Rica: Prov. Guanacaste, Taboga, 26–29.VI.1967, colls. Flint and Ortiz (2 larvae; USNM).
- Coraliomela* Jacobson: Bruch, 1939.
- Corynispia* Uhhmann: Bondar, 1938.
- Craspedonispia* Weise: Maulik, 1932.
- Craspedontia* Chevrolat (= *Calopepla* Hope): Weise, 1901; Garthwaite, 1939; Beeson, 1941; Zaitsev and Medvedev, 1982; Sen-Sarma and Ahmed, 1984; Cox, 1988, 1994a; Zaitsev, 1992; Świętojańska and Ghate, 2003. **Specimens examined:** *Craspedontia leayana* Latreille (= *Calopepla leayana* Latreille). Locality: India, Mangalore, ex Gmelina, VIII.1926, coll. J.C. Bridwell (1 larva, 1 pupa; USNM). *Craspedontia mouhoti* (Baly). Locality: CPB YSKm C HH Yana, 2.12.78, coll. L.N. Medvedev (2 larvae; CSCC, gift of collector).
- Cryptonychus* Gyllenhal: Maulik, 1932.
- Cteisella* Weise: Fiebrig, 1910; Buzzi, 1988.
- Cyperispia* Gressitt: Gressitt, 1960a.
- Dactylispia* Weise: Maulik, 1929, 1931, 1932; Kalshoven, 1951; Gressitt, 1963b; Gressitt and Kimoto, 1963; Chen et al., 1986; Kimoto and Takizawa, 1994, 1997; H. Ghate, personal commun. *Delocrania* Guérin-Ménéville: Bondar, 1940c; Zenner, 1968; Genty et al., 1978; Buzzi, 1988; Mariau, 2004.
- Deloyala* Chevrolat: Riley, 1870a. **Specimens examined:** *Deloyala guttata* (Olivier). Locality: U.S.: Massachusetts, Middlesex Co., Lincoln, 3.VIII.1984, coll. E.T. Armstrong (1 larva, 1 adult; MCZ); Delaware, Wilmington, coll. A.F. McDermott (4 larvae, USNM).
- Demotispia* Baly: Strong, 1977a, 1977b. **Specimens examined:** *Demotispia nevei*. Locality: Brazil, Bahia, Agua Preta, 25.V.1946, damaging coconut, coll. Pedoria Silva (7 larvae; USNM).
- Di cladispa* Gestro: Gressitt, 1963b; Gressitt and Kimoto, 1963; Alam, 1964; Sen and Chakravorty, 1970; Budraja, 1979; Clark, 1983; Chen et al., 1986; Vadadia et al., 1989; Kimoto and Takizawa, 1994, 1997.
- Discomorphia* Chevrolat: Candèze, 1861; Windsor et al., 1992.
- Dorynota* Chevrolat: Costa Lima, 1955; Buzzi, 1976b; Buzzi, 1988. **Specimens examined:** *Dorynota (Dorynota) pubescens* Blake. Locality: Haiti: Kenscoff, 3.III.1950, no collector (1 egg mass, 2 larvae, 1 pupa; USNM).
- Dorynota (Paranota)* undetermined species. Locality: not provided (5 larvae, 1 pupa; USNM).
- Downesia* Baly: Chen et al., 1986.
- Echoma* Chevrolat: Ferris and Nissen, 1927; Maulik, 1948b; Buzzi, 1988; Steinhausen, 1994a.
- Enischnispia* Gressitt: Gressitt, 1963b; Gressitt and Kimoto, 1963.
- Epistictia* Boheman: Gressitt, 1952; Takizawa, 1983.
- Epistictina* Hincks: Zaitsev and Medvedev, 1982; Chen et al., 1986; Ghate and Rane, 2002. **Specimens examined:** Undetermined species. Locality: Gynreoiseyoi, 24.V.85, coll. L.N. Medvedev (3 larvae; CSCC, gift of collector).
- Estigmene* Hope: Maulik, 1932; Beeson, 1941; Kalshoven, 1951; Chen et al., 1986.
- Eugenysa* Chevrolat: Windsor et al., 1992; Chaboo, 2002. **Specimens examined:** *Eugenysa columbiana* (Boheman). Localities and repositories listed in Chaboo (2002). *Eugenysini* undetermined. Locality: Colombia: Santa Rosa de Sucumbios, Kefan Indian Village, Rio San Miquel, Int. Putumayo, 400m, 2.IX.1971, coll. B. Malkin (1 larva, 1 adult; USNM).
- Eurispia* Baly: Gressitt, 1963b; Gressitt and Kimoto, 1963; Hawkeswood, 1991; Hawkeswood and Takizawa, 1997; Mathews and Reid, 2002. **Specimens examined:** *Eurispia vittata* Baly. Locality: Australia: NSW: 800 m up road from Pt. Piper, Brown Mountain, 36°36'S, 149°23'E, wet sclerophyll, ex *Gahnia* (Cyperaceae), 11.I.2003, coll. C. Reid (1 larva; CSCC, gift of collector).
- Eurypedus* Gistel: Windsor et al., 1992; Gómez, 1997, 2004; Gómez et al., 1999; Chaboo and Gómez, in prep. **Specimens examined:** *Eurypedus nigrosignatus* (Boheman). Locality: Panama, Soberania National Park, October 2003, coll. N. Gómez (>100 eggs, larvae, pupae; CSCC, gift of collector).
- Eurypepla* Boheman: Böving and Craighead, 1931; Woodruff, 1976a; Chaboo, 2004. **Specimens examined:** *Eurypepla calochroma* Boheman. Locality: U.S.: Florida, Broward Co., Ft. Lauderdale Convention Centre, ex *Cordia sebestema* (Geiger tree), 24.XI.2002, coll. C. Chaboo (>100; CSCC); Monroe Co., Big Pine Key, 29.III.1979, colls. E.G. Riley and D. LeDoux (6; UMRM). *Eurypepla jamaicensis* Linnaeus. Locality: U.S.: Florida, Miami, ex *Cordia sebestema* (Geiger tree), 12/IV.1940; no collector (5 larvae, 1 pupa, 1 adult; USNM).
- Euxema* Baly: Strong, 1977a, 1977b.
- Freycinetispia* Gressitt: Gressitt, 1960a, 1963b.
- Glyphocassis* Spaeth: Zaitsev, 1988; Kalaichelvan and Verma, 2000.
- Gonophora* Chevrolat: Kalshoven, 1951; Gressitt, 1963b; Gressitt and Kimoto, 1963.
- Gratiana* Spaeth: Frers, 1925; Rolston et al., 1965; Siebert, 1975; Kvasina and Ponce de Leon, 1985; Albuquerque and Becker, 1986; Windsor et al., 1992; Medeiros and Moreira, 2005. **Specimens examined:** Undetermined species. Locality: Paraguay, San Bernardino (1 larva; USNM).
- Gyllenhalus* Weise: Maulik, 1932.
- Hemisphaerota* Chevrolat: Candèze, 1861; Olliff, 1884; Sharp, 1899; Fiebrig, 1910; Bruch, 1939; Böving and Craighead, 1931; Costa Lima, 1955; Woodruff, 1965; Beshear, 1969; Jackman, 1976; Buzzi, 1988; Chaboo and Nguyen, 2004. **Specimens examined:** *Hemisphaerota fallax* Suffrian. Localities and re-

- positories are listed in Chaboo and Nguyen (2004). *Hemisphaerota cyanea* (Say). Localities and repositories are listed in Chaboo and Nguyen (2004). *Hemisphaerota palmarum* (Boheman). Localities and repositories are listed in Chaboo and Nguyen (2004).
- Heptispa* Weise: Uhmman, 1949b.
- Heterispa* Chapuis: Uhmman, 1949a.
- Hilarocassis* Spaeth: Windsor et al., 1992.
- Hispa* Linnaeus: Maxwell-Lefroy, 1906; Harris, 1835; Needham et al., 1928; Kalshoven, 1951.
- Hispellinus* Weise: Gressitt and Kimoto, 1963; Mathews and Reid, 2002.
- Hispodonta* Baly: Gressitt, 1960a, 1960b, 1963a; Gressitt and Kimoto, 1963. **Specimens examined:** *Hispodonta chapuisi* Gestro. Locality: New Guinea: Kassem Pass 5, 1500 m, 4.I.1965, ex betel palm, coll. J.L. Gressitt (16 larvae; MCZ).
- Homolispa* Baly: Bondar, 1938.
- Hybosa* Duponchel and Chevrolat: Windsor et al., 1992.
- Hypocassida* Weise: Steinhausen, 1950; Kosior, 1975; Brovdi, 1983.
- Imatidium* Fabricius: Bondar, 1940a, 1940b, 1941, 1942, 1943; Gilbert et al., 2001. **Specimens examined:** *Imatidium* prob. *rubricatum*. Locality: Suriname, ex bird-of-paradise flower, colls. A.M. Potter and T.H. Russel (1 larva; USNM).
- Ischnocodia* Spaeth: Windsor et al., 1992.
- Ischyronota* Weise: Medvedev and Radzivilovskaja, 1971.
- Ischyrosomyx* Sturm. **Specimens examined:** *Ischyrosomyx discipennis* Boheman. Locality: Panama: Ancon, C.Z., 6.VII.1919, coll. H.F. Dietz (1 larva, 1 adult; USNM). *Ischyrosomyx oblonga* Boheman. Locality: Brazil, coll. D. Yanega (1 larva, 1 adult; UCRC).
- Isopedispa* Spaeth: Gressitt, 1960b.
- Jonthonota* Spaeth: Lawson, 1991.
- Lacoptera* Boheman: Muir and Sharp, 1904; Schultze, 1908; Hingston, 1928; Hoffman, 1933; Beeson, 1941; Maulik, 1948b; Gressitt and Kimoto, 1963; Takizawa, 1982; Nakamura et al., 1992; Zaitsev, 1992; Kimoto and Takizawa, 1994, 1997; Heron, 2004b; Ranade et al., 2004.
- Lasiochila* Weise: Kimoto and Takizawa, 1997.
- Leptispa* Baly: Maxwell-Lefroy, 1906; Froggatt, 1914; Fletcher, 1914; Maulik, 1919; Kalshoven, 1951; Chen et al., 1986; Vorovna and Zaitsev, 1982; Chen, 1973; Chen et al., 1986; Kimoto and Takizawa, 1994, 1997.
- Macromonycha* Spaeth: Matis, 1970.
- Mecistomela* Jacobson: Bondar, 1913; Macêdo et al., 1994; Grenha et al., 2004. **Specimens examined:** *Mecistomela marginata* (Thunberg). Locality: Brazil: Agua Preta, Bahia, IX.1944, folded leaves of coconut palm, coll. P. Silva (4 larvae; USNM).
- Megapyga* Boheman. **Specimens examined:** Undetermined species. Locality: Africa, no date, no collector (1 larva; USNM).
- Metaxycera* Baly: Bondar, 1938.
- Metriona* Weise: Schultze, 1908; Frers, 1922a, 1922b; Kalshoven, 1951; Woodruff, 1976b; Buzzi, 1988; Morelli et al., 1994; Medeiros et al., 2005. **Specimens examined:** *Metriona elatior* (Klug). Locality: Brazil, Minas Gerais, V. Monte Verde, 14.VII.1961, coll. F. Halik (2 larvae; USNM); Paraguay, San Bernardino: coll. K. Fiebrig (1 larva, 2 pupae; USNM).
- Metrionella* Spaeth: Windsor et al., 1992.
- Micrispa* Gestro: Gressitt, 1963a.
- Microctenochira* Spaeth: Windsor et al., 1992; Teixeira and Casari, 2003.
- Microhropala* Chevrolat: Harris, 1835; Chittenden, 1902; Needham et al., 1928; Hendrickson, 1930; McCauley, 1938; Uhmman, 1949b; Peterson, 1951; Clark, 1983; Ford and Cavey, 1985; Cox, 1988, 1994a; Lawson, 1991; Damman, 1994; Hespeneheide and Dang, 1999; Staines, 2006; R. Hoebeke, personal commun. **Specimens examined:** *Microhropala rubrolineata* (Mannerheim). Locality: U.S.: California, Coronado, 21.IV.1947, coll. Algert (18 larvae, 2 pupae; USNM).
- Notosacantha* Chevrolat: Hawkeswood, 1989; Monteith, 1991; Zaitzev and Medvedev, 1982; Medvedev and Eroshkina, 1988; Kimoto and Takizawa, 1997; Rane et al., 2000; Reid, unpublished illustrations.
- Nuzonia* Spaeth. **Specimens examined:** *Nuzonia* Spaeth prob. *pallidula*? Locality: U.S.: Missouri (1 larva, 1 adult; USNM).
- Nympharescens* Weise: Maulik, 1937; Wang, 1977; Seifert and Seifert, 1979; Strong, 1977a, 1977b; 1981, 1982a, 1982b; Strong and Wang, 1977; Morrison and Strong, 1981; McCoy, 1984, 1985; Staines, 1996; Wilf et al., 2000.
- Octhispa* Chapuis: Bondar, 1938; Uhmman, 1949a; Hespeneheide and Dang, 1999.
- Octodonta* Chapuis: Gressitt, 1960a, 1963b; Gressitt and Kimoto, 1963; Kogan and Kogan, 1979.
- Octotoma* Dejean: Sanderson, 1902; Needham et al., 1928; Böving and Craighead, 1931; Bruch, 1933; Uhmman, 1949a; Ford and Cavey, 1985; Broughton, 1999; Jolivet and Hawkeswood, 1995; Staines, 2006. **Specimens examined:** *Octotoma scabripennis* Guérin-Ménéville. Locality: Mexico: Cuernavaca, Morelos, VIII.1995, mining leaves of shrub prob. *Lippia umbellata*, coll. N.H.L. Krauss (1 larva, 1 adult; USNM).
- Octuroplata* Uhmman: Teixeira et al., 1999; Casari and Queiroz, 2005.
- Odontota* Chevrolat: Harris, 1835; Chittenden, 1902; Kogan and Kogan, 1979; Wheeler, 1980; Ford and Cavey, 1985; Wheeler and Snook, 1986; Lawson, 1991; Lawson, 1991. **Specimens examined:** *Odontota arizonicus*. Locality: U.S.: Arizona, Douglas Co., 26.VIII.1942, coll. W.W. Jones (8 larvae; USNM). *Odontota dorsalis* Thunberg. Locality: not available (3 pupal skins; USNM).
- Oediopalpa* Baly (= *Amplipala*): Bruch, 1906; Monrós and Viana, 1947. **Specimens examined:** *Oediopalpa guerini* (Baly). Locality: Panama, Barro Colorado Island, VI.1939, coll. J. Zetek (3 larvae; USNM).
- Ogdoecosta* Spaeth: Windsor et al., 1992.
- Omaspides* Chevrolat: Ohaus, 1899, 1900; von Lengerken, 1939; Sturm, 1961; O'Toole and Preston-Mafham, 1985; Windsor et al., 1992; Windsor and Choe, 1994; Rodriguez, 1994; Frierio-Costa, 1995; Frierio Costa and Vasconcellos-Neto, 2000. **Specimens examined:** Undetermined species. Locality:

- Brazil: Minas Gerais, coll. D. Yanega (2 larvae, 1 pupa, 1 adult; UCRC).
- Omoecerus* Chevrolat: Fiebrig, 1910.
- Omocephala* Agassiz: Kimoto and Takizawa, 1997; H. Ghate, personal commun.
- Oocassida* Weise: Schultze, 1908; Maulik, 1919; Beeson, 1941; Gressitt, 1952; Rawat and Modi, 1972; Takizawa, 1980; Chen et al., 1986; Kalai-chelvan and Verma, 2000; Chaboo, in review.
- Oxycephala* Desbrochers: Gressitt, 1960a, 1955.
- Oxyroplata* Uhmman: Uhmman, 1949b.
- Parachirida* Spaeth: Windsor et al., 1992.
- Paranota* Monrós and Viana: Fiebrig, 1910.
- Paraselenis* Spaeth: Weyenburg, 1874; Monte, 1932; Buzzi, 1988; Vaconcellos-Neto and Jolivet, 1989; Windsor et al., 1992.
- Paratrikona* Spaeth. **Specimens examined:** *Paratrikona lerouxii* (Boheman). Locality: Cuba, Matas, Mercedes, ex *Tabebuia*, 20.VI.1940, coll. L. Scaramunoz (2 larvae, 1 pupa; USNM).
- Parorectis* Spaeth. **Specimens examined:** *Parorectis callosa* (Boheman). Locality: U.S.: Texas, Brownsville, 24.V.1938, ex *Physalis*, no collector (4 larvae, USNM).
- Pentispa* Chapuis: Uhmman, 1949a, 1949b; Boldt and Staines, 1993; Staines, 2006.
- Physonota* Boheman: Riley, 1870a; Sanderson, 1948; Simmonds, 1949a, 1949b; Peterson, 1951; Stehr, 1991. **Specimens examined:** *Physonota attenuata* Boheman. Locality: Mexico: Oax, Tehuantepec, no date, coll. F. Knab (5 egg masses, 15 pupal skins on sticks; USNM). *Physonota alutacea* Boheman. Locality: U.S.: Texas, Mercedes, ex *Ipomoea* sp., V.1939, coll. G.M. Jones (1 larva, 1 adult; MCZ); Panama: Panama, Soberania National Park, nr. Gamboa, Pipeline Rd., 15.V.1995, coll. C. Chaboo (5 larvae; CSCC); Mexico: Sn. Jacinto to km 44 Carrete Ra Norte Man, Mic, 6.26.1963, colls. Sequiera and Lempira (3 larvae, 5 pupae; USNM). *Physonota citrinella* Boheman. Locality: Mexico, Huipulco, ex *Eupatorium*, VIII.1922, coll. E.G. Smyth (5 larvae, USNM). *Physonota helianthi* Boheman. Locality: U.S.: Indiana: Hessville, 4.VII.1906, ex milkweed, coll. A.B. Wolcott (1 larva, 1 adult; USNM); MO: Birch tree, 29.V.1932 (1 pupal skin; USNM); not available (1 egg case; USNM).
- Physonota unipunctata* (Say). Locality: U.S.: Missouri, Boone Co., Rockbridge St. Park, 1.VI.1976, ex mint, coll. A.A. Borski (3; UMRM); S. Ill. [South Illinois], St. Clair Co., 19.VI, coll. D.G. Bock (6 larvae, 2 pupae; USNM). Undetermined species 1. Locality: Mexico: Ciudad Victoria (20 miles), Tamaulipas, 17.VI.1941, coll. H. Dybas (1 larva; FMNH). Undetermined species 2. Locality: Guatemala: Petten coll. (1 larva; CSCC). Undetermined species 3. Locality: Guatemala, coll. F. Knab (1 larva; UNMM). Undetermined species 4. Locality: Guatemala, Alta Paz, Trece Aguas, 16.IV. 1906 (1 larva; USNM). Undetermined species 5. Locality: Costa Rica: Guanacaste Prov., Fca. La Pacifica, 7 km N Cañas, VIII.1969, coll. D. H. Janzen (1 larva; USNM). Undetermined species 5. Locality: Mexico: Vera Cruz, 15.VII.1907 (2 pupal skins; USNM). Undetermined species 6. Locality: U.S.: New York, Ithaca (1 egg mass, 3 pupal skins; USNM). Undetermined species 7. Locality: Mexico: Oaxaca, near Totolapan, 5.VIII.1965, colls. Flint and Ortiz (2 larvae; USNM). Undetermined species 8. Locality: Mexico: Tehuantepec, coll. F. Knab (2 pupal skins on stem; USNM).
- Phytodectoidea* Spaeth. **Specimens examined:** *Phytodectoidea quatuordecimpunctata* (Boheman). Locality: Mexico: Mexico City, 10.VII.1897, coll. A. Koebele (1 larva, 1 adult; USNM).
- Pistosia* Weise (= *Wallaceana* Maulik): Kalshoven, 1951; Kimoto and Takizawa, 1997.
- Plagiometriona* Spaeth: Fiebrig, 1910; Woodruff, 1975; Lawson, 1991; Windsor et al., 1992; Nogueira-de-Sá and Trigo, 2005.
- Platyauchenia* Sturm: Maulik, 1933.
- Platycycla* Boheman. **Specimens examined:** *Platycycla deruta* Boheman. Locality: Guat. [Guatemala], 1955, no collector (1 pupa; USNM).
- Platypria* Guérin-Ménéville: Stebbing, 1914; Beeson, 1941; Gressitt, 1963b; Gressitt and Kimoto, 1963; Chen et al., 1986; Kimoto and Takizawa, 1994; H. Ghate, personal commun.
- Plesispa* Chapuis: Kalshoven, 1951; Gressitt, 1960a, 1963b; Gressitt and Kimoto, 1963.
- Polychalca* Chevrolat: Fiebrig, 1910.
- Polychalma* Barber and Bridwell: Buzzi, 1988; Windsor et al., 1992. **Specimens examined:** *Polychalma multicava* (Latreille). Locality: Panama: Canal Zone, La Pita Signal Stn, 29.VI.1976, coll. E. Riley (1 larva; CSCC, gift of collector).
- Prioptera* Hope: Schultz, 1908.
- Probaenia* Weise: Bruch, 1928; Bondar, 1938; Uhmman, 1949a.
- Promecotheca* Blanchard: Maulik, 1919; Taylor, 1937; Kalshoven, 1951; Gressitt, 1960a, 1963b; Gressitt and Kimoto, 1963; Chen et al., 1986. **Specimens examined:** New Britain: Gazelle Pen, Vunakunan, ex *Cocos*, 21.V.1956, coll. J.L. Gressitt (3 larvae, MCZ).
- Prosopodonta* Baly: Chen et al., 1986; D. McKenna, personal commun. **Specimens examined:** *Prosopodonta corallina*. Locality: Costa Rica: ex *Miltonia endresii* leaf [Orchidaceae], coll. Cogswell (1 larva; USNM).
- Psalidonota* Boheman. **Specimens examined:** *Psalidonota contemta*. Locality: Brazil: Minas Gerais, coll. D. Yanega (1 larva, 1 adult; UCRC).
- Sceloenopla* Chevrolat: Bondar, 1938; Uhmman, 1949a; Costa et al., 1988; Jolivet and Hawkeswood, 1995; Casari and Queiroz, 2005.
- Silana* Spaeth: Takizawa, 1980; Mohamedsaid and Sajap, 1996.
- Sindia* Weise: Hingston, 1928; Maulik, 1948a; Gressitt, 1952.
- Sindiola* Spaeth: Zaitsev and Medvedev, 1983; Zaitsev, 1992.
- Spaethiella* Barber and Bridwell: Olliff, 1884; Bruch, 1939a; Bondar, 1940; Monrós and Viana, 1951; Costa Lima, 1955; Genty et al., 1978; Buzzi, 1988; Windsor et al., 1992; Garcia et al., 1996; de Lima, 1997; Barbosa et al., 1999; Chaboo and Nguyen, 2004. **Specimens examined:** *Spaethiella crassicornis* (Spaeth). Localities and repositories are listed in Chaboo and Nguyen (2004).

<i>Spaethiella pulchella</i> Baly. Localities and repositories are listed in Chaboo and Nguyen (2004).	CMNC	Canadian Museum of Nature Collection, Ottawa, Canada; R.S. Anderson
<i>Stenispa</i> Baly: Riley and Enns, 1979; Ford and Cavey, 1985; Staines, 2006.	CNDC	Catherine N. Duckett Collection, New Brunswick, USA; C.N. Duckett
<i>Stenopodius</i> Horn: Needham et al., 1928.	CSCC	Caroline S. Chaboo Collection, New York, USA; C.S. Chaboo
<i>Stephanispa</i> Gressitt: Gressitt, 1960b.	CUIC	Cornell University Insect Collection, Ithaca, USA; J.K. Liebherr and R. Hoebeke
<i>Sternostena</i> Weise: Bruch, 1933.	EGRC	Edward G. Riley Collection, College Station, USA; E.G. Riley
<i>Stethispa</i> Baly: Bondar, 1938. Specimens examined: <i>Stethispa bruchi</i> . Locality: [Country?], Serra de Batarite (Cêara), I. 1895, coll. Gounelle (1 larva; USNM).	FMNH	Field Museum of Natural History, Chicago, USA; A. Newton
<i>Stoiba</i> Spaeth. Specimens examined: <i>Stoiba swartzii</i> Shönherr. Locality: Jamaica, Cinchona, on vine, 13.VI.1931, coll. M. Kisliuk (1 larva; USNM).	FSCA	Florida State Collection of Arthropods, Gainesville, USA; M.C. Thomas and B. Beck
<i>Stolas</i> Billberg: Fiebrig, 1910; Buzzi, 1975a, 1975b, 1977, 1988; Buzzi and Garcia, 1983; Buzzi and Miyazaki, 1999; Carroll, 1978; Habib and Vasconcellos-Neto, 1979; Boldt et al., 1991; Windsor et al., 1992; Medeiros et al., 2005; Vencl et al., 2005.	IMLA	Fundación e Instituto Miguel Lillo, Tucúman, Argentina; A.L. Terán
<i>Sumitrosis</i> Butte (= <i>Anoplitis</i>): Harris, 1835; Uhmman, 1949a; Butte, 1969; Ford and Cavey, 1985; Wheeler and Snook, 1986; Staines, 2006.	INBIO	Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica; A. Solís
<i>Syngambria</i> Spaeth: Fiebrig, 1910; Buzzi, 1988.	INHS	Illinois Natural History Survey, Champaign, USA; K.R. Zeiders and C. Favret
<i>Teretrispa</i> Gressitt: Gressitt, 1960b.	IRSNB	Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; M. Cludts
<i>Thlaspida</i> Weise: Takizawa, 1980; Zaitsev, 1988; Lee and Park, 1996; Kimoto and Takizawa, 1994, 1997.	KSEM	Snow Entomology Museum, Lawrence, USA; S. Ashe and R. Brooks
<i>Uroplata</i> Chevrolat: Maulik, 1932; Bondar, 1938; Uhmman, 1949a; Broughton, 1999.	LBC	Lech Borowiec Collection, Wrocław, Poland; L. Borowiec
<i>Vietocassis</i> Medvedev and Eroshkina: Zaitsev, 1988.	MACN	Museo Argentina de Ciencias Naturales, Buenos Aires, Argentina; A.O. Bachman
<i>Xenarescus</i> Weise: Maulik, 1937; Wang, 1977; Seifert and Seifert, 1979; Strong, 1977a, 1977b; 1981, 1982a, 1982b; Strong and Wang, 1977; Morrison and Strong, 1981; McCoy, 1984, 1985; Staines, 1996; Wilf et al., 2000.	MAIC	Michael A. Ivie Collection, Bozeman, USA; M. Ivie
<i>Xenocassis</i> Spaeth: Windsor et al., 1992.	MCZC	Museum of Comparative Zoology Collection, Boston, USA; P. Perkins
<i>Xenochalepus</i> Weise: Bondar, 1938; Uhmman, 1949a, 1949b. Specimens examined: <i>Xenochalepus ater</i> Weise. Locality: U.S.: Arizona, in string bean leaves, 24.VIII.1945, coll. H.S.B. (1 larva, exuvial skins, 1 pupa; USNM); Arizona, Douglas, 20.IX.1942, reared on soybeans, (3 pupal skins; USNM).	MMUE	University of Manchester Collection, Manchester, U.K.; C. Johnson and P. Rispin
	MNHC	Museo Nacional de Historia Natural, Havana, Cuba; J. Genaro
	MNHUB	Museum für Naturkunde der Humboldt Universität, Berlin, Germany; M. Uhlig and H. Wendt

APPENDIX 3

INSTITUTIONAL ABBREVIATIONS: LIST OF INSTITUTIONS AND RESPONSIBLE INDIVIDUALS WHO PROVIDED SPECIMENS FOR THIS STUDY

AMNH	American Museum of Natural History, New York, USA; L. Herman and S. Lodhi
BMNH	British Museum (Natural History), London, UK; M. Brendell and S. Shute
BPBM	Bernice P. Bishop Museum, Honolulu, USA; A. Samuelson

MUCR	University of Costa Rica, Costa Rica; P. Hanson
MZHF	University of Helsinki, Helsinki, Finland; O. Biström
NHRS	Naturhistoriska Riksmuseet, Stockholm, Sweden; B. Viklund
PPRI	Plant Protection Research Institute, Pretoria, South Africa; E. Grobbelaar
RHTC	Robert H. Turnbow Collection, Fort Rucker, USA; R. Turnbow
RMCA	Musee Royal de l'Afrique Centrale, Tervuren, Belgium; M. de Meyer
SMCC	Shawn M. Clark Collection, Provo, USA; S.M. Clark
TAMU	Texas A&M University, College Station, USA; E.G. Riley
UCRC	University of California, Riverside, USA; D. Yanega
UGCA	University of Georgia, Athens, USA; J. McHugh and C. L. Smith
UMRM	University of Missouri, W.R. Enns Entomology Museum, Missouri, USA; R. W. Sites and K. Simpson
USNM	U.S. National Museum, Washington, D. C., USA; A. Konstantinov, S. Lingafelter and D. Furth

APPENDIX 4

CHARACTER LIST

EGG

0. Egg: Stalked = 0; Sessile = 1.
1. Fecal case: Present = 0; Absent = 1.

LARVA

2. Feeding: Endophagous = 0; Exophagous = 1.
3. Miners, food choice: Stem = 0; Leaf = 1.
4. Terrestrial, exophagous larvae, microhabitat: Rolled-leaf tubes = 0; Flowers = 1; Open feeders = 2; Leaf shelter type I (folded leaf) = 3; Leaf shelter type II (two leaves glued together) [non-additive].
5. Body: Cylindrical or subcylindrical = 0; Dorsoventrally flattened = 1.
6. Flattened larva: Heavily sclerotized = 0; Reduced sclerotization = 1.
7. Leg length: Elongate, extend beyond lateral margin of body = 0; Short, hidden in dorsal aspect = 1.

8. Abdomen: Straight = 0; Sharply recurved = 1.
9. Abdomen, tergum of terminal segment: Concave, hind end shovel-shaped = 0; Flat = 1.
10. Abdominal tergum IX, processes: Developed = 0; Not developed = 1.
11. Abdominal tergum IX, number of processes: Single = 0; Anterior pair = 1; Posterior = 2. [nonadditive].
12. Anus position: Terminal = 0; Ventral = 1; Dorsal = 2. [nonadditive].
13. Anus shape: Elongated as anal telescope = 0; Simple pore = 1.
14. Shield: Retained = 0; Not retained = 1.
15. Shield architecture: Wet coat = 0; Exuvial stack, with or without feces = 1; Basket arrangement = 2. [nonadditive].
16. Individuals: Solitary = 0; Gregarious = 1.
17. Gregarious larvae, cycloalexy: Present = 0; Absent = 1.

PUPA

18. Pupation site: Within leaf mine = 0; Externally, on stem or leaves = 1; Within stem gall = 2. [nonadditive].
19. Fecal case: Retained = 0; Not retained = 1.

ADULTS

20. Maternal care of immature stages: Absent = 0; Present = 1.
21. Body, shape: Elongate, three or more times longer than wide = 0; Not so elongate = 1.
22. Body, profile in dorsal aspect: Continuous = 0; Discontinuous = 1.
23. Body, dorsum in lateral aspect: Flattened = 0; Rounded, arcuate or convex = 1.
24. Body, venter in lateral aspect: Flattened, pleuron in same plane as sternum = 0; Rounded or angular, pleuron angled vertically from sternum = 1.
25. Body, dorsal surface: Glabrous or sparse = 0; Densely pubescent = 1.
26. Head, dorsal exposure: Not exposed, hidden by pronotum = 0; Partially exposed, overlapped by pronotum = 1; Completely exposed = 2. [non-additive].
27. Mouth position: Prognathous = 0; Hypognathous = 1.
28. Head, supra-optic ridge or groove: Present = 0; Absent = 1.
29. Head, midcranial suture: Present = 0; Absent = 1.
30. Head, midfrontal sulcus: Extended to frons = 0; Terminates before antenna = 1.
31. Head, posterior section of midcranial suture: Terminates at or before posterior eye margin = 0; Terminates beyond posterior eye margin = 1.
32. Head, coronal carina: Present = 0; Absent = 1.
33. Head, broadly projected beyond eye margin = 0; Not projected = 1.
34. Head, supraantennal plate: Present = 0; Absent = 1.
35. Head, orbital sulcus: Present = 0; Absent = 1.
36. Head, supraorbital sulcus: Present = 0; Absent = 1.

37. Head, frontoclypeal suture: Deeply incised, \, /, or \wedge shaped = 0; Absent or Faint = 1.
38. Eye: Protuberant = 0; Not protuberant = 1.
39. Eye, medial margin: Elevated = 0; Not elevated = 1.
40. Eye, medial margin: Sinuate = 0; Continuous = 1.
41. Eye, dorsal aspect: Greatly projected from genae and corona = 0; Continuous with genae and corona = 1.
42. Eye, dorsomedial margin: With adjoining row of punctures = 0; Lacking row of punctures = 1.
43. Eye, cornea of ommatidia: Convex = 0; Flat = 1.
44. Supra-orbital puncture: Present = 0; Absent = 1.
45. Supra-orbital puncture, position: At or on eye margin = 0; Closer to midline, midfrontal sulcus or coronal carina = 1.
46. Gular sutures: Extend to mouth = 0; Terminate before mouth = 1.
47. Gula shape: Longer than wide = 0; Wider than long = 1; As long as wide = 2. [nonadditive].
48. Antennal insertions: On tubercles = 0; Not on tubercles = 1.
49. Antenna length: Equal or less than pronotal length = 0; Exceeding pronotal length = 1.
50. Antenna, position of insertions: Above frons = 0; Between eye and mouth = 1; Between eyes and frons = 2. [nonadditive].
51. Antenna, distance between insertions: Proximate, less than scape length = 0; Separated, distance about equal in length to scape length = 1; Separated, distance more than twice scape length = 2. [nonadditive].
52. Antennomere I: As long as or longer than antennomere II = 0; Shorter than antennomere II = 1.
53. Antennomere I, apical margin: Straight = 0; Lobate = 1.
54. Antennomere I, surface: Impunctate = 0; Punctate = 1.
55. Antennomere II: As long as or longer than antennomere III = 0; Shorter than antennomere III = 1.
56. Antennomere III: As long as or longer than antennomere IV = 0; Shorter than antennomere IV = 1.
57. Antenna: Spinose = 0; Aspinose = 1.
58. Antenna: Longitudinally striate = 0; Not striate = 1.
59. Antenna, ventromarginal grooves: Present = 0; Absent = 1.
60. Antennomere, shape: Apex wider than base = 0; Apex as wide as base = 1.
61. Distal antennomeres, shape: Longer than broad = 0; Broader than long = 1.
62. Distal antennomeres, shape: Enlarged, forming a club = 0; Not enlarged = 1.
63. Distal antennomeres: Separated = 0; Partially or entirely fused = 1.
64. Terminal antennomere: As long as or longer than penultimate antennomere = 0; Shorter than penultimate antennomere = 1.
65. Relative lengths of frontoclypeus to hypostomal areas: Frontoclypeus shorter than hypostomal area = 0; Frontoclypeus longer than or equal to hypostomal area = 1.
66. Clypeus: Discrete, separate from frons = 0; Fused to frons, apparent or not = 1.
67. Frontoclypeus: Flat = 0; Protuberant = 1.
68. Frontoclypeus: In same plane or slightly protuberant from antennal bases = 0; Distinctly protuberant from antennal bases = 1.
69. Mouth fossa, shape: Rounded = 0; Transverse rectangle = 1.
70. Mouth, margins: Protuberant = 0; Simple = 1.
71. Mouth position: Close to antennal insertions = 0; Distant from antennal insertions = 1.
72. Hypognathous head, anterior margin of mouth: Posterior to or reaching eye margin = 0; Extended between eyes = 1.
73. Mouth: Projected from surrounding area (gena, frons, gula) = 0; In same plane as gena = 1.
74. Mouthparts: Completely exposed, mouthparts free = 0; Partially hidden = 1; Mostly hidden, only labrum partially exposed = 2. [nonadditive].
75. Mouthparts: Oriented antieriad = 0; Oriented in same plane as gula = 1.
76. Labrum, shape: Longer than wide = 0; Wider than long or as wide as long = 1.
77. Labrum, dorsal surface: Carinate = 0; Acarinate = 1.
78. Labrum, distal margin: Entire = 0; With narrow medial emargination = 1; Broadly concave = 2. [nonadditive].
79. Mandible, shape: Triangular or pyramidal = 0; Palmate = 1.
80. Triangular or pyramidal mandible: Bi- or tridentate = 0; Multiple dens = 1; Unidentate = 2. [nonadditive].
81. Palmate mandible: Blade undifferentiated = 0; Blade dentate = 1.
82. Quadrate mandible: Uni- or bidentate = 0; Multiple dens = 1.
83. Prementum, apical margin: Extended beyond base of submentum = 0; Contiguous with base of submentum = 1.
84. Pronotum (dorsal aspect): Parallel or subparallel-sided, apical and basal margins equal = 0; Base distinctly wider than apex = 1; Apex distinctly wider than base = 2. [nonadditive].
85. Pronotum, lateral margins parallel or subparallel: Medially constricted = 0; Medially expanded = 1; Straight = 2. [nonadditive].
86. Pronotum, lateral edges: Margined = 0; Rounded = 1.
87. Pronotum, lateral margination: Complete = 0; Incomplete, evanescent posteriorly = 1; Incomplete, evanescent medially = 2; Incomplete, evanescent anteriorly = 3. [nonadditive].
88. Pronotum, lateral margins: Narrow gutter or bead = 0; Explanate = 1.
89. Pronotum, humeral protuberance: Present = 0; Absent = 1.
90. Pronotum, anterior margin: Continuous or shallowly concave = 0; Broadly concave = 1; Broadly convex = 2. [nonadditive].
91. Pronotum, anterolateral angle: Broadly extended antieriad, enclosing head laterally = 0; Not so extended = 1.
92. Pronotum, lateral edge: Aspinose = 0; Spinose = 1.

93. Pronotum, lateral edge: Serrate = 0; Aserrate = 1.
94. Pronotum, basal margin: Straight = 0; Evenly curved or broadly sinuous = 1; Bisinuate = 2. [nonadditive].
95. Pronotum, postero-lateral angle: Projected posteriad = 0; Not so projected = 1.
96. Pronotum, posterior angle: Straight or slightly convex = 0; Concave = 1; Acuminate or rounded = 2. [nonadditive].
97. Pronotum, disc: Spinose = 0; Aspinose = 1.
98. Pronotum, dorsal spines: Branched = 0; Unbranched = 1.
99. Pronotum, anterior pore with bristle: Present = 0; Absent = 1.
100. Pronotum, position of anterior trichobothrium: Anterolateral angle = 0; Anteromedial angle = 1.
101. Pronotum, posterior trichobothrium: Present = 0; Absent = 1.
102. Pronotum, transverse basal groove: Present = 0; Absent = 1.
103. Prosternum, length at midline: Equal or shorter than mesosternal length = 0; Longer than mesosternal length = 1.
104. Prosternum, anterior marginal teeth: Absent = 0; Present = 1.
105. Prosternum, anterior margin: Expanded anteriorly, overlapping mouth = 0; Not expanded, mouth exposed = 1.
106. Prosternum, prepectus at medial margin of procoxa: Shorter than length of post-coxal lobe = 0; As long as or longer than length of post-coxal lobe = 1.
107. Prosternum, anterior prepectus length: Short, anterior prosternal margin and coxal margin close = 0; Long, anterior prosternal margin and coxal margin distant = 1.
108. Prosternal process: Slender, two or more times longer than breadth at apex = 0; Broad, as long as breadth at apex = 1.
109. Prosternal process: Inflated posteriorly = 0; Not so inflated = 1.
110. Prosternal process, apex: Laterally expanded, reaching below procoxae = 0; Apex not expanded = 1.
111. Prosternal process, apex: Tuberculate laterally = 0; Rounded = 1; Angular = 2; Broad = 3. [nonadditive].
112. Prosternal process, surface: With broad angular depression = 0; Flat, slightly grooved or slightly protuberant = 1.
113. Prosternal process: Flat; base, medial section and apex in same plane = 0; Projected medially from base and apex planes = 1.
114. Mesoscutellum, anterior margin: Not expanded, not overlapping pronotal posterior angle = 0; Straight, overlapping pronotal posterior angle = 1; Concave, overlapping pronotal posterior angle = 2. [nonadditive].
115. Mesoscutellum, anterior margin: Depressed from posterior margin = 0; Not depressed, in same plane as posterior margin = 1.
116. Mesoscutellum, posterior margin: Truncate = 0; Acute or rounded = 1.
117. Mesosternum, anterior portion: Exposed, shallowly overlapped by prosternal process = 0; Exposure limited, hidden by prosternal process = 1.
118. Mesosternum, surface: Notched, receiving prosternal process = 0; Flat or grooved medially, not receiving process = 1.
119. Mesosternum, process: Slender, two or more times longer than width = 0; Broad, less than or equal to width = 1.
120. Mesosternum, process: Apex protuberant from base = 0; Apex not protuberant, in same plane as base = 1.
121. Mesosternum, surface: Grooved, receiving legs = 0; Not grooved = 1.
122. Metepimeron: Hidden by elytra = 0; Exposed = 1.
123. Metasternum, anterolateral lobe: Developed, projecting over mesepimeron = 0; Absent = 1.
124. Metasternum, lateral section: Hidden = 0; Exposed = 1.
125. Metasternum, length at midline: Shorter than one half of width = 0; as long as or longer than one half of width = 1.
126. Metasternum, anterior intercoxal process: Flat or weakly notched = 0; Deeply notched, receiving mesocoxal process = 1.
127. Elytra, coverage of abdomen: Complete, pygidium hidden = 0; Incomplete, pygidium exposed = 1.
128. Elytra, ratio of length to width: Elongate, 2-3 times longer than wide = 0; Rounded, 1-1.5 times longer than wide = 1.
129. Elytra, lateral margins: Parallel or subparallel = 0; Rounded, base wider than apex = 1; Wedge-shaped, apex wider than base = 2. [nonadditive].
130. Elytra, anterolateral angle and humeral angle: Coincident = 0; Separated = 1.
131. Elytra, anterolateral angle: Broad lobe produced anteriorly = 0; Not produced = 1.
132. Elytra, anterolateral angle: Shallowly extended anteriorly along pronotal margin = 1; Not extended, pronotum free laterally = 2.
133. Elytra, margin: Narrow bead or gutter = 0; Explanate = 1.
134. Elytra, width of explanate margin: Less than width of disc = 0; Equal to or greater than width of disc = 1.
135. Elytra, lateral edge: Smooth = 0; Serrate or dentate = 1; Spinose = 2. [nonadditive].
136. Elytra, basal margin: Continuous with pronotal basal margin = 0; Wider than pronotal basal margin = 1.
137. Elytra, basal margin: Straight, transverse = 0; Straight, angled anteriorly = 1; Arched medially = 2; Sinuate or bisinuate = 3. [nonadditive].
138. Elytra, arched basal margin: Pronotal margin partially hidden = 0; Pronotal margin exposed = 1.
139. Elytra, basal margin: Smooth = 0; Crenulate = 1.
140. Elytra, apical margin: Round = 0; Truncate = 1.
141. Elytra, apical margin: Developed into posterior spine = 0; Spine absent = 1.
142. Elytra, apical angle at sutural margin: Continuous or slightly concave = 0; Deeply indented = 1.
143. Elytra, suture at apical angle: Denticulate = 0; Not denticulate = 1.

144. Elytra, punctuation: In rows on striae, intervals apparent = 0; Randomly distributed, intervals not apparent = 1; In round clusters, intervals not apparent = 2. [nonadditive].
145. Punctate-striate elytra, parascutellar stria: Present = 0; Absent = 1.
146. Punctate-striate elytra, intervals: Convex = 0; Flat = 1.
147. Elytra, discal punctuation: Deeply impressed, some fenestrate or porous = 0; Shallowly impressed = 1.
148. Elytra, deeply impressed punctuation: Fenestrate or porous = 0; Not fenestrate or porous = 1.
149. Elytra, sutural margin: With postscutellar protuberance = 0; Without postscutellar protuberance = 1.
150. Elytra, post-scutellar umbo or spine: Present = 0; Absent = 1.
151. Elytra, dorsum: Spinose or tuberculate = 0; Aspinose and atuberculate = 1.
152. Elytra, epipleural ridge: Transverse internal ridge present = 0; Transverse internal ridge absent = 1.
153. Elytra, epipleural ridge: Transverse external ridge present = 0; Transverse external ridge absent = 1.
154. Elytra, epipleura: Internal longitudinal carina present = 0; Internal longitudinal carina absent = 1.
155. Elytra, epipleural brace and internal carina: Connected = 0; Separated = 1.
156. Hindwing: Present, fully developed = 0; Reduced or absent = 1.
157. Hindwing, CuA cell 1: Closed = 0; Open = 1.
158. Hindwing, CuA cell 2: Closed = 0; Open = 1.
159. Procoxae: Rounded = 0; Elongate = 1.
160. Procoxae: Protuberant = 0; Set into cavity = 1.
161. Mesocoxae: Protuberant = 0; Set into cavity = 1.
162. Femur, shape: Strongly bowed = 0; Straight = 1.
163. Femur, basal margins: Spinose = 0; Aspinose = 1.
164. Mesotibia, shape: Bowed = 0; Straight = 1.
165. Tibia, lateral margins: Spinose = 0; Aspinose = 1.
166. Tibia, dorsal surface of apex: Deeply notched, receiving tarsus = 0; Flattened, transverse, or slightly depressed = 1.
167. Deep tibial notch: Short, less than one-third of tibial length = 0; Longer, more than one half of tibial length = 1.
168. Tibia, apex: Aspinose = 0; Spinose, spines in a row = 1; Spinose, spine single or few = 2. [nonadditive].
169. Tarsomere I, apical margin in dorsal aspect: Deeply bilobed = 0; Straight or sinuate = 1.
170. Tarsomere I, shape: Expanded laterally, as wide as tarsomere II = 0; Not expanded, tarsomere II wider than tarsomere I = 1.
171. Tarsomere I, length: As long as or longer than tarsomere II = 0; Shorter than tarsomere II = 1.
172. Tarsomere II, apical margin in dorsal aspect: Bilobed = 0; Straight or sinuate = 1.
173. Tarsomere II, width: Expanded laterally, as wide as tarsomere III = 0; Not so expanded, width less than tarsomere III = 1.
174. Tarsomere II, lateral margins: Rounded = 0; Parallel = 1.
175. Tarsomere III, length: Longer than total length of tarsomeres I–II = 0; Less than or equal to length of tarsomeres I–II = 1.
176. Tarsomere III, lobes: Symmetrical = 0; Asymmetrical = 1.
177. Tarsomere I, ventral setation: Bifid = 0; Simple = 1.
178. Tarsomere II, ventral setation: Bifid = 0; Simple = 1.
179. Tarsomere III, ventral setation: Bifid = 0; Simple = 1.
180. Tarsomere IV: Distinct, tarsal formula 5-5-5 = 0; Absent, tarsal formula 4-4-4 = 1.
181. Tarsomere V, length: Long, reaching well beyond apex of tarsomere III = 0; Short, terminating at or before apex of tarsomere III = 1.
182. Tarsomere V, ventral projection: Present = 0; Absent = 1.
183. Tarsomere V, projection: Single = 0; Paired = 1.
184. Tarsomere V, apical margin: Expanded, hiding claw base in dorsal aspect = 0; Not expanded, claw base exposed dorsally = 1.
185. Claws, number: Two = 0; One = 1.
186. Claws: Divergent = 0; Parallel = 1.
187. Claw, ventral margin: Pectinate = 0; Single tooth = 1; Simple, without projections = 2. [nonadditive].
188. Abdomen, lateral profile: Rounded = 0; Flattened = 1.
189. Abdominal intercoxal process: Shallowly extended between metacoxae = 0; Deeply extended, reaching beyond anterior metacoxal margin = 1.
190. Abdomen sterna I and II: Separate = 0; Fused = 1.
191. Ejaculatory duct: Loosely folded = 0; Tightly coiled = 1.
192. Tegmen: Complete = 0; Incomplete = 1.
193. Tegmen, attachment: At median foramen = 0; Distal from median foramen = 1.
194. Aedeagus, apex: Asetose = 0; Setose = 1.
195. Tegmen, manubrium: Developed as vertical plate = 0; Not so developed = 1.
196. Female, rectal kotpresse: Present = 0; Absent = 1.
197. Vaginal pouches: Present = 0; Absent = 1.
198. Spermatheca, apical appendix: Present = 0; Absent or very small = 1.
199. Spermatheca, receptacle appendix: Present = 0; Absent = 1.
200. Spermatheca, receptacle chambers: Single = 0; More than one = 1.
201. Single-chambered spermatheca: Receptacle separated from pump = 0; Receptacle broadly joined to pump = 1.
202. Spermatheca, relative position of entries of gland and duct: Proximate = 0; Separate but close = 1; Separate and distant = 2. [nonadditive].
203. Spermatheca with separated gland and duct entries: Entries on different chambers = 0; entries on same chamber = 1.
204. Spermatheca, position of duct and gland entries: On unspecialized proximal section of duct = 0; On short expanded section of proximal duct = 1; On long expanded section of proximal duct = 2. [nonadditive].

- 205. Spermatheca, insertion of duct and gland: Continuous with surface or everted into a short projection = 0; Inverted, in a depression = 1.
- 206. Spermatheca, duct length: Short, 2–3 times spermathecal length = 0; Long, 10 or more times longer than spermathecal length = 1.
- 207. Spermathecal duct: Coiled = 0; Not coiled = 1.
- 208. Spermatheca, coiled duct: Tightly coiled = 0; Loosely folded = 1; Sinuous, but not coiled or folded = 2. [nonadditive].
- 209. Spermatheca, duct: With sclerotized sac = 0; Without sclerotized sac = 1.

APPENDIX 5

CLADE SUPPORT UNDER ACCELERATED (FAST) AND DELAYED (SLOW) CHARACTER TRANSFORMATIONS

Support under unambiguous optimization is shown in figures 81–90. Clade numbers correspond to those given on figure 78. Character numbers and their states are indicated below as “character no. (state no.)” and correspond to those listed in table 7. Bold text indicates unique features; regular text indicates homoplasies.

- CLADE 1. *Lamprosoma* + (*Pachybrachis* + ((*Plateumaris* + (*Lema* + *Sagra*)) + (*Ophraella* + Cassidinae)))
- CLADE 2.
Fast: 49(1) **50(2)**, 55(1), **62(1)**, 144(1), **153(1)**, 157(1), 158(1), **162(1)**, 168(1), 170(1), 173(1), 197(1), 202(1).
Slow: 49(1) **50(2)**, 55(1), **62(1)**, **153(1)**, 158(1), **162(1)**, 170(1), 173(1).
- CLADE 3. (*Plateumaris* + (*Lema* + *Sagra*)) + (*Ophraella* + Cassidinae)
Fast: **1(1)**, **7(1)**, **8(1)**, **19(1)**, 22(1), 26(2), **37(0)**, **40(1)**, **46(1)**, 106(1), **121(1)**, 128(0), 136(1), **191(1)**, **207(0)**, **208(0)**.
Slow: **1(1)**, **7(1)**, **8(1)**, **19(1)**, 22(1), **40(1)**, **46(1)**, 106(1), **121(1)**, **191(1)**, **208(0)**.
- CLADE 4. *Plateumaris* + (*Lema* + *Sagra*)
Fast: 38(0), 41(0), 70(0), 80(0), **89(0)**, 144(0), **209(0)**.
Slow: 26(2), 37(0), 38(0), 41(0), 70(0), **89(0)**, 128(0), 136(1), **209(0)**.
- CLADE 5. *Lema* + *Sagra*
Fast: 30(1), 78(1), 107(1), 109(1), 186(1).
Slow: 78(1), 107(1), 109(1), 186(1), 197(1).
- CLADE 6. *Ophraella* + Cassidinae
Fast: **2(1)**, 23(1), **35(1)**, **50(0)**, 56(0), 76(0), 120(1), 157(0), 168(0), 192(0), 197(1), 202(0), **206(1)**.
Slow: 23(1), **35(1)**, **50(0)**, **51(0)**, 56(0).
- CLADE 7. *Areoscus* + other Cassidinae
Fast: **5(1)**, 12(1), 21(0), **24(0)**, 26(1), **27(1)**, 29(1), 37(1), **69(1)**, **73(1)**, **75(1)**, **103(1)**, 110(0), 158(0), 173(0), **177(0)**, **178(0)**, **180(1)**, **188(1)**, 201(1).

- Slow: **5(1)**, 12(1), 21(0), **24(0)**, **27(1)**, 29(1), **69(1)**, **73(1)**, **75(1)**, **103(1)**, 110(0), 129(0), 136(0), **177(0)**, **178(0)**, **180(1)**, **188(1)**, 201(1), **206(1)**, **207(0)**.
- CLADE 8. *Alurnus* + derived Cassidinae
Fast: 2(0), 9(0), 94(1), 108(1), 119(1), 159(1), 160(1), 161(1), 171(1), **190(1)**.
Slow: 2(0), **3(1)**, 94(1), 108(1), 119(1), 159(1), 160(1), 161(1), 171(1), **190(1)**.
- CLADE 9. Prosopodontine clade + derived cassidines
Fast: 23(0), 32(0), 76(1), 107(1), 144(0), 158(1), 197(1).
Slow: 23(0), **32(0)**, 173(0).
- CLADE 10. *Prosopodonta* + (*Promecothea* + (*Lasiochila* + (*Anisodera* + *Estigmena*)))
Fast: 66(0), 78(1).
Slow: 9(0), 66(0), 78(1), 197(1).
- CLADE 11. *Promecothea* + (*Lasiochila* + (*Anisodera* + *Estigmena*))
Fast: 170(0), 172(0), 193(0).
Slow: 101(1), 170(0), 172(0), 193(0).
- CLADE 12. *Lasiochila* + (*Anisodera* + *Estigmena*)
Fast: 29(0), **43(0)**, 83(0), 94(0), 101(1), 108(0), 145(0), 147(0), 175(0).
Slow: 29(0), **43(0)**, 94(0), 101(1), 145(0), 175(0).
- CLADE 13. *Anisodera* + *Estigmena*
Fast: 3(0), 201(0), 203(0).
Slow: 3(0), 201(0), 203(1).
- CLADE 14. (*Cephaloleia* + *Oediopalpa*) + (Sceloenopline clade + derived Cassidinae)
Fast: 9(1), 79(1), 181(1).
Slow: 79(1), 107(1), 181(1).
- CLADE 15. *Cephaloleia* + *Oediopalpa*
Fast: 2(1), 13(2), 68(1), 77(0), 116(0), 200(1), 201(0).
Slow: 2(1), 68(1), 77(0), 116(0).
- CLADE 16. Sceloenopline clade + derived Cassidinae
Fast: 101(1), 137(2), 145(0), 197(0).
Slow: 101(1), 137(2).
- CLADE 17. *Sceloenopla* + clade 18
Fast: 71(1), 117(1), 135(1), 147(0), 172(0), 175(0).
Slow: 71(1), 117(1), 147(0), 175(0).
- CLADE 18. CLADE 19 + clade 26
Fast: 18(0), 29(0), 113(1).
Slow: 18(0), 29(0), 145(0).
- CLADE 19. CLADE 20 + clade 21
Fast: 106(0), 107(0), 135(0), 137(0), 203(1).
Slow: 106(0), 203(1).
- CLADE 20. *Botryonopa* + *Callistola*
Fast: 9(0), 54(1), 99(1), 147(1), 152(0).
Slow: 64(1), 99(1), 107(0), 137(1), 147(1).
- CLADE 21. (*Cyperispa* + *Klitispa*) + (*Trichispa* + (*Dactylispa* + (*Asamangula* + *Dorcathispa*)))
Fast: 39(0), 79(0), 87(3), 101(0), 157(1), 201(0), 202(1).
Slow: 87(3), 101(0), 202(1).
- CLADE 22. *Cyperispa* + *Klitispa*
Fast: 29(1), 113(0), 137(2), 145(1), 148(0), 170(0).
Slow: 29(1), 107(0), 145(1), 148(0), 170(0), 172(0).

- CLADE 23. *Trichispa* + (*Dactylispa* + (*Asamangula* + *Dorcathispa*))
Fast: 25(1), 28(0), 72(0), 107(1), 120(0), **135(2)**, 172(1), 197(1).
Slow: 28(0), 39(0), 72(0), 113(1), 120(0), **135(2)**, 137(0).
- CLADE 24. *Dactylispa* + (*Asamangula* + *Dorcathispa*)
Fast: 61(1), 65(1), **97(0)**, 102(0), 106(1), **151(0)**, 186(1), 196(0), 198(0).
Slow: 65(1), 106(1), **151(0)**.
- CLADE 25. *Asamangula* + *Dorcathispa*
Fast: 25(0), **57(0)**, 94(0), 115(0), 163(0).
Slow: **57(0)**, 79(0), 94(0), 115(0), 163(0), 196(0), 197(1), 198(0).
- CLADE 26. CLADE 27 + clade 30
Fast: 115(0), 116(0), 181(0).
Slow: 115(0), 116(0), 135(1).
- CLADE 27. *Baliosus* + (*Anoplites* + (*Microrhopala* + *Octotoma*))
Fast: 30(1), 32(1), 55(0), 62(0), 81(1), 182(0), 183(1).
Slow: 30(1), 55(0), 62(0), 81(1), 172(0), 181(0), 183(1).
- CLADE 28. *Anoplites* + (*Microrhopala* + *Octotoma*)
Fast: 21(1), 60(1), 61(1), 82(1), 113(0).
Slow: 21(1), 60(1), 61(1).
- CLADE 29. *Microrhopala* + *Octotoma*
Fast: 63(1), 68(1), 145(1).
Slow: 32(1), 63(1), 68(1), 82(1).
- CLADE 30. *Anisostena* + (*Cephalodonta* + ((*Chalepus* + *Uroplata*) + (*Odontota* + *Xenochalepus*)))
Fast: 67(1), 68(1), 101(0), 134(1), 146(0), 172(1).
Slow: 67(1), 68(1), 113(1).
- CLADE 31. *Cephalodonta* + ((*Chalepus* + *Uroplata*) + (*Odontota* + *Xenochalepus*))
Fast: 84(1), 147(1), 186(1), 201(0).
Slow: 84(1), 181(0), 186(1).
- CLADE 32. (*Chalepus* + *Uroplata*) + (*Odontota* + *Xenochalepus*)
Fast: 152(0), 182(0).
Slow: 152(0), 182(0).
- CLADE 33. *Chalepus* + *Uroplata*
Fast: 61(1), 63(1), 140(1), 175(1).
Slow: 61(1), 63(1), 140(1), 175(1), 201(0).
- CLADE 34. *Odontota* + *Xenochalepus*
Fast: 21(1), 29(1), 157(1).
Slow: 21(1), 29(1), 101(0).
- CLADE 35. CLADE 36 + clade 39
Fast: **98(1)**, 136(0), 193(0).
Slow: 145(0), 193(0).
- CLADE 36. *Eurispa* + (*Aproidea* + *Exothispa*)
Fast: 29(0), 32(1), 59(0), 83(1), 86(1), 87(1), **141(0)**.
Slow: 29(0), 32(1), 83(0).
- CLADE 37. *Aproidea* + *Exothispa*
Fast: 26(2), 47(0), 51(1), 101(0), 136(1).
Slow: 26(2), 47(0), 51(1), 101(0).
- CLADE 38. *Stenispa* + clade 39
Fast: 2(1), 44(1), 79(0), 100(1), 170(0).
Slow: 44(1), 100(1), 136(0), 170(0).
- CLADE 39. *Leptispa* + clade 40
Fast: 22(0), 67(1), 99(1), 138(1), 158(0), 172(0).
Slow: 67(1), 79(0), 99(1), 138(1), 172(0).
- CLADE 40. (*Ceratispa* + *Palmispa*) + (*Plautyauchenia* + clade 43)
Fast: 2(0), 29(0), 71(1), 80(0), 137(0).
Slow: 71(1), 80(0).
- CLADE 41. *Ceratispa* + *Palmispa*
Fast: 28(0), 59(0), 65(1), 68(1), 94(0), 168(2), 193(1).
Slow: 22(0), 28(0), 29(0), 59(0), 65(1), 68(1), 94(0), 168(2).
- CLADE 42. *Plautyauchenia* + clade 43
Fast: 21(1), 22(1), 84(1), **88(1)**.
Slow: 21(1), 84(1), **88(1)**, 137(0), 158(0).
- CLADE 43. *Callispa* + clade 44
Fast: 23(1), 29(1), 82(1), 101(0), 128(1).
Slow: 23(1), 101(0), 128(1).
- CLADE 44. *Hispodonta* + clade 45
Fast: 13(2), 129(1), **133(1)**, 193(1).
Slow: 129(1), **133(1)**.
- CLADE 45. *Calliaspis* + clade 46
Fast: 22(0), 67(0), 90(1), 99(0), 130(0), 152(0), 181(0).
Slow: 22(0), 67(0), 90(1), 99(0), 152(0), 193(1).
- CLADE 46. *Demotispa* + clade 47
Fast: 2(1), 6(1), 80(2), 117(1), 170(1).
Slow: 2(1), 117(1), 170(1).
- CLADE 47. *Imatidium* + clade 48
Fast: 72(0), 91(0), 101(1), 181(1).
Slow: 91(0), 101(1), 130(1).
- CLADE 48. derived Cassidinae
Fast: 6(0), 10(0), **13(0)**, 14(0), 29(0), 32(1), 65(1), 74(1), 99(1), 100(0), 125(1), 158(1), **167(0)**, 193(0).
Slow: 29(0), 32(1), 100(0), 158(1), 193(0).
- CLADE 49. *Delocrania* + (*Hemisphaerota* + *Spaethiella*)
Fast: 12(0), 65(0), 72(0), 74(0), 107(0), 122(0), **124(0)**, 125(1), 166(0).
Slow: 10(0), 12(0), 13(0), 14(0), 107(0) 122(0), 166(0), **167(1)**.
- CLADE 50. *Hemisphaerota* + *Spaethiella*
Fast: **15(2)**, 31(0), 55(0), 99(0), 109(1), 110(1), 111(2), **112(0)**, **114(1)**, 118(0), 126(1), 137(1), 154(0), 158(0), **185(1)**.
Slow: **15(2)**, 55(0), 109(1), 111(2), **112(0)**, **114(1)**, 118(0), 126(1), 137(1), 158(0), **185(1)**.
- CLADE 51. (*Calyptocephala* + *Spilophora*) + clade 53
Fast: 44(0), 59(0), 79(1), 81(1), 90(0), 91(1), 96(2), 104(0).
Slow: 10(0), 13(0), 14(0), 44(0), 65(1), 74(1), 79(1), 81(1), 90(0), 91(1), 96(2), **98(1)**, 104(0), 125(0).
- CLADE 52. *Calyptocephala* + *Spilophora*
Fast: 22(1), 72(1), 77(0), 82(0), 99(0), 101(0), 116(0), 136(1), 157(1), 200(1).
Slow: 22(1), 59(0), 101(0), 116(0), 136(1), 157(1).
- CLADE 53. *Ischyrosomyx* + clade 54
Fast: 12(0), 26(0), 31(0), 67(1), 118(0), **139(1)**, 154(0), 197(1), 201(0).

Slow: 12(0), **26(0)**, 31(0), 72(0), 82(1), 99(1), 118(0), 126(1), 139(1), 154(0), 197(1).

CLADE 54. Derived Cassidineae

Fast: 56(1), 59(1), 68(1), 78(1), 137(1), 144(1), 145(1), 181(0), **187(1)**.

Slow: 67(1), 68(1), 78(1), 137(1), 144(1), 145(1), 181(0).

CLADE 55. *Chelymorpha* + *Phytodectoidea*

Fast: 16(1), 95(0), 158(0).

Slow: 16(1), 56(1), 95(0), 158(0), 187(1), 201(0).

CLADE 56. *Elytrogona* + *Stoiba*

Fast: 155(0), **156(1)**, **189(1)**.

Slow: 155(0), **156(1)**, 187(1), **189(1)**, 201(0).

CLADE 57. *Eurypepla* + (*Dorynota* + *Paratrikona*)

Fast: 22(1), 30(1), 67(0), 68(0), 90(2), 96(1), 136(1), 187(2), 201(1).

Slow: 22(1), 30(1), 56(1), 68(0), 90(2), 136(1).

CLADE 58. *Dorynota* + *Paratrikona*

Fast: 45(1), 84(2), **114(2)**, 131(0), 132(0), 147(0), **150(0)**, 158(0), 175(0), 181(1), 186(1), 194(0).

Slow: 45(1), 84(2), **114(2)**, 131(0), 132(0), 147(0), **150(0)**, 158(0), 175(0), 181(1), 186(1), 194(0).

CLADE 59. *Asteriza* + (*Aspidimorpha* + *Conchylotenia*)

Fast: 49(0), 56(0), 68(0), 90(2), 155(0), 175(0), 187(0), 193(1).

Slow: 49(0), 90(2), 193(1).

CLADE 60. *Aspidimorpha* + *Conchylotenia*

Fast: 45(1), 154(1), 158(0), 197(0), 199(1).

Slow: 45(1), 154(1), 187(0), 201(0).

CLADE 61. *Zatrephina* + (*Poecilaspis* + *Stolas*)

Fast: 2(1), 49(0), 137(0).

Slow: 22(1), 49(0), 56(1), 137(0), 187(1).

CLADE 62. *Poecilaspis* + *Stolas*

Fast: 158(0), 201(1).

Slow: 158(0).

CLADE 63. (*Basiprionota* + *Epistictina*) + (*Prenea* + (*Polychalca* + (*Canistra* + *Oxynoder*)))

Fast: 26(1), 137(3), 155(0), 187(2), 201(1).

Slow: 56(1), 137(3).

CLADE 64. *Basiprionota* + *Epistictina*

Fast: 54(1), 72(1), 152(1), 154(1).

Slow: 26(1), 54(1), 72(1), 152(1), 154(1).

CLADE 65. *Prenea* + (*Polychalca* + (*Canistra* + *Oxynoder*))

Fast: 172(1), **199(2)**.

Slow: 155(0), 172(1), **199(2)**.

CLADE 66. *Polychalca* + (*Canistra* + *Oxynoder*)

Fast: 26(0), 30(1), 67(0), 95(0), 193(1).

Slow: 30(1), 95(0), 193(1).

CLADE 67. *Canistra* + *Oxynoder*

Fast: 22(1), 56(0), 59(0), 76(0), 94(2), 111(0).

Slow: 22(1), 56(0), 59(0), 94(2), 111(0).

CLADE 68. (*Lacoptera* + *Psalidonota*) + ((*Jonthonota* + (*Charidotella* + *Orexita*)) + (*Metrionella* + (*Amythra* + *Anepsiomorpha*)))

Fast: 56(0), 90(2), 132(1), 145(0), 201(1).

Slow: 90(2), 132(1), 145(0).

CLADE 69. *Lacoptera* + *Psalidonota*

Fast: 187(0), 203(1).

Slow: 187(0).

CLADE 70. (*Jonthonota* + (*Charidotella* + *Orexita*)) + (*Metrionella* + (*Amythra* + *Anepsiomorpha*))

Fast: 139(0).

Slow: 139(0).

CLADE 71. *Jonthonota* + (*Charidotella* + *Orexita*)

Fast: 144(0), 157(1), 187(2).

Slow: 157(1).

CLADE 72. *Charidotella* + *Orexita*

Fast: 193(1).

Slow: 144(0), 193(1).

CLADE 73. *Metrionella* + (*Amythra* + *Anepsiomorpha*)

Fast: 126(0).

Slow: 126(0), 187(1).

CLADE 74. *Amythra* + *Anepsiomorpha*

Fast: 22(1), 49(0), 108(0), 119(0), 137(0).

Slow: 22(1), 49(0), 108(0), 119(0), 137(0).

CLADE 75. *Hilarocassis* + *Ogdoecosta* + *Omaspides* + (*Echoma* + (*Paraselenis* + (*Acromis* + *Eugenysini*)))

Fast: 16(1), **17(0)**, 22(1), 30(1), 56(0), 132(1), 136(1).

Slow: 16(1), **17(0)**, 22(1), 30(1), 132(1), 136(1), 187(1), 201(0).

CLADE 76. *Omaspides* clade

Fast: 0(0), 20(1), 56(1), 106(0), 137(0).

Slow: 0(0), 20(1), 56(1), 106(0), 137(0).

CLADE 77. *Echoma* + (*Paraselenis* + (*Acromis* + *Eugenysini*))

Fast: 131(0), 134(1).

Slow: 131(0), 134(1).

CLADE 78. *Echoma* clade

Fast: 11(0), 30(0), 193(1), 198(0), 199(1).

Slow: 11(0), 30(0), 193(1), 198(0), 199(1).

CLADE 79. *Paraselenis* + (*Acromis* + *Eugenysini*)

Fast: 20(1), 119(0).

Slow: 20(1), 119(0).

CLADE 80. *Acromis* + *Eugenysini*

Fast: 108(0), 126(0).

Slow: 126(0).

CLADE 81. *Eugenysini*

Fast: 30(0), 139(0), **184(0)**, 201(1), **205(1)**.

Slow: 30(0), 139(0), **184(0)**, 201(1), **205(1)**.

CLADE 82. *Miocalaspis* + *Eugenysa*

Fast: 108(1), 119(1), 131(1), 195(1).

Slow: 119(1), 131(1), 195(1).

CLADE 83. *Eugenysa* clade

Fast: 158(0), 198(0).

Slow: 158(0), 198(0).