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Systematics and phylogenetic relationships of the Australian Agaristinae (Lepidoptera: Noctuidae) based on morphology, including a revised checklist of the subfamily

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Abstract. The subfamily Agaristinae from Australia comprise a small group of largely diurnal and brightly coloured moths, but their phylogenetic relationships are largely unknown. Cladistic analysis of nearly all extant genera (20 out of 21, or 95%) and most described species (38 out of 45, or 84%) based on 39 male genitalic and adult morphological characters revealed several incongruencies with the current generic classification. Strict consensus and 50% majority rule analyses confirmed monophyly of the subfamily. The monotypic genus *Cremnophora* Hampson, 1901 (type species: *Apina angasii* Walker, 1855, a junior synonym and secondary homonym of *Agrista* [sic] *angasii* Angas, 1847) is excluded from the Agaristinae because the morphology of the male genitalia suggest it probably belongs in the Amphipyrinae. Except for a few species-groups, deep level relationships among most clades were largely unresolved. Most genera were monophyletic, but *Zalissa* Walker, 1865, *Leucogonia* Hampson, 1908, *Argyrolepidia* Hampson, 1901 and *Idalima* Turner, 1903 were all non-monophyletic. Sister-group relationships were recovered between the monotypic genera *Apina* Walker, 1855 and *Agaristodes* Hampson, 1908, and between *Phalaenoides* Lewin, 1805 and *Comocrus* Jordan, 1896. Morphological and other evidence suggest each of these pairs are congeneric; thus, we propose the following new combinations following synonymy of *Agaristodes* **syn. nov.** with *Apina* and *Comocrus* **syn. nov.** with *Phalaenoides*: *Apina feisthamelii* (Herrich-Schäffer, [1853]) **comb. nov.** and *Phalaenoides behri* (Angas, 1847) **comb. nov.** *Idalima* (type species: *Agarista affinis* Boisduval, 1832) emerged as polyphyletic, with *Idalima affinis* (Boisduval, 1832) and *Idalima metasticta* Hampson, 1910 showing a closer relationship to *Periscepta* Turner, 1920 than to *Idalima aethrias* (Turner, 1908) or *Idalima leonora* (Doubleday, 1846). Thus, we synonymise *Periscepta* **syn. nov.** with *Idalima* and transfer *Periscepta polysticta* (Butler, 1875) and *Periscepta butleri* (Swinhoe, 1892) to this genus, resulting in the following new combinations: *Idalima polysticta* (Butler, 1875) **comb. nov.** and *Idalima butleri* (Swinhoe, 1892) **comb. nov.** A revised checklist of the Australian fauna is presented, including nomenclature for all valid subspecies.

Keywords: classification, day-moth, Insecta, phylogeny
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Introduction

The moth subfamily Agaristinae (Lepidoptera: Noctuidae) has a pantropical distribution (Hampson, 1901, 1910; Strand, 1912; Jordan, 1912; Kiriakoff, 1977; Kitching, 1984; Scoble, 1992). They exhibit an array of life-history traits, including adults with diurnal, crepuscular and nocturnal activity; cryptic, mimetic and warningly coloured wing patterns; audible sound-production; aposematic larvae; and univoltine and bivoltine generations with protracted pupal dormancy. Many agaristines are day-flying (hence, the common name 'day-moth'), and the diurnal species have bright, aposematic wing colour patterns (Figs 1–2), as well as aposematic larvae (Kitching, 1984; Common, 1990; Nielsen & Common, 1991) that are assumed to be toxic to most predators (but see Talianchich *et al.,* 2003).

Agaristines are informally classified as 'trifine' noctuids in which vein M_2 of the hindwing is absent (obsolescent) (Kitching, 1984). Holloway (1989) considered that the majority of trifine genera comprise a natural group based on this unusual hindwing venation, the presence of a pair of complex hair-pencils or brush-organs at the base of the male abdomen (scent-organs which disseminate pheromones—Edgar *et al.* 1978), ornamentation of the bursa copulatrix in females with longitudinal band-like signa, and the presence of a costal process associated with the harpe in the male genitalia. Phylogenies based on molecular data also support the 'trifine' classification (Mitchell *et al.,* 1997; 2000, 2006). Recent, large-scale phylogenetic analysis of Noctuidae and Noctuoidea suggest Agaristinae are most closely related to either Oncocnemidinae (Mitchell *et al.,* 2006; Keegan *et al.,* 2021) or Acronictinae and Amphipyrinae (Regier *et al.,* 2016; Li *et al.,* 2024).

Traditionally, Agaristinae were considered to be a separate family closely related to Noctuidae (e.g., Hampson, 1901, 1910; Jordan, 1912; Kiriakoff, 1977). In contrast, Strand (1912) and Turner (1920) treated Agaristinae as a subfamily of Noctuidae, but universal adoption of this taxonomic rank did not occur until the 1980's following publication of a major checklist and revision of the North American Noctuidae (Franclemont & Todd, 1983) and Kitching's (1984) global review of the higher classification of Noctuidae. The Agaristinae are widely regarded to be monophyletic (Kiriakoff, 1977; Kitching, 1984; Holloway, 1989), but the relative importance of characters delineating the group has varied among workers. For example, Hampson (1901, 1910) considered the filiform structure of the antennae to be the primary character for distinguishing agaristines from other noctuids, whereas Jordan (1912) and Turner (1920) found little structural evidence to diagnose agaristines, although both acknowledged that they comprised a distinct natural group. Jordan (1912) included genera with filiform, ciliate and bipectinate antenna in his revision and classification of the Indo-Australian fauna. Warren (1913-1937) found wing neuration to be "surprisingly consistent" and concluded that the separation of agaristines from other day-flying Noctuidae was "purely one of convenience" (Warren, 1913-1937, p. 31). However, Kiriakoff (1963, 1977) noted that agaristines are a very homogeneous group morphologically; he observed that they possess enlarged tympanal organs similar to some other noctuids, but are distinguished by the presence of a paired vesicle (bulla abdominalis) at the base of the abdomen, a synapomorphy he considered to be a reliable character for differentiating the lineage.

Strand (1912) recognised just over 500 valid species of Agaristinae referred to 137 genera in his global checklist of the fauna, although that work is now considerably outdated. More recently, Scoble (1992) estimated around 300 species in the subfamily. In Australia, there are currently 45 described species (and at least a further eight undescribed species, Braby, 2025) referred to 21 genera (Edwards, 1996; Braby, *et al.* 2018; Braby & Heath, 2024), excluding the genus *Cremnophora* Hampson, 1901 (containing the single species *Cremnophora angasii* (Angas, 1847)) that was added to the Australian agaristine fauna by Nye (1975). Kiriakoff (1977) provisionally classified the Palaearctic, Oriental and Australian agaristine fauna into several informal 'subgroups', of which eight included the Australian genera, based on features of the male genitalia. However, the classification of genera, and to some extent species, has been unstable over the past 125 years (Table 1) and is in need of review (Kitching 1984; Edwards 1996). For example, the generic classification of *Argyrolepidea thoracophora* Turner, 1920; *Coenotoca subaspersa* (Walker, [1865]); *Platagarista macleayi* (W.J. Macleay, 1864); *Periopta ardescens* (Butler, 1884); *Periopta diversa* (Walker, [1865]); and *Burgena varia* (Walker, 1854), as well as several species currently assigned to *Idalima* Turner, 1903 (i.e., *I. aethrias* (Turner, 1908); *I. leonora* (Doubleday, 1846); and *I. tasso* (Jordan, 1912)), have been particularly unstable (Table 1). Edwards (1996) revised the status of four taxa to full species (i.e., *Cruria latifascia* Jordan, 1912; *Cruria tropica* (T.P. Lucas, 1891); *Idalima butleri* (Swinhoe, 1892); *Idalima tasso* (Jordan, 2012)), and synonymised the genus *Prostheta* Turner, 1922, proposed for *Prostheta acrypta* Turner, 1922, a junior synonym of *Hecatesia exultans* Walker, [1865], under *Hecatesia* Boisduval, 1829. Many of the genera erected in the early twentieth century by G.F. Hampson, H.E.K. Jordan and A.J. Turner were based on a relatively narrow concept with few reliable distinguishing characters, resulting in a high proportion of genera (11 or 52%) endemic to Australia or the Australian region that are either monotypic (*Agarista* Leach, 1814; *Agaristodes* Hampson, 1908; *Apina* Walker, 1855; *Comocrus* Jordan, 1896; *Ipanica* Hampson, 1908; *Platagarista* Jordan, 1912) or contain only two species (*Coenotoca* Turner, 1903; *Eutrichopidia* Hampson, 1901; *Periopta* Turner, 1920; *Periscepta* Turner, 1920; *Radinocera* Hampson, 1908). The delineation of so many genera in the Australian fauna is unlikely to reflect true phylogenetic relationships and evolutionary history of the constituent species, but there have been no previous phylogenetic studies undertaken to investigate the robustness of the current classification. Thus, the main aim of this study is to reconstruct the phylogeny of the Australian Agaristinae using cladistic analysis of morphological characters (male genitalia and external features of the adult). Our results are then compared with the generic classifications of previous workers, particularly the more recent studies by Kiriakoff (1977) and Edwards (1996).

Materials and methods

Taxon sampling

Thirty-eight ingroup species (Figs 1–2), of the 45 described species of Australian Agaristinae, were sampled for phylogenetic analysis. The seven missing species (*Sarbanissa diana* Sugi, 1996; *Cruria latifascia*; *C. tropica* (T.P. Lucas, 1891); *C. epicharita* (Turner, 1911); *C. darwiniensis* (Butler, 1884); *Mimeusemia simplex* (T.P. Lucas, 1891); and *Idalima tasso*) were not examined due to paucity of material. *Cremnophora angasii* has been placed in the Agaristinae (Nye, 1975; Common, 1990; Edwards, 1996), but it was found to be misplaced in this subfamily based on morphology of the male genitalia (Fig. 24C), frons shape (with a small, rounded prominence), and wing pattern elements, which resemble those of Amphipyrinae to which it appears to belong. Indeed, Hampson (1901) classified *C. angasii* well outside the Agaristinae in his revision of the Noctuidae, which was followed by McFarland (1979) in his compilation of larval food plants. This taxon was therefore omitted from the analysis altogether. An additional four species (Fig. 2) from the Noctuidae were included as outgroups to estimate ingroup relationships and determine character polarity, *viz*: *Neumichtis saliaris* (Guenée, 1852); *Proteuxoa sanguinipuncta* (Guenée, 1852); *Helicoverpa punctigera* (Wallengren, 1860); and *Heliothis punctifera* Walker, 1857. *Neumichtis* Hampson, 1906 and *Proteuxoa* Hampson, 1903 represent large and divergent genera within the Australian Amphipyrinae, whereas *Helicoverpa* Hardwick, 1965 and *Heliothis* Ochsenheimer, 1816 represent significant genera in the Heliothinae (Matthews 1999). Morphological and molecular phylogenetic studies of the Noctuidae consider the ‘trifine’ subfamilies, which include the Amphipyrinae, Heliothinae and Agaristinae, to be a monophyletic group (Kitching, 1984; Holloway, 1989; Speidel *et al.,* 1996; Mitchell *et al.,* 1997*,* 2000, 2006).

Material examined

The material that was examined for morphological characters in the Australian National Insect Collection, Canberra (ANIC) is listed in Appendix 1. Each specimen was examined, especially the male genitalia, but also wing pattern elements and other external features. We also examined, identified and sorted material, including name-bearing types, in the Australian Museum, Sydney, Museums Victoria, Melbourne, and South Australian Museum, Adelaide.

Male genitalia

Genitalia dissections were examined for all ingroup and outgroup species. The male genitalia were prepared following the method described by Hardwick (1950), except that all structures were stained in orcein and the abdomens cut open to reveal the sclerotisation and hair-pencils (pheromone-disseminating hair brushes) of abdominal segments VII and VIII. The abdomen of each specimen was removed and boiled for 4–10 mins in 10% KOH. Following maceration, each abdomen was transferred to 15% propanol for cleaning and dissection. The genitalia were removed from each abdomen; the phallus was then removed from the tegumen and vinculum. The vesica of each phallus was everted using the Vesica Everter apparatus (Matthews 1998). The valvae were cleaned of extraneous scales and membrane, and the pelt cleaned of scales and internal organs, and opened with a cut along the right-hand side. The cleaned pelt and valvae were flattened with small glass weights and, together with the phallus and vesica, dehydrated for a few minutes in 100% propanol, stained for 2–3 mins in orcein, and returned to 100% propanol to leach out excess stain. The genitalia were then transferred to Euparal Essence prior to mounting in Euparal, with the pelt opened and flattened, the phallus and its everted vesica block mounted in lateral orientation, and the tegumen, vinculum, and valvae block-mounted in posterior orientation, with the valvae slightly opened and flattened to reveal the internal features of the genitalia. Dissections were not made for three species (*Hecatesia exultans*, *Coenotoca unimacula* (Lower, 1903), and *Periscepta butleri*) due to scarcity of material, but previously prepared genitalia slides were examined; however, the vesicas were not everted in these preparations.

At least one male of each species was dissected and the vesica everted to examine and score characters. For 21 species at least two preparations were available for character scoring (Appendix 1), while for others published illustrations were also available (see Kiriakoff, 1977). The basic structure of the male genitalia of Agaristinae is shown in Figures 3A–B. For each species, except two outgroups, the male genitalia were illustrated to assist with character assessment and scoring.

The membranous vesicas of noctuids are often highly specific in shape, with sclerotised spines (cornuti) and blind-ending sacs (diverticula) that have proved highly important in resolving species level differences, and have enhanced phylogenetic studies (Kitching, 1984; Common, 1990; Dang, 1993). The shape of the membranous vesica was not available to Kiriakoff (1977) because the organ is contained within the hollow tube of the phallus, which is small in Agaristinae and difficult to evert manually without specialised apparatus, such as the Vesica Everter (Matthews, 1998).

The detailed illustrations and descriptions of the male genitalia of Australian Agaristinae by Kiriakoff (1977) were also assessed, and for each species reference to this work is given where previous preparations have been published.

Character scoring

During a preliminary investigation, a large number of morphological characters were investigated, but many of these were discarded *a posteriori* because they showed high levels of homoplasy and were thus phylogenetically uninformative. These discarded characters included hair pencils, sclerotisation of sclerites and tergites VII and VIII, abdominal markings, internal sclerotised structures of the vesica, tibial spurs, maxilla, eye and other cranial features, wing: body ratio and forewing: hindwing ratio. The female genitalia of six species (*Agaristodes feisthamelii* (Herrich-Schäffer, [1853]); *Apina callisto* (Angas, 1847); *Phalaenoides tristifica* (Hübner, 1818); *Phalaenoides glycinae* Lewin, 1805; *Platagarista macleayi*; *Idalima metasticta* Hampson, 1910) were also examined (Appendix 1), but no potentially informative characters (e.g., signa on the corpus bursae) were found.

Our final data dataset consisted of 39 unordered and equally weighted external morphological characters (Appendix 2), of which 21 concerned the male genitalia.

Figure 1. Species of Australian Agaristinae examined in this study: (A) *Phalaenoides behri* **comb. nov.**; (B) *Phalaenoides glycinae*; (C) *Phalaenoides tristifica*; (D) *Apina feisthamelii* **comb. nov.**; (E) *Apina callisto*; (F) *Ipanica cornigera*; (G) *Periopta diversa*; (H) *Periopta ardescens*; (I) *Burgena varia*; (J) *Cruria donowani*; (K) *Cruria synopla*; (L) *Cruria kochii*; (M) *Platagarista macleayi*; (N) *Eutrichopidia latina*; (O) *Agarista agricola*; (P) *Idalima aethrias*; (Q) *Idalima leonora*; (R) *Argyrolepidia fracta*; (S) *Idalima polysticta* **comb. nov.**; (T) *Idalima butleri* **comb. nov.**; (U) *Idalima metasticta*; (V) *Idalima affinis*. Scale bar = 20 mm.

Figure 2. Species of Australian Agaristinae and five outgroups examined in this study: (A) *Radinocera maculosa*; (B) *Radinocera vagata*; (C) *Argyrolepidia aequalis*; (D) *Coenotoca unimacula*; (E) *Coenotoca subaspersa*; (F) *Mimeusemia centralis*; (G) *Mimeusemia econia*; (H) *Argyrolepidia thoracophora*; (I) *Hecatesia thyridion*; (J) *Hecatesia fenestrata*; (K) *Hecatesia exultans*; (L) *Leucogonia cosmopis*; (M) *Zalissa pratti*; (N) *Zalissa catocalina*; (O) *Zalissa stichograpta*; (P) *Leucogonia ekeikei*; (Q) *Heliothis punctifera* (Heliothinae); (R) *Heliocoverpa punctigera* (Heliothinae); (S) *Neumichtis saliaris* (Amphipyrinae); (T) *Cremnophora angasii*; (U) *Proteuxoa sanguinipuncta* (Amphipyrinae). Scale bar = 20 mm.

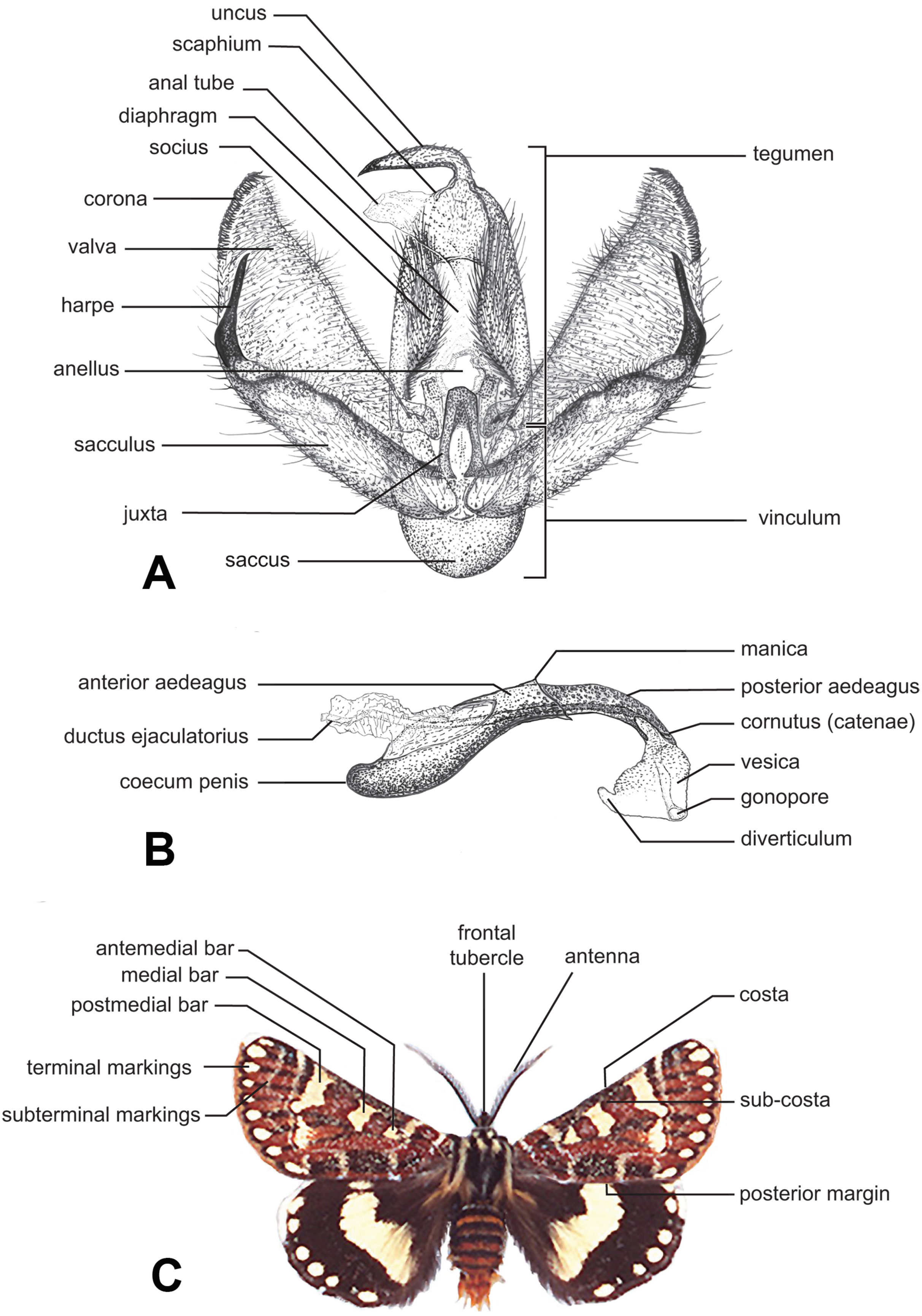

Figure 3. Diagrams of representative male genitalia and adult Agaristinae, based on *Apina callisto*: (A) posterior view of valvae, tegumen and vinculum; (B) lateral view of phallus; (C) wing colour pattern elements of adult.

The male genitalia (Figs 3A–B), in particular the vesica, are considered to be one of the most phylogenetically informative character complexes in systematic studies of Lepidoptera and, in the Noctuidae, their use is standard best practice in describing new species, resolving species-level differences in taxonomically complex groups, and determining their evolutionary relationships (Hardwick, 1965; Kitching, 1984; Common, 1990; Rawlins, 1992; Poole, 1994). Character states for several structures of the male genitalia are illustrated for ease of reference, particularly the vesica type (Fig. 4), shape of the apical diverticulum (Fig. 5), shape of the phallus (Fig. 6), sclerotised extensions of the phallus into the vesica (Fig. 7), shape of juxta (Fig. 8), and width and shape of the valvae (Fig. 9).

The 18 other morphological characters (Appendix 2) included wing pattern elements (Fig. 3C), features of the antennae, frons, and markings on the thorax (Fig. 10). The generalised forewing pattern of a typical noctuid (*Euxoa* sp.) given by Poole (1994) was used to assess wing characters. This basic pattern is present in most nocturnal species of Agaristinae and in the outgroup subfamilies. In order to ensure scoring of homologous wing patterns, the forewing was divided into four areas where wing markings in the form of spots, bars, lines etc. were typically expressed, and these areas each formed the basis of a polymorphic character (Fig. 11). In the diurnal species, only the antemedial, medial, postmedial bars, and subterminal markings are prominent, and each of these four areas of the forewing was scored as a multi-state character. Patterns of iridescence, ground colours, and extraneous bars were also scored, as well as markings and colours of the hindwing. However, species with cryptic wing patterns could not be satisfactorily categorised as having bars or spots and were instead lumped into a generalised state. It should be noted that in these taxa

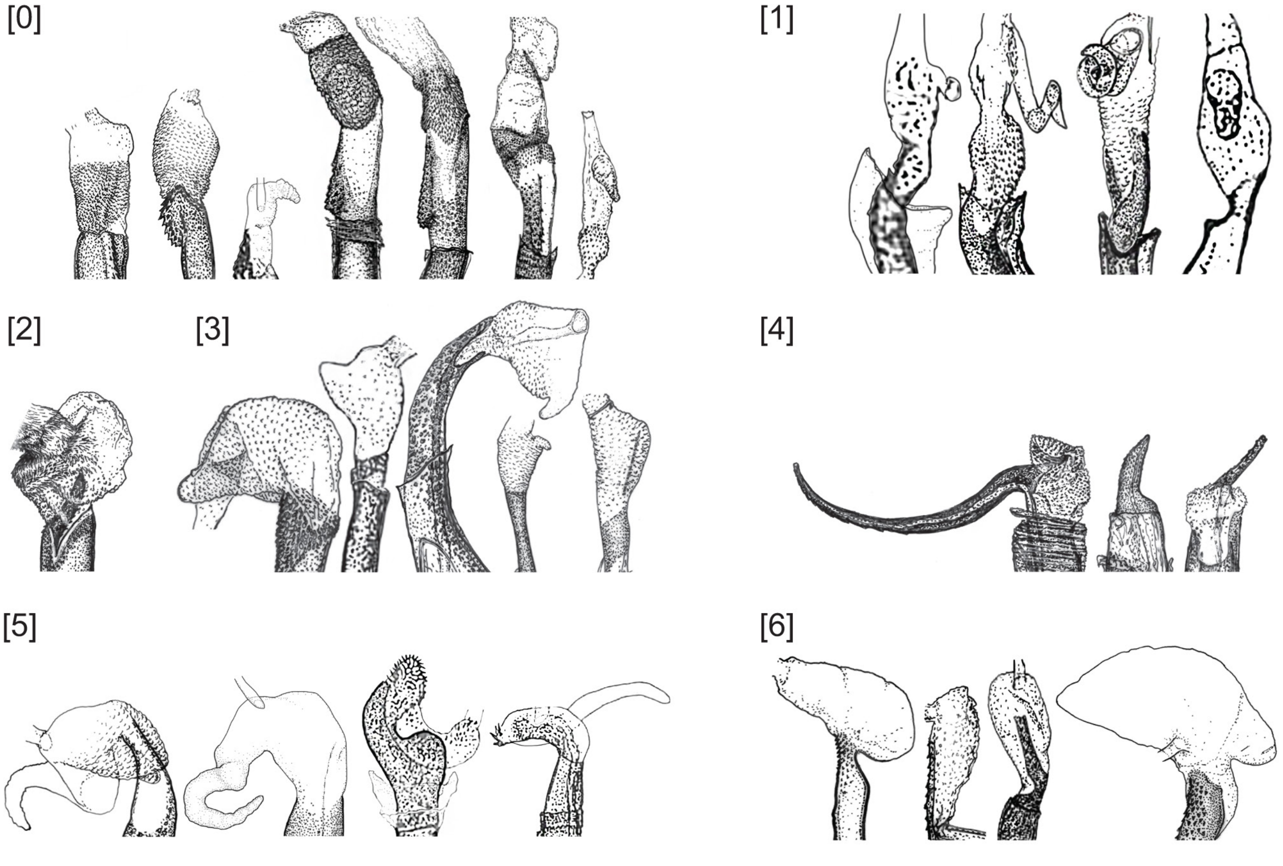

Figure 4. Character states for vesica type of male genitalia: [0] tubular, extending posteriorly; [1] tubular, extending posteriorly, small broadening medially; [2] tubular, extending posteriorly, large broadening laterally; [3] tubular, extending posteriorly, broadening distally; [4] permanently everted with a single, sclerotised process enclosing ductus seminalis; [5] tubular or "C" shaped, recurved anteriorly or laterally; [6] expanded anteriorly, ovoid or anvil shaped.

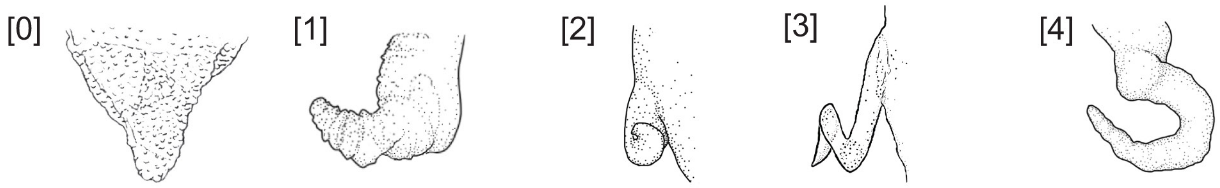

Figure 5. Character states for shape of apical diverticulum of male genitalia: [0] straight; [1] weakly curved apically; [2] tightly curved apically; [3] spiralled; [4] "C"-shaped.

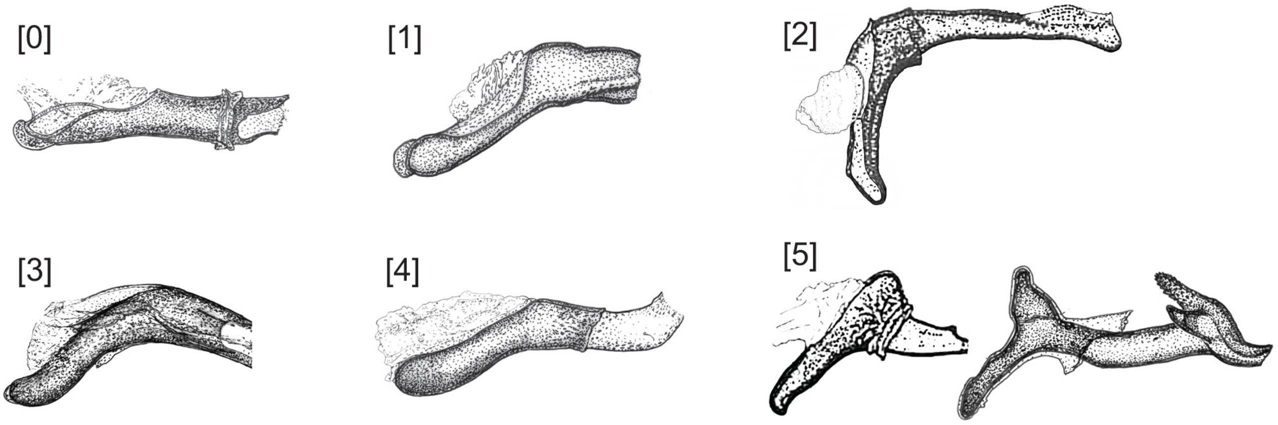

Figure 6. Character states for shape of phallus of male genitalia: [0] straight; [1] anteriorly curved ventrally <45º; [2] anteriorly curved ventrally >45º; [3] weakly anteriorly and posteriorly curved ventrally; [4] posteriorly curved dorsally, anteriorly curved ventrally; [5] anteriorly strongly curved ventrally with dorsoposterior lobe.

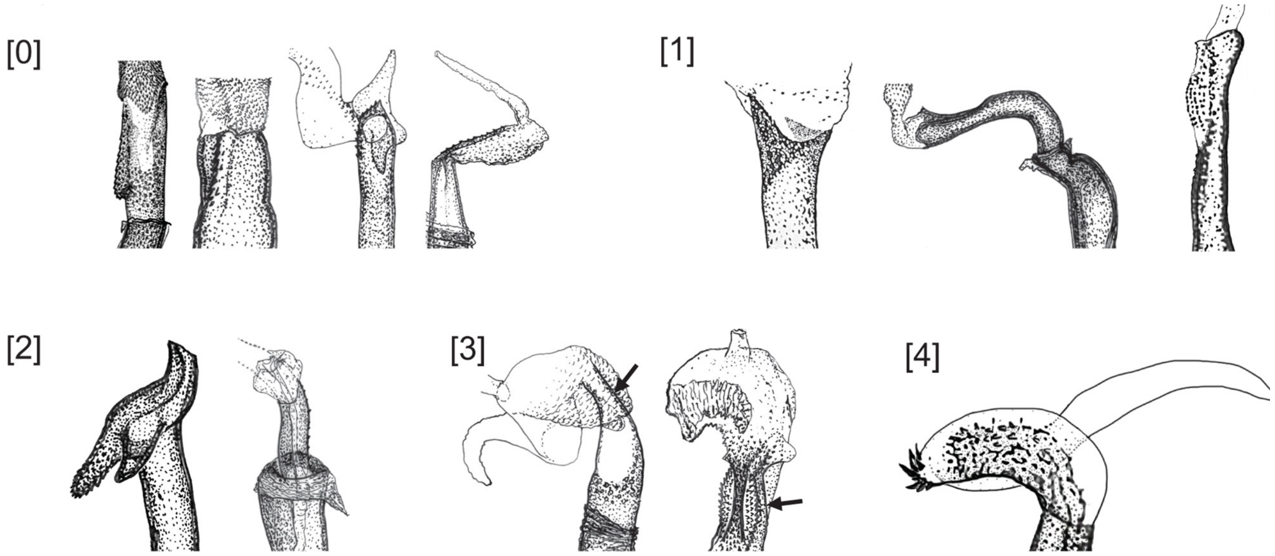

Figure 7. Character states for sclerotised extensions of phallus into vesica of male genitalia: [0] with a spined ridge; [1] with two lateral, weakly sclerotised extensions into vesica; [2] with a strongly sclerotised, evenly ending, cylindrical extension into vesica; [3] with constricting lateral extensions resulting in invagination of vesica; [4] with a long, flat sclerotised plate extending into vesica.

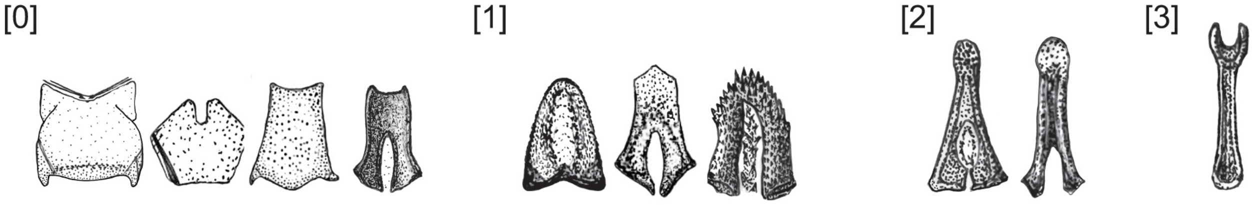

Figure 8. Character states for shape of juxta of male genitalia: [0] flat, square, or "M"-shaped; [1] triangular and flat-topped or indented dorsally; [2] narrowly triangular, tapering sharply dorsally; [3] pillar-shaped.

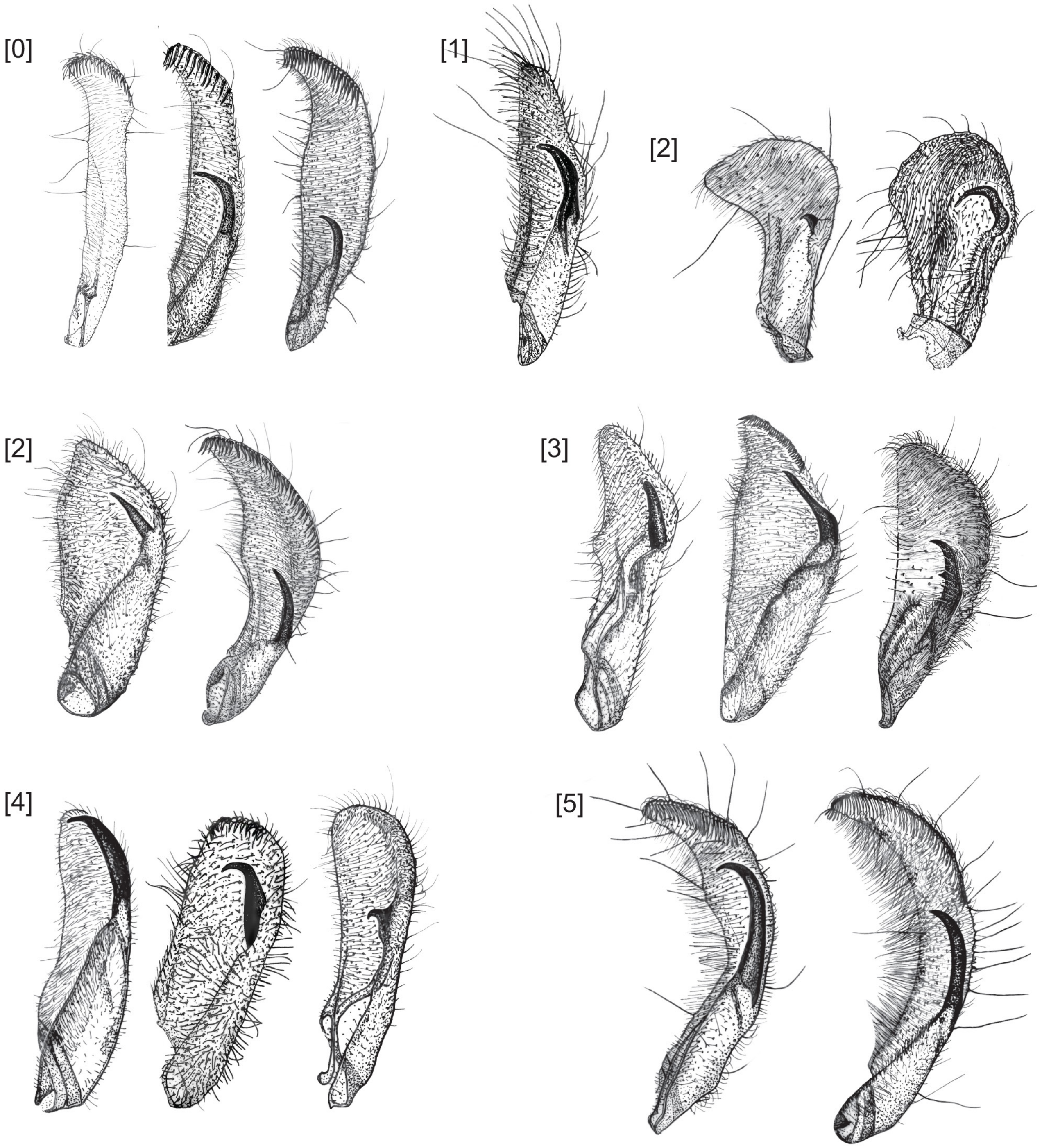

Figure 9. Character states for width and shape of valva of male genitalia: [0] narrow, apex sharply pointed, inner margin straight, angularly inward-curved at apex; [1] narrow, apex sharp, inner margin straight, outer margin angularly inward-curved at median; [2] more than twice as broad distally than proximally, apex rounded; [3] width with a medial bulge, apex sharp or produced; [4] width consistent, less than vinculum, margins straight, apex squarish or gently rounded; [5] slender, "crescent" shaped, both margins strongly curved medially, apex pointed.

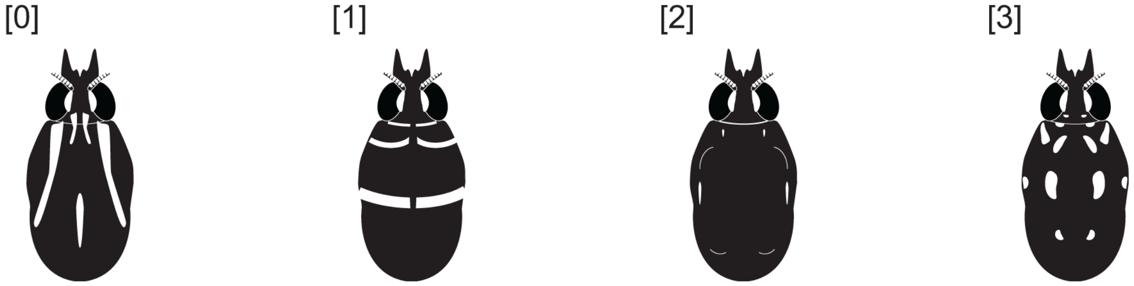

Figure 10. Character states for markings of thorax: [0] predominantly longitudinal bands; [1] predominantly transverse bands; [2] predominantly faint markings; [3] predominantly large spots.

multiple scoring of cryptic markings lends undue weight to the analysis.

Most characters regarded to be phylogenetically informative were, to some degree, continuous, and sometimes it was difficult to determine homology in both external and genitalia characters. In addition, many potentially useful binary characters were homoplasious in the absence state, and a number of species and species groups were highly apomorphic; the states of many of the characters for such taxa were therefore not useful for estimating relationships. Therefore, an attempt was made to maximise phylogenetic information in polymorphic characters by re-scoring characters shown to be homoplasious in initial phylogenetic estimates. Other quantitative characters such as wing and body ratios were plotted to determine whether natural gaps between the values were present—these characters were discarded if the values did not fall into discernible clusters.

Phylogenetic analysis

The final dataset, which consisted of 39 characters and 42 taxa (38 ingroups, 4 outgroups) (Appendix 3), was subjected to cladistic analyses using PAUP version 4.0d64 (Swofford, 1999) based on the parsimony criterion to estimate the phylogeny. This method assumes the best phylogenetic estimate is the one that employs the least number of evolutionary changes, to maximise character congruence and summarise the dominant hierarchal signal as a bifurcating tree (Maddison, 1997). The parsimony analysis was executed on a Power Macintosh 5500/250 using 1000 random addition sequences; only 500 trees were saved at each replicate. Due to the size of the dataset the use of exhaustive methods to generate the most parsimonious tree was found to be impractical, so the data were analysed with heuristic settings and the branch-swapping algorithm tree-bisection-reconnection (TBR). The algorithm employed for heuristic searches in PAUP does not generate every possible tree, nor guarantee the most parsimonious tree.

A number of character exploration techniques were used to investigate homoplasy in the dataset and to measure the goodness of fit of the dataset to the trees. Homoplasious characters were identified by plotting characters on trees with the program McClade (Maddison & Maddison, 1992) and re-examined to determine whether scoring could be improved. The program SPLITSTREE 2.2.1 (Huson & Wetzel, 1997) was used to depict the relationship of species groups, and reverse successive weighting (Trueman, 1998) was used to determine whether the data contained more than one signal which could be interpreted as hierarchy. Reverse successive weighting investigates datasets or partitions in datasets for conflicting hierarchal structure by down-weighting non-homoplasious characters relative to homoplasious characters, weakening the initial structure of the tree and allowing a rival signal to dominate. The best alternative tree from the weighted dataset can then be tested for significant structure with bootstrap analysis or other standard test. Multiple hierarchal signals may occur if a group of characters (such as wing-pattern characters) show convergence and parallelisms by tracking a variable other than the phylogeny (e.g., mimicry), causing concerted homoplasy (Trueman, 1998). External morphological characters, primarily wing patterns and colour, were tested separately against genitalia characters for congruence in a partition homogeneity test. Three widely used tests were employed to determine the robustness of nodes and hence confidence in the topology: bootstrap value (Felsenstein, 1985), Bremer support or Decay Index (Bremer, 1988, 1994), and T-PTP test (topology-dependent cladistic permutation tail probability test) (Faith, 1991; Faith & Cranston, 1991).

Results

Two phylogenetic trees were generated from the cladistic analyses: a strict consensus of 13,710 most parsimonious trees of length 257 (CI = 0.409, RI = 0.687) (Fig. 12); and a 50% majority rule tree (Fig. 13). Tree topology from both estimates were congruent with each other. Monophyly of Agaristinae (i.e., ingroup clade) was supported by T-PTP test ($P< 0.01$) and Bremer support value (1), but had low bootstrap support (55). The male genitalia of each species are shown in Figures 14–24. Synapomorphies distinguishing Agaristinae from the outgroup taxa (Amphipyrinae and Heliothinae) were primarily genitalic (Appendices 2–3). The outgroups all shared several plesiomorphic traits, including phallus simple and straight [character 9, state 0]; sacculus poorly defined with harpe reduced or absent [12, 0]; juxta flat and square-shaped [16, 0], without spines [17, 0] and internally sclerotised [18, 0]; and hindwing markings absent [36, 0]. The genitalia of the outgroups *Proteuxoa sanguinipuncta* (Fig. 24B) and *Neumichtis saliaris* (not illustrated) possessed a pair of elongated, sclerotised structures on the sacculus—these structures were interpreted to be not homologous with the harpe due to the presence in *N. saliaris* of another pair of weakly sclerotised structures closely resembling the shape and position of the harpe in the ingroup taxa.

The base or backbone of both trees was largely unresolved, and many clades formed polytomies. The

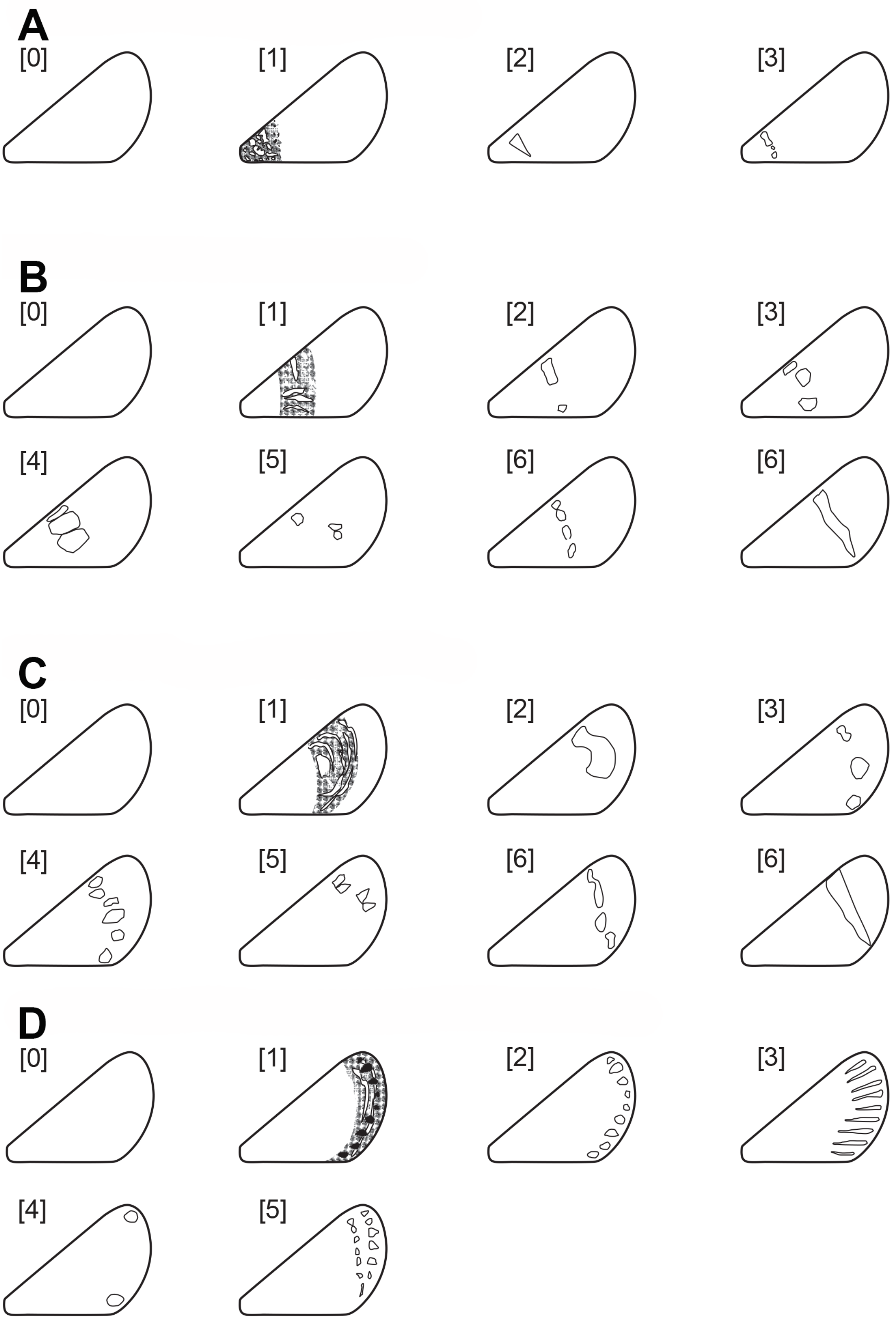

Figure 11. Character states of forewing for: (A) antemedial markings; (B) medial markings; (C) postmedial markings; (D) subterminal and terminal markings. See text and Appendix 2 for explanation of character states.

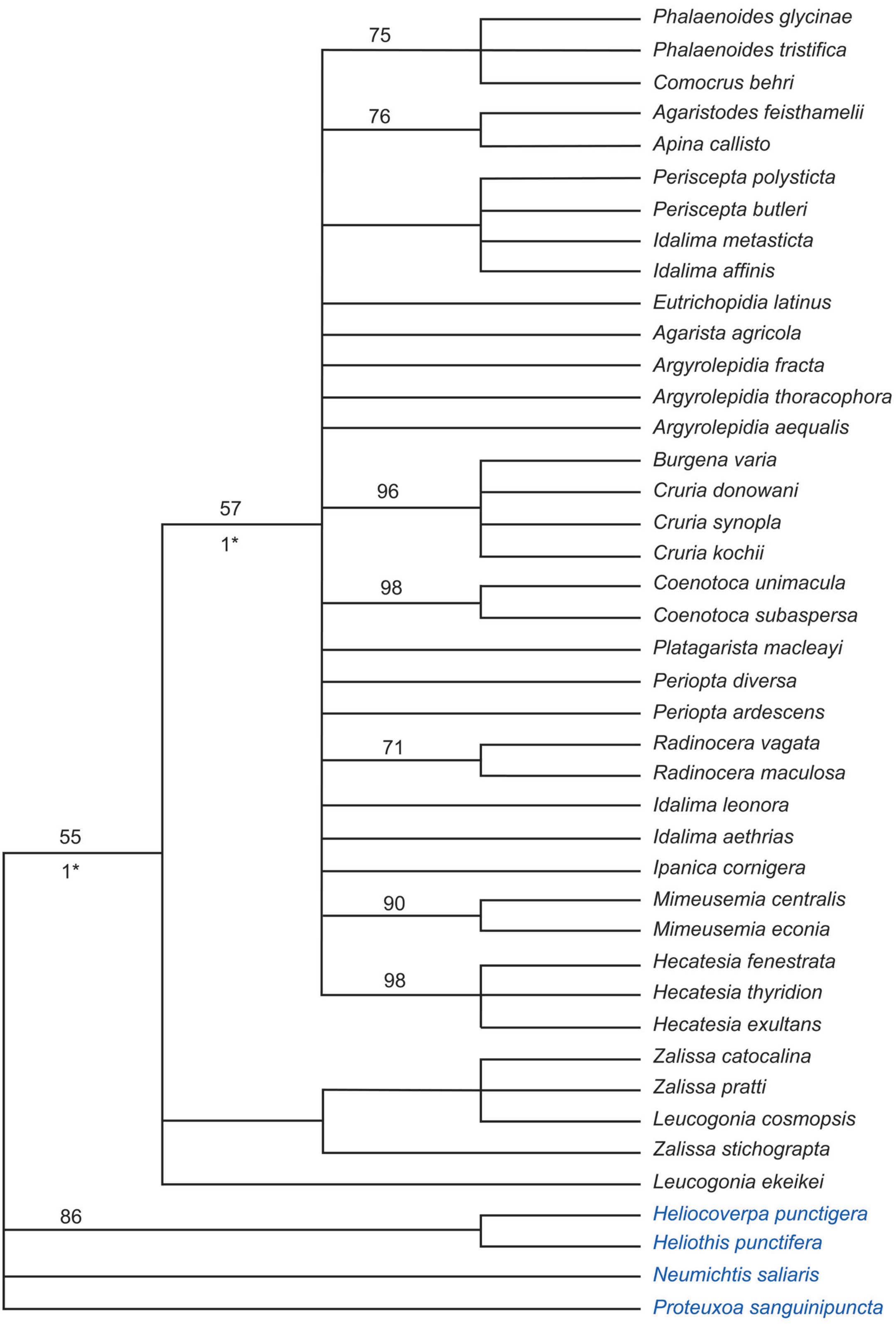

Figure 12. Strict consensus tree based on morphological characters (*n* = 39 characters; 13,710 trees; tree length= 257; 16 islands of length 257; CI = 0.409; RI = 0.687). Only 500 trees per replicate were saved. Numbers above the nodes are bootstrap values (Heuristic setting, 100 x 10 random addition sequences; only values of 50 and above are shown). Additional measures of support were estimated for only two nodes, with numbers below the nodes being Bremer support values, and asterisks denoting nodes for which T-PTP tests corroborate a prior hypothesis of monophyly. Outgroup taxa are highlighted in blue.

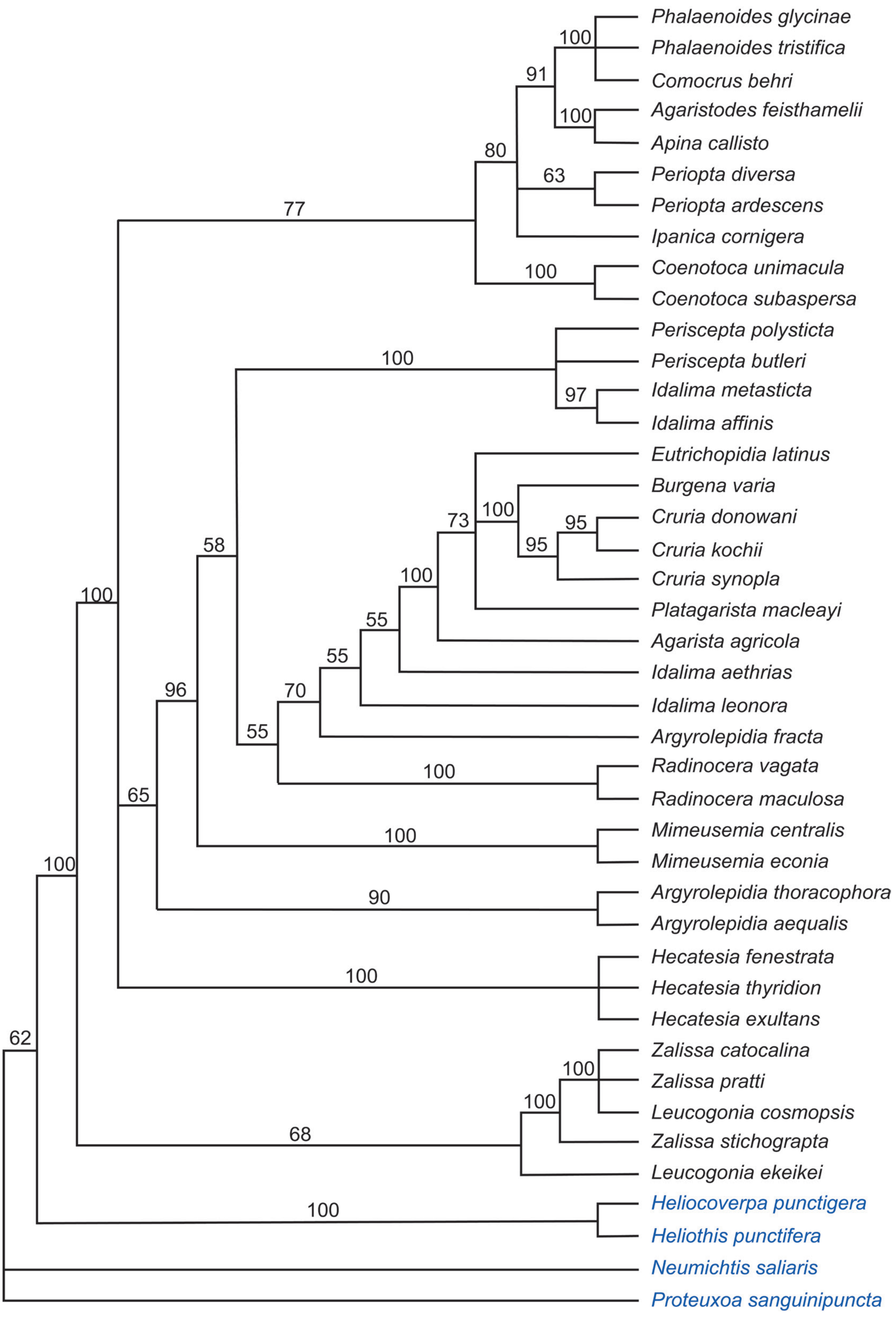

Figure 13. 50% majority rule tree using morphological characters ($n = 39$ characters; 13,232 trees; tree length= 257; over 90 islands of length 257; Cl = 0.409; RI = 0.687). Only 500 trees per replicate were saved. Numbers above the nodes are the percentage of trees in which that node occurs. Outgroup taxa are highlighted in blue.

morphological character partition gave no significant difference in maximum parsimony estimates in a partition homogeneity test, indicating that homoplasy in the tree was not due to conflicting hierarchal signal across these character types. The program SPLITSTREE 2.2.1 yielded a 'bush' structure in which species groups showed some definition but relationships between them were largely unresolved, and this is reflected in the high degree of polytomy in the strict consensus tree.

The nocturnal genera *Zalissa* + *Leucogonia* were recovered in a separate clade sister to the remaining agaristines with significant T-PTP test ($P < 0.01$) and high Bremer support (1), although bootstrap support was low (68). The divergent genitalia of *Leucogonia ekeikei* (Bethune-

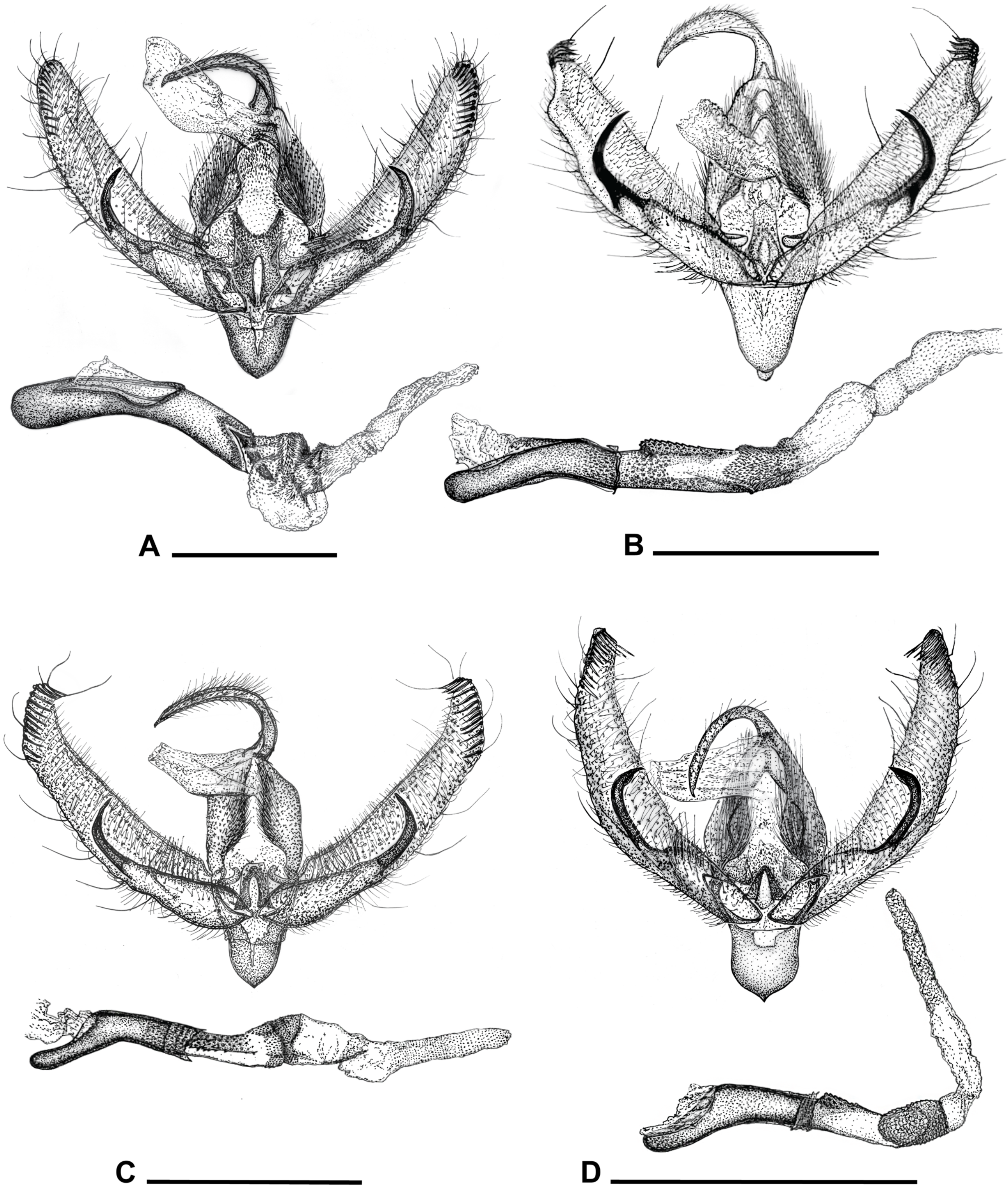

Figure 14. Male genitalia of Australian Agaristinae: (A) *Zalissa stichograpta*; (B); *Zalissa pratti* (C) *Zalissa catocalina*; (D) *Leucogonia cosmopis*. Shown here, and Figs 15–24, are valvae, tegumen and vinculum in posterior view, and phallus in lateral view. Scale bars = 2.0 mm.

Baker, 1906) (Fig. 15A) appears to have resulted in its placement outside of, or sister to, this clade, suggesting doubt over the monophyly of both *Leucogonia* Hampson, 1908 and *Zalissa* Walker, 1865. However, there was no significant support for the polyphyly of *Leucogonia*. The plesiomorphic character states separating *Zalissa* and *Leucogonia* from the other largely diurnal agaristine taxa were forewing marking pattern cryptic [characters 31–34, state 1]; forewing marking colour predominantly brown [35, 0]; and frons with a small, rounded prominence [23, 0] as opposed to a truncate or spatulate state.

Within the largely 'diurnal' agaristines, there was strong evidence supporting the monophyly or sister group relationships of *Cruria* + *Burgena* (bootstrap value = 96), *Apina* + *Agaristodes* (bootstrap value = 76), and *Phalaenoides* + *Comocrus* (bootstrap value = 75). The close relationship between *Burgena* Walker, [1865] (Fig. 19D) and *Cruria* Jordan, 1896 (Figs 19A–C) was characterised by several synapomorphies, including vesica permanently everted with a single, sclerotised process enclosing the ductus

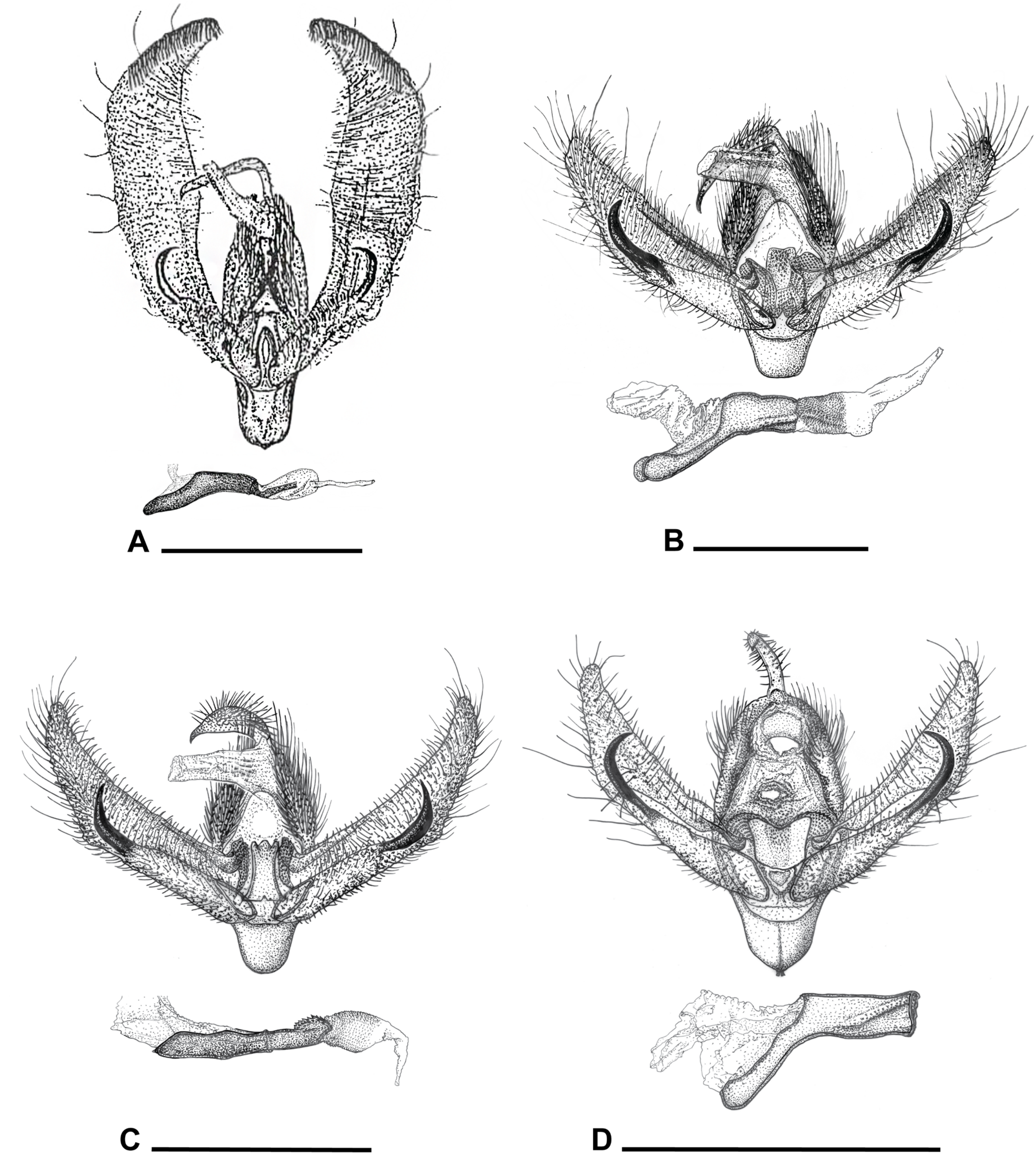

Figure 15. Male genitalia of Australian Agaristinae: (A) *Leucogonia ekeikei*; (B) *Hecatesia thyridion*; (C) *Hecatesia fenestrata*; (D) *Hecatesia exultans*. Scale bars = 2.0 mm.

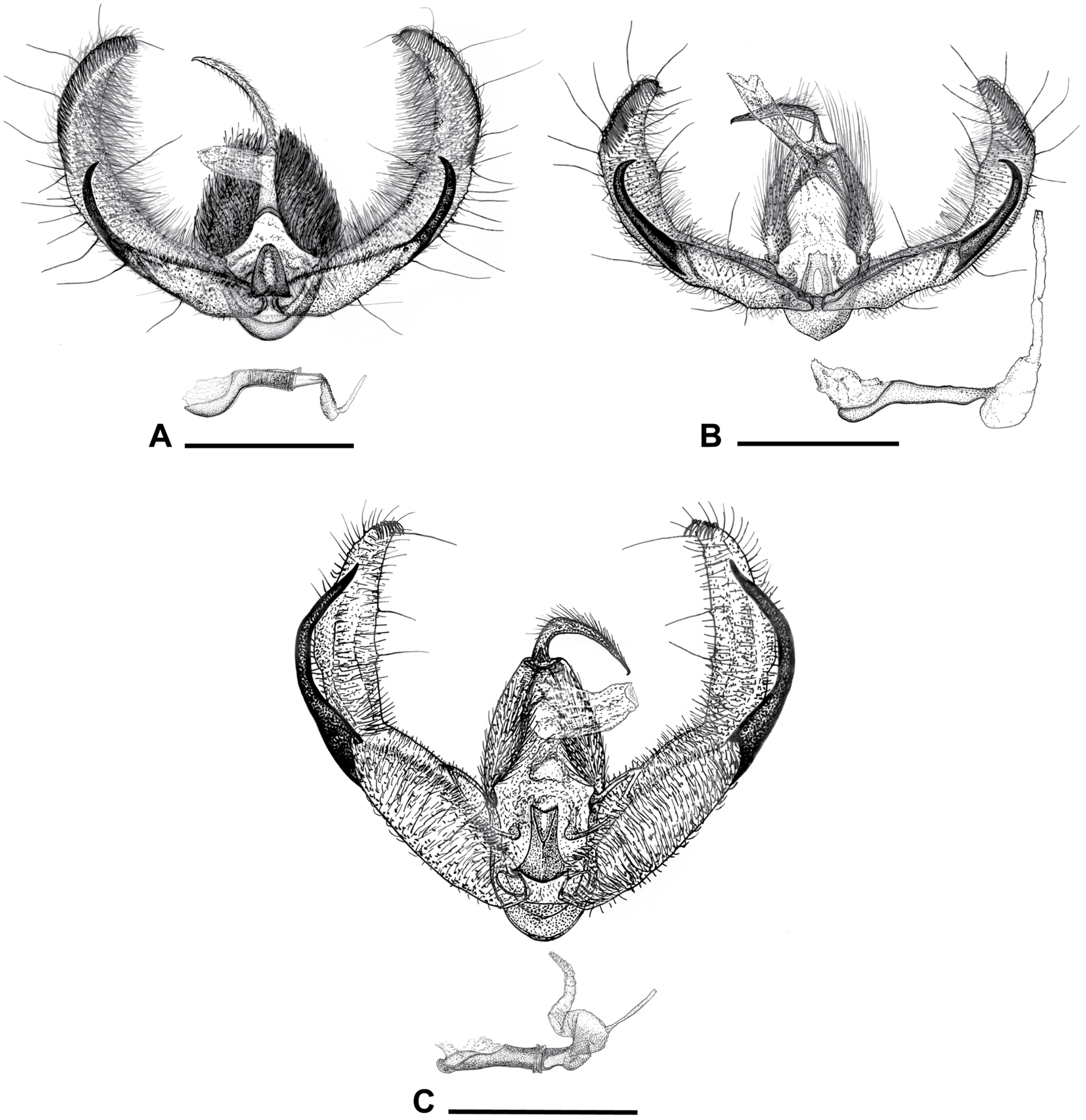

Figure 16. Male genitalia of Australian Agaristinae: (A) *Argyrolepidia thoracophora*; (B) *Argyrolepidia aequalis*; (C) *Argyrolepidia fracta*. Scale bars = 2.0 mm.

seminalis [character 1, state 4]; apex of valva rounded, more than twice as broad distally than proximally [19, 2]; uncus equal or greater in length than tegumen [20, 2]; postmedial markings of forewing comprising two pairs of elongate spots [33, 5]; and hindwing markings comprising two bars or bands [36, 3].

Most genera for which two or more species were included were recovered as monophyletic with high bootstrap support (>70), *viz*: *Hecatesia*, *Mimeusemia* Butler, 1875, *Radinocera*, *Coenotoca* and *Cruria*. However, several genera were non-monophyletic, most notably *Leucogonia*, *Zalissa*, *Argyrolepidia* and *Idalima*. In particular, *Idalima affinis* (Boisduval, 1832) and *Idalima metasticta* showed a closer relationship to *Periscepta polysticta* (Butler, 1875) and *Periscepta butleri* with good support than to *Idalima leonora* or *I. aethrias*.

Taxonomy

A revised classification of the Australian Agaristinae is presented in Tables 1–2 based on the cladistic analysis of morphological data and other evidence. The following taxonomic changes are made concerning the synonymy of several genera and new combinations of species.

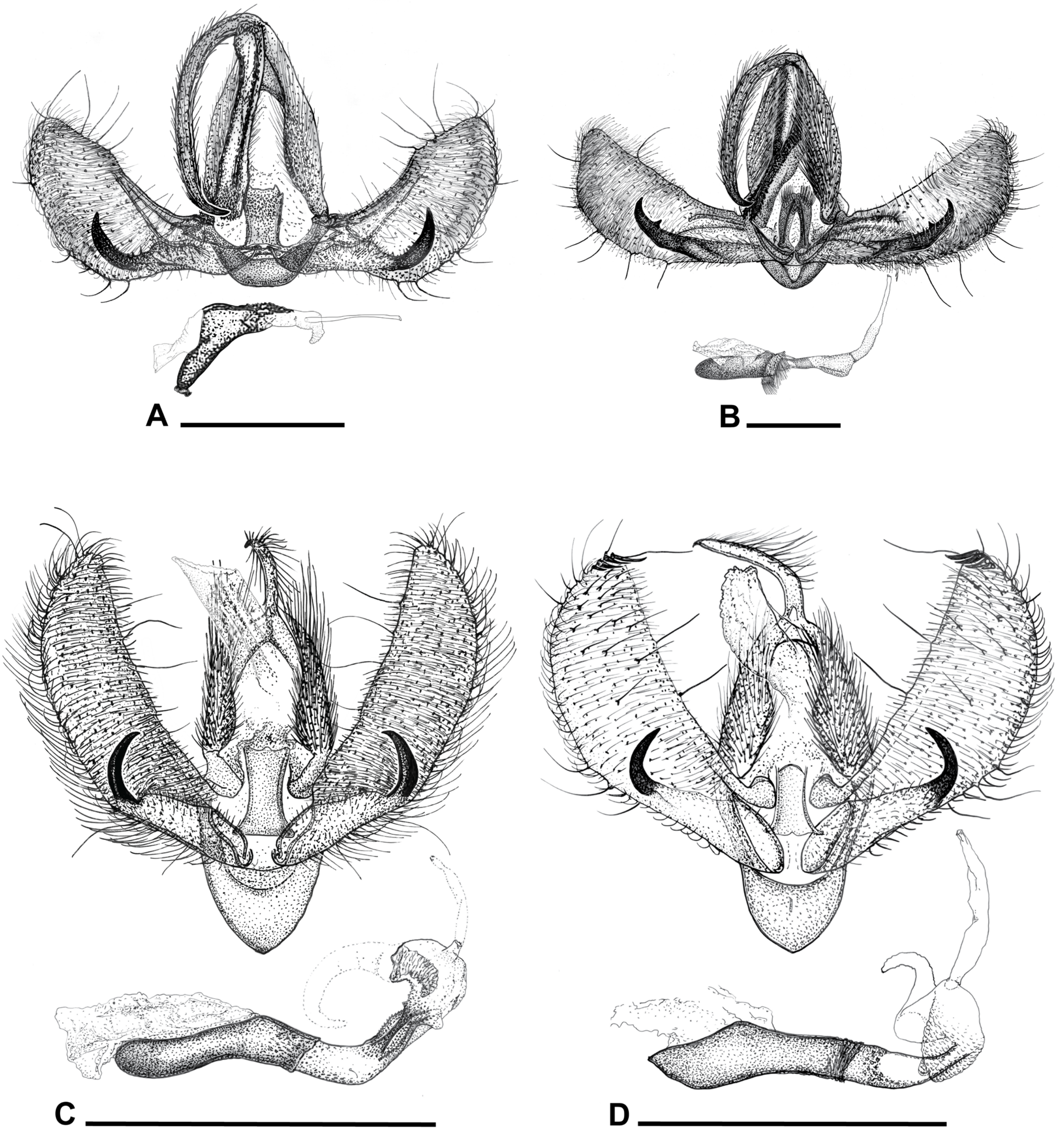

Figure 17. Male genitalia of Australian Agaristinae: (A) *Mimeusemia econia*; (B) *Mimeusemia centralis*; (C) *Radinocera maculosa*; (D) *Radinocera vagata*. Scale bars = 2.0 mm.

Order Lepidoptera Linnaeus, 1758

Family Noctuidae Latreille, 1809

Subfamily Agaristinae Boisduval, 1833

Genus *Apina* Walker, 1855

Amazela Boisduval, 1874
Agaristodes Hampson, 1908 **syn. nov.**

Type species: *Apina callisto* Walker, 1855, a junior synonym and junior secondary homonym of *Agarista callisto* Angas, 1847 (by subsequent designation).

Remarks. Hampson (1908) introduced the name *Agaristodes* in a key, which included several characters, namely eyes small and reniform, palpi porrect, frontal prominence large, proboscis fully developed, frons without truncate process in middle of prominence, prothorax without crest. He subsequently provided a detailed description (Hampson 1910) and considered the genus to be monotypic, containing the type species *Agarista feisthamelii* Herrich-Schäffer,

Table 1. History of nomenclature of the Australian Agaristinae according to five major revisionary classifications published over the past 125 years. Species names are listed in their original combination and spelling. For each species, only generic names are listed where the species group name did not change between the various workers. Synonyms are listed only in cases where the species group name changed between workers. Note, the genera *Cremnophora* and *Sarbanissa* listed in the Australian agaristine fauna by Nye (1975) and Braby and Heath (2024), respectively, were not included in the works by Hampson (1901, 1910), Jordan (1912), Turner (1920) or Kiriakoff (1977).

Species name	Hampson (1901, 1910)	Jordan (1912)	Turner (1920)	Kiriakoff (1977)	Edwards (1996)	this work
Zalissa ekeikei Bethune-Baker, 1906	*Leucogonia eceicei*	—	—	—	*Leucogonia*	*Leucogonia ekeikei*
Birtha cosmopis Lower, 1897	*Metaxanthia*	—	—	—	*Leucogonia*	*Leucogonia cosmopis*
Zalissa stichograpta Turner, 1943	—	—	—	—	*Zalissa*	*Zalissa stichograpta*
Zalissa catocalina Walker, 1865	*Zalissa*	*Zalissa*	—	*Zalissa*	*Zalissa*	*Zalissa catocalina*
Hypocala pratti Bethune-Baker, 1906	*Zalissa*	*Zalissa catocalina pratti*	—	*Zalissa catocalina pratti*	*Zalissa pratti*	*Zalissa pratti*
Sarbanissa diana Sugi, 1996	—	—	—	—	—	*Sarbanissa diana*
Hecatesia fenestrata Boisduval 1829	*Hecatesia*	*Hecatesia*	*Hecatesia*	*Hecatesia*	*Hecatesia*	*Hecatesia fenestrata*
Hecatesia thyridion Feisthamel, 1839	*Hecatesia*	*Hecatesia*	*Hecatesia*	*Hecatesia*	*Hecatesia*	*Hecatesia thyridion*
Hecatesia exultans Walker, [1865]	*Hecatesia*	*Hecatesia*	*Hecatesia*	*Hecatesia*	*Hecatesia*	*Hecatesia exultans*
Agarista aequalis Walker, [1865]	*Argyrolepidia, aequalis. A caeruleotincta*	*Argyrolepidia*	*Argyrolepidia caeruleotincta*	*Argyrolepidia*	*Argyrolepidia*	*Argyrolepidia aequalis*
Phalaenoides thoracophora Turner, 1920	—	—	*Phalaenoides*	*Phalaenoides*	*Argyrolepidia*	*Argyrolepidia thoracophora*
Phalaenoides fractus Rothschild, 1899	*Argyrolepidia*	*Argyrolepidia*	*Argyrolepidia*	*Argyrolepidia*	*Argyrolepidia*	*Argyrolepidia fracta*
Melanochroia subaspersa Walker, [1865]	*Coenotoca*	*Idalima*	*Argyrolepidia*	*Coenotoca*	*Coenotoca*	*Coenotoca subaspersa*
Argyrolepidia unimacula Lower, 1903	—	—	—	*Argyrolepidia*	*Coenotoca*	*Coenotoca unimacula*
Mimeusemia centralis (Rothschild, 1896)	*Mimeusemia*	*Mimeusemia*	*Argyrolepidia*	*Mimeusemia*	*Mimeusemia*	*Mimeusemia centralis*
Mimeusemia econia Hampson, 1900	*Mimeusemia*	*Mimeusemia*	*Argyrolepidia*	*Mimeusemia*	*Mimeusemia*	*Mimeusemia econia*
Agarista simplex T.P. Lucas, 1891	—	*Mimeusemia*	—	*Mimeusemia*	*Mimeusemia*	*Mimeusemia simplex*
Agarista ardescens Butler, 1884	*Phalaenoides*	*Idalima*	*Periopta*	*Periopta*	*Periopta*	*Periopta ardescens*
Agarista diversa Walker, [1865]	*Radinocera*	*Idalima*	*Periopta*	*Periopta*	*Periopta*	*Periopta diversa*
Aegocera cornigera (Butler, 1886)	*Ipanica*	*Ipanica*	*Ipanica*	*Ipanica*	*Ipanica*	*Ipanica cornigera*
Agarista callisto Angas, 1847	*Apina*	*Apina*	*Apina*	*Apina*	*Apina*	*Apina callisto*
Agarista feisthamelii Herrich-Schäffer, [1853]	*Agaristodes*	*Agaristodes*	*Agaristodes*	*Agaristodes*	*Agaristodes*	*Apina feisthamelii* **comb. nov.**
Eutactis tristifica Hübner, 1818	*Phalaenoides*	*Phalaenoides*	*Phalaenoides*	*Phalaenoides*	*Phalaenoides*	*Phalaenoides tristifica*
Phalaenoides glycinae Lewin, 1805	*Phalaenoides*	*Phalaenoides*	*Phalaenoides*	*Phalaenoides*	*Phalaenoides*	*Phalaenoides glycinae*
Agarista behri Angas, 1847	*Comocrus*	*Comocrus*	*Comocrus*	*Comocrus*	*Comocrus*	*Phalaenoides behri* **comb. nov.**
Nyctemera vagata Walker, [1865]	*Radinocera*	*Radinocera*	*Radinocera*	*Radinocera*	*Radinocera*	*Radinocera vagata*
Phalaenoides maculosus Rothschild, 1896	*Radinocera maculosa,* *R. placodes*	*Radinocera*	*Radinocera*	*Radinocera*	*Radinocera*	*Radinocera maculosa*
Papilio agricola Donovan, 1805	*Agarista*	*Agarista*	*Agarista*	*Agarista*	*Agarista*	*Agarista agricola*

Table 1. *Continued...*

Table 1. *Continued*.

Species name	Hampson (1901, 1910)	Jordan (1912)	Turner (1920)	Kiriakoff (1977)	Edwards (1996)	this work
Agarista macleayi W.J. Macleay, 1864	*Phalaenoides tetrapleura*	*Platagarista Idalima tetrapleura*	*Platagarista tetrapleura*	*Platagarista tetrapleura*	*Platagarista macleayi*	*Platagarista macleayi*
Phalaena latinus Donovan, 1805	*Eutrichopidia*	*Eutrichopidia*	*Eutrichopidia*	*Eutrichopidia*	*Eutrichopidia*	*Eutrichopidia latina*
Damias varia Walker, 1854	*Burgena*	*Damias*	*Burgena*	*Damias*	*Burgena*	*Burgena varia*
Cruria synopla Turner, 1903	—	*Cruria*	*Cruria*	*Cruria*	*Cruria*	*Cruria synopla*
Cruria latifascia Jordan, 1912	—	*Cruria synopla latifascia*	*Cruria sthenozona*	*Cruria synopla latifascia,* *C. sthenozona*	*Cruria latifascia*	*Cruria latifascia*
Agarista tropica T.P. Lucas, 1891	*Cruria platyxantha*	*Cruria darwiniensis platyxantha*	*Cruria platyxantha*	—	*Cruria tropica*	*Cruria tropica*
Agarista darwiniensis Butler, 1884	*Cruria darviniensis*	*Cruria*	*Cruria*	*Cruria*	—	*Cruria darwiniensis*
Agarista donowani Boisduval, 1832	*Cruria donovani*	*Cruria*	*Cruria*	*Cruria*	*Cruria*	*Cruria donowani*
Agarista kochii W.J. Macleay, 1866	*Cruria neptioides*	*Cruria neptioides*	*Cruria neptioides*	*Cruria neptioides*	*Cruria kochii*	*Cruria kochii*
Cruria epicharita Turner, 1911	—	*Cruria*	*Cruria*	*Cruria*	*Cruria*	*Cruria epicharita*
Agarista affinis Boisduval, 1832	*Idalima*	*Idalima*	*Idalima*	*Idalima*	*Idalima*	*Idalima affinis*
Idalima metasticta Hampson, 1910	*Idalima*	*Idalima*	*Idalima*	*Idalima*	*Idalima*	*Idalima metasticta*
Agarista polysticta Butler, 1875	*Phalaenoides*	*Phalaenoides*	*Periscepta*	*Periscepta*	*Periscepta*	*Idalima polysticta* **comb. nov.**
Phalaenoides butleri Swinhoe, 1892	*Idalima hemiphragma*	*Phalaenoides polysticta butleri,* *Idalima hemiphragma*	*Idalima hemiphragma*	—	*Periscepta butleri*	*Idalima butleri* **comb. nov.**
Argyrolepidia aethrias Turner, 1908	*Idalima cyanobasis*	*Argyrolepidia*	*Idalima*	*Argyrolepidia*	*Idalima*	*Idalima aethrias*
Agarista leonora Doubleday, 1846	*Idalima*	*Argyrolepidia*	*Idalima*	*Coenotoca*	*Idalima*	*Idalima leonora*
Argyrolepidia tasso Jordan, 1912	—	*Argyrolepidia leonora tasso*	—	*Coenotoca leonora tasso*	*Idalima tasso*	*Idalima tasso*
Agarista angasii Angas, 1847	—	—	—	—	*Cremnophora*	—

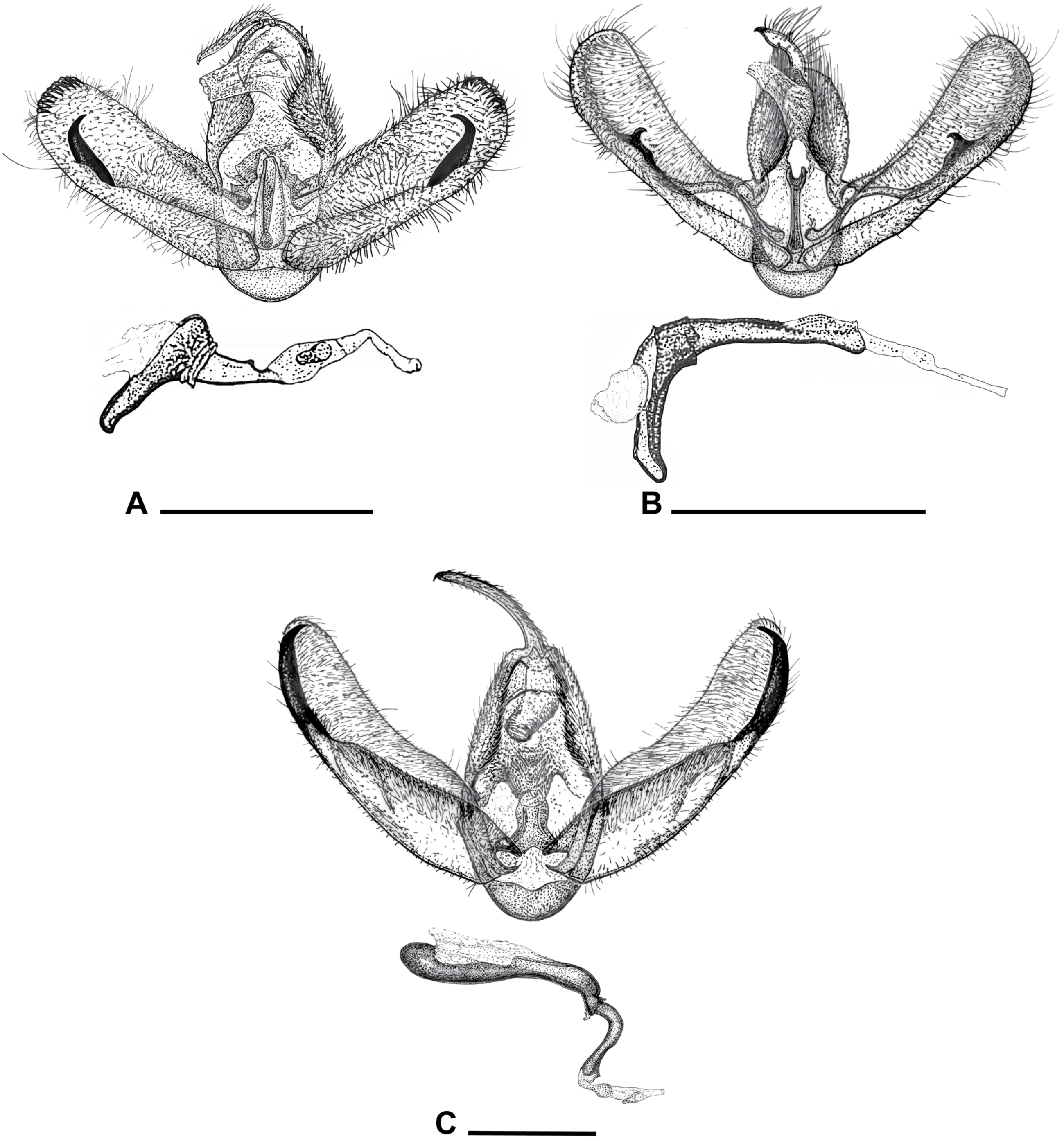

Figure 18. Male genitalia of Australian Agaristinae: (A) *Eutrichopidia latina*; (B) *Platagarista macleayi*; (C) *Agarista agricola*. Scale bars = 2.0 mm.

[1853]. However, he did not diagnose the genus and indicate how it differed from *Apina*. In this work, morphological evidence indicates that *Agaristodes* should be synonymised with *Apina*. The clade *Apina* + *Agaristodes* shares numerous synapomorphies, including: tubular vesica, broadening distally [character 1, state 3]; ventral curve in the distal phallus [9, 2]; sacculus terminating in the distal portion of the valvae [12, 2]; male antennae bipectinate [22, 0]; coarse white scales widely scattered over the forewing [30, 1]; and hindwing with a prominent patch [36, 1] that is coloured white or cream. Although there is no question that *Apina callisto* and *Agaristodes feisthamelii* are specifically distinct, the male genitalia of these two species (Figs 20A–B) are otherwise very similar. In addition, the pupae of these two genera are similar in that they possess a pronounced frontal projection on the head, and lack hooked setae on the cremaster (S.A. Wragg, unpub. data). Thus, two species are now recognized in *Apina*, as follows:

Apina callisto (Angas, 1847)
= *Apina callisto* Walker, 1855 [junior synonym & junior homonym]
= *Amazela calisto* Boisduval, 1874

Apina feisthamelii (Herrich-Schäffer, [1853]) **comb. nov.**

Table 2. Revised systematic checklist of the Agaristinae from Australia according to this study. A more detailed species level synonymy is provided by Edwards (1996).

- *Leucogonia* Hampson, 1908
- = *Metaxanthiella* Collins, 1962
    - *Leucogonia ekeikei* (Bethune-Baker, 1906)
    - *Leucogonia cosmopis* (Lower, 1897)
- *Zalissa* Walker, 1865
    - *Zalissa stichograpta* Turner, 1943
    - *Zalissa catocalina* Walker, 1865
    - *Zalissa pratti* (Bethune-Baker, 1906)
- *Sarbanissa* Walker, 1865
    - *Sarbanissa diana* Sugi, 1996
- *Hecatesia* Boisduval, 1829
- = *Prostheta* Turner, 1922
    - *Hecatesia fenestrata* Boisduval 1829
    - *Hecatesia thyridion* Feisthamel, 1839
    - *Hecatesia exultans* Walker, [1865]
- *Argyrolepidia* Hampson, 1901
    - *Argyrolepidia aequalis* (Walker, [1865])
        - *Argyrolepidia aequalis caeruleotincta* (Lucas, 1891)
    - *Argyrolepidia thoracophora* (Turner, 1920)
    - *Argyrolepidia fracta* (Rothschild, 1899)
- *Coenotoca* Turner, 1903
    - *Coenotoca subaspersa* (Walker, [1865])
    - *Coenotoca unimacula* (Lower, 1903)
- *Mimeusemia* Butler, 1875
    - *Mimeusemia centralis* (Rothschild, 1896)
    - *Mimeusemia econia* Hampson, 1900
        - *Mimeusemia econia econia* Hampson, 1900
    - *Mimeusemia simplex* (T.P. Lucas, 1891)
        - *Mimeusemia simplex simplex* (T.P. Lucas, 1891)
- *Periopta* Turner, 1920
    - *Periopta ardescens* (Butler, 1884)
    - *Periopta diversa* (Walker, [1865])
- *Ipanica* Hampson, 1908
    - *Ipanica cornigera* (Butler, 1886)
- *Apina* Walker, 1855
- = *Amazela* Boisduval, 1874
- = *Agaristodes* Hampson, 1908 **syn. nov.**
    - *Apina callisto* (Angas, 1847)
    - *Apina feisthamelii* (Herrich-Schäffer, [1853]) **comb. nov.**

Table 2. *Continued...*

Table 2. *Continued.*

- *Phalaenoides* Lewin, 1805
- = *Eutactis* Hübner, 1818
- = *Comocrus* Jordan, 1896 **syn. nov.**
    - *Phalaenoides tristifica* (Hübner, 1818)
    - *Phalaenoides glycinae* Lewin, 1805
    - *Phalaenoides behri* (Angas, 1847) **comb. nov.**
- *Radinocera* Hampson, 1908
    - *Radinocera vagata* (Walker, [1865])
    - *Radinocera maculosa* (Rothschild, 1896)
- *Agarista* Leach, 1814
    - *Agarista agricola* (Donovan, 1805)
        - *Agarista agricola agricola* (Donovan, 1805)
        - *Agarista agricola daemonis* Butler, 1876
        - *Agarista agricola biformis* Butler, 1884
- *Platagarista* Jordan, 1912
    - *Platagarista macleayi* (W.J. Macleay, 1864)
- *Eutrichopidia* Hampson, 1901
    - *Eutrichopidia latina* (Donovan, 1805)
- *Burgena* Walker, [1865]
    - *Burgena varia* (Walker, 1854)
        - *Burgena varia varia* (Walker, 1854)
- *Cruria* Jordan, 1896
    - *Cruria synopla* Turner, 1903
    - *Cruria latifascia* Jordan, 1912
    - *Cruria tropica* (T.P. Lucas, 1891)
    - *Cruria darwiniensis* (Butler, 1884)
    - *Cruria donowani* (Boisduval, 1832)
        - *Cruria donowani donowani* (Boisduval, 1832)
        - *Cruria donowani xanthosoma* Jordan, 1912
    - *Cruria kochii* (W.J. Macleay, 1866)
    - *Cruria epicharita* Turner, 1911
- *Idalima* Turner, 1903
- = *Periscepta* Turner, 1920 **syn. nov.**
    - *Idalima affinis* (Boisduval, 1832)
    - *Idalima metasticta* Hampson, 1910
    - *Idalima polysticta* (Butler, 1875) **comb. nov.**
    - *Idalima butleri* (Swinhoe, 1892) **comb. nov.**
    - *Idalima aethrias* (Turner, 1908)
    - *Idalima leonora* (Doubleday, 1846)
    - *Idalima tasso* (Jordan, 1912)

Genus *Phalaenoides* Lewin, 1805

Eutactis Hübner, 1818
Comocrus Jordan, 1896 **syn. nov.**

Type species: *Phalaenoides glycinae* Lewin, 1805 (by monotypy).

Remarks. Karl Jordan in Rothschild and Jordan (1896) described the monotypic genus *Comocrus* (type species: *Agarista contorta* Walker, [1865], a junior synonym of *Agarista behri* Angas, 1847) and noted that it was distinguished from other genera by the hind tibiae bearing long hairs at the outer edge (dorsal surface), although this feature also occurs in *Phalaenoides* (Turner 1920). Further, he noted that it differed from *Phalaenoides* in that vein R_2 of the forewing was stalked with veins R_3 and R_4 instead of being separate with the discal cell. However, in this study we found that *Comocrus* and *Phalaenoides* show a close resemblance in morphology of the male genitalia (Figs 20C–D, 21A) and adult, as well as the immature stages. The clade *Phalaenoides* + *Comocrus* was defined by several characters, including: apical diverticulum spiral-shaped [character 4, state 3]; antennae filiform, dilated at the extremity to appear club-shaped [22, 3]; and forewing with a row of parallel lines along veins of the terminal edge [34, 3]. In addition, morphology of the immature stages of these genera are similar. For instance, the larvae of both have five or six white transverse bands per segment, and the pupae lack a pronounced frontal projection on the head (S.A. Wragg, unpub. data). Although the wing patterns of *P. glycinae* are highly variable, they are somewhat intermediate

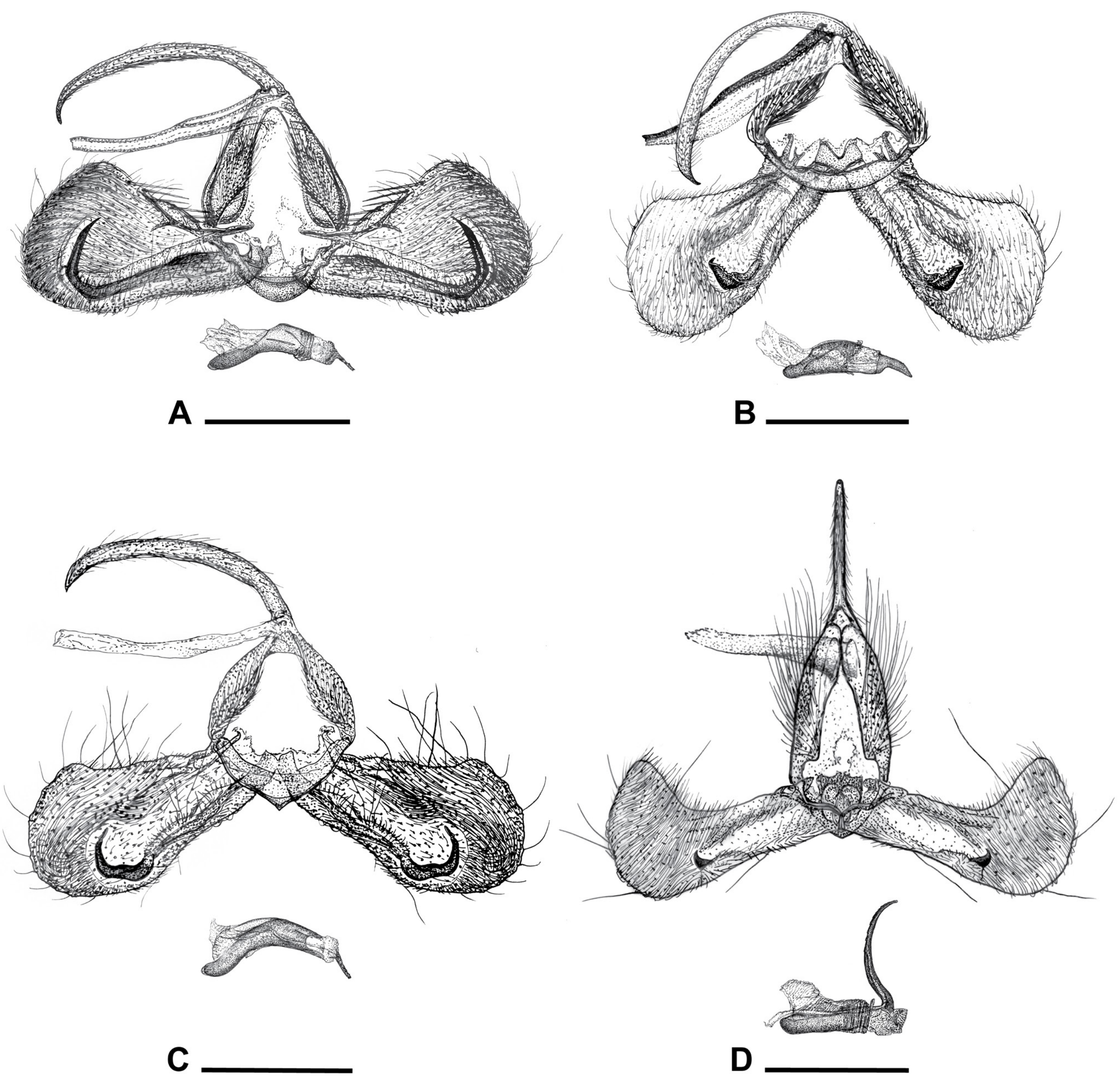

Figure 19. Male genitalia of Australian Agaristinae: (A) *Cruria donowani*; (B) *Cruria synopla*; (C) *Cruria kochii*; (D) *Burgena varia*. Scale bars = 2.0 mm.

between those of *C. behri* and *P. tristifica*—specimens from the northern areas of the range typically lack markings except the postmedial bar, whereas those from the southern areas of the range closely resemble *C. behri*. The relationships of these three species could not be satisfactorily resolved, but the male genitalia of *P. glycinae* (Fig. 20C) appear more similar to those of *P. tristifica* (Fig. 20D) than to *C. behri* (Fig. 21A). Following the synonymy of *Comocrus* three species are now recognised in *Phalaenoides*:

Phalaenoides tristifica (Hübner, 1818)
= *Agarista lewinii* Boisduval, 1832
= *Agarista ephyra* Angas, 1847
= *Agarista ephyra* Herrich-Schäffer, 1853
= *Agarista ephyra* Walker, 1854

Phalaenoides glycinae Lewin, 1805

Phalaenoides behri (Angas, 1847) **comb. nov.**
= *Agarista casuarinae* Scott, 1864
= *Agarista flexuosa* Walker, [1865]
= *Agarista contorta* Walker, [1865]

Genus *Idalima* Turner, 1903

Periscepta Turner, 1920 **syn. nov.**

Type species: *Agarista affinis* Boisduval, 1832 (by original designation).

Remarks. Turner (1920) erected the genus *Periscepta* to accommodate the species *Agarista polysticta* Butler, 1875, although he placed the very closely related *Cruria hemiphragma* Lower, 1903, a junior synonym of *Phalaenoides butleri* Swinhoe, 1892, in the genus *Idalima*.

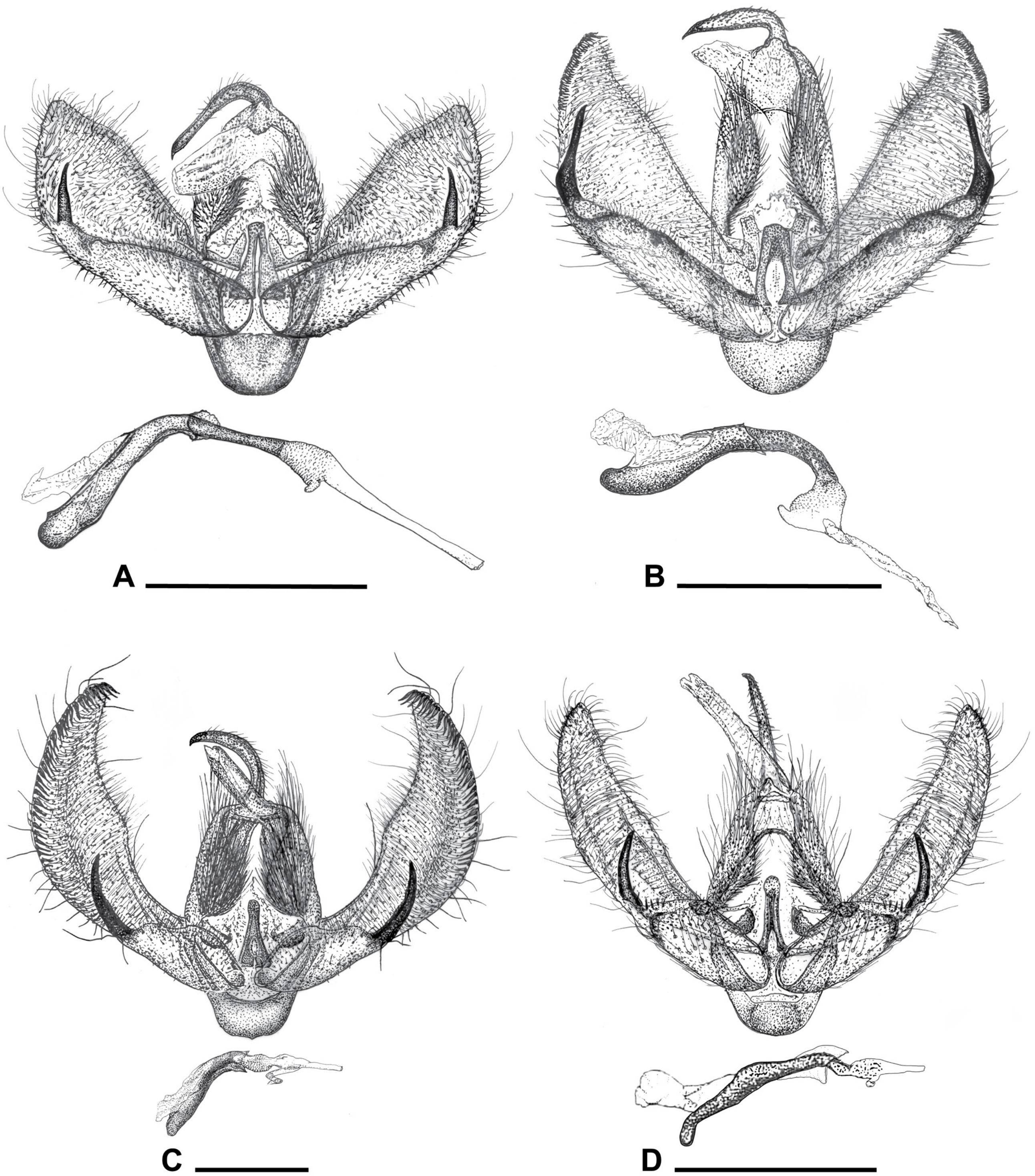

Figure 20. Male genitalia of Australian Agaristinae: (A) *Apina feisthamelii* **comb. nov**.; (B) *Apina callisto*; (C) *Phalaenoides glycinae*; (D) *Phalaenoides tristifica*. Scale bars = 2.0 mm.

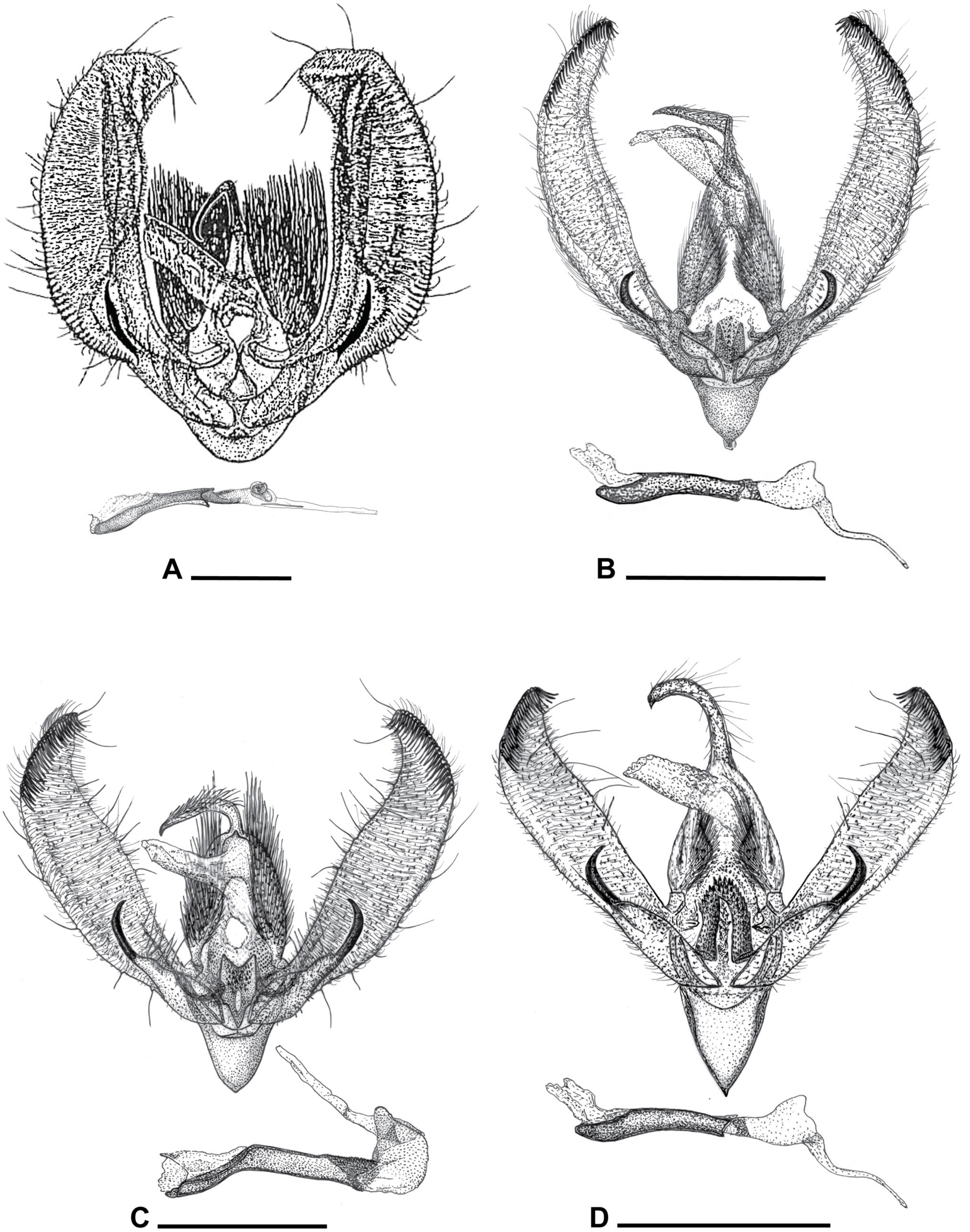

Figure 21. Male genitalia of Australian Agaristinae: (A) *Phalaenoides behri* **comb. nov**.; (B) *Ipanica cornigera*; (C) *Periopta ardescens*; (D) *Periopta diversa*. Scale bars = 2.0 mm

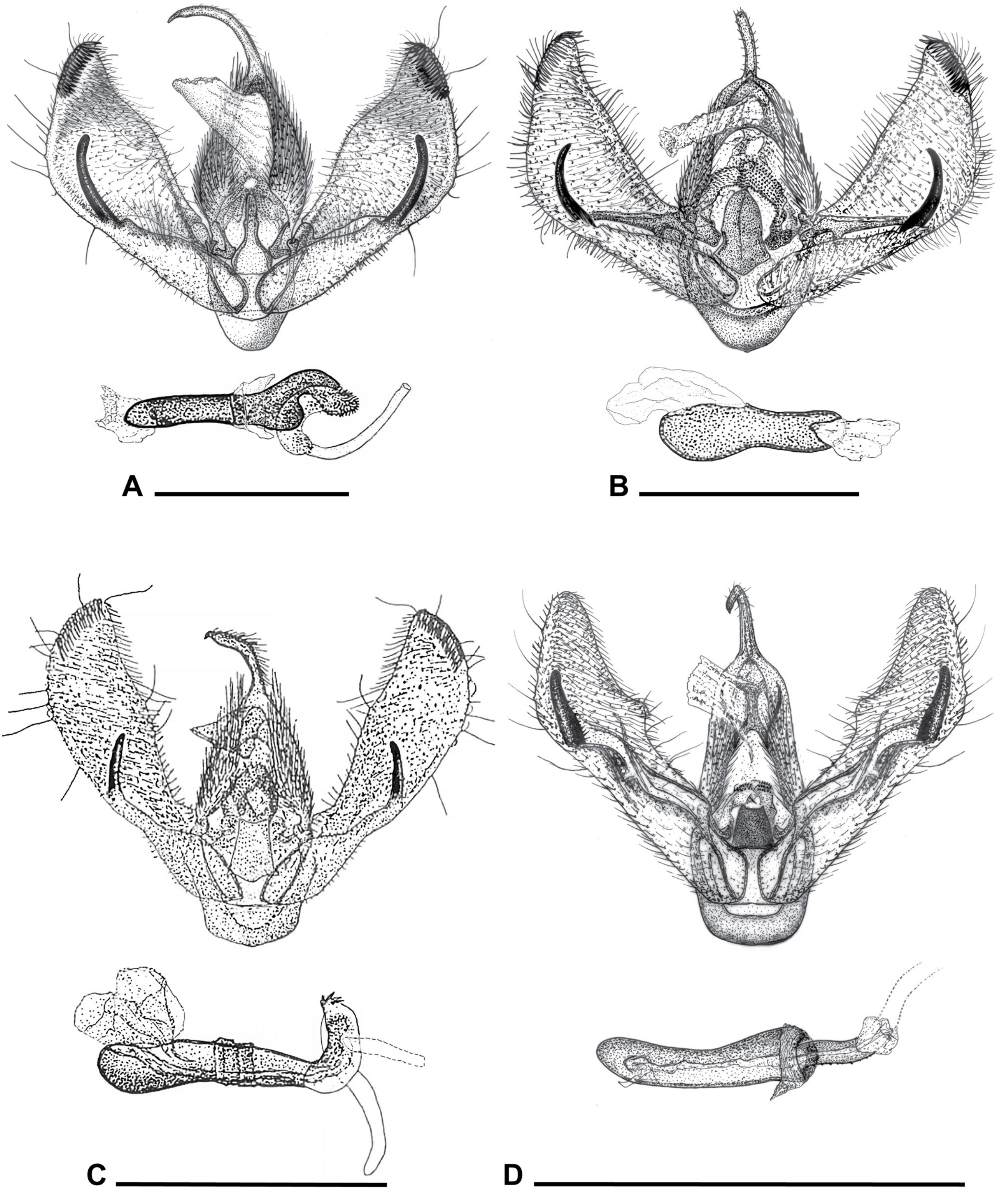

Figure 22. Male genitalia of Australian Agaristinae: (A) *Idalima polysticta* **comb. nov**.; (B) *Idalima butleri* **comb. nov**.; (C) *Idalima affinis*; (D) *Idalima metasticta*. Scale bars = 2.0 mm.

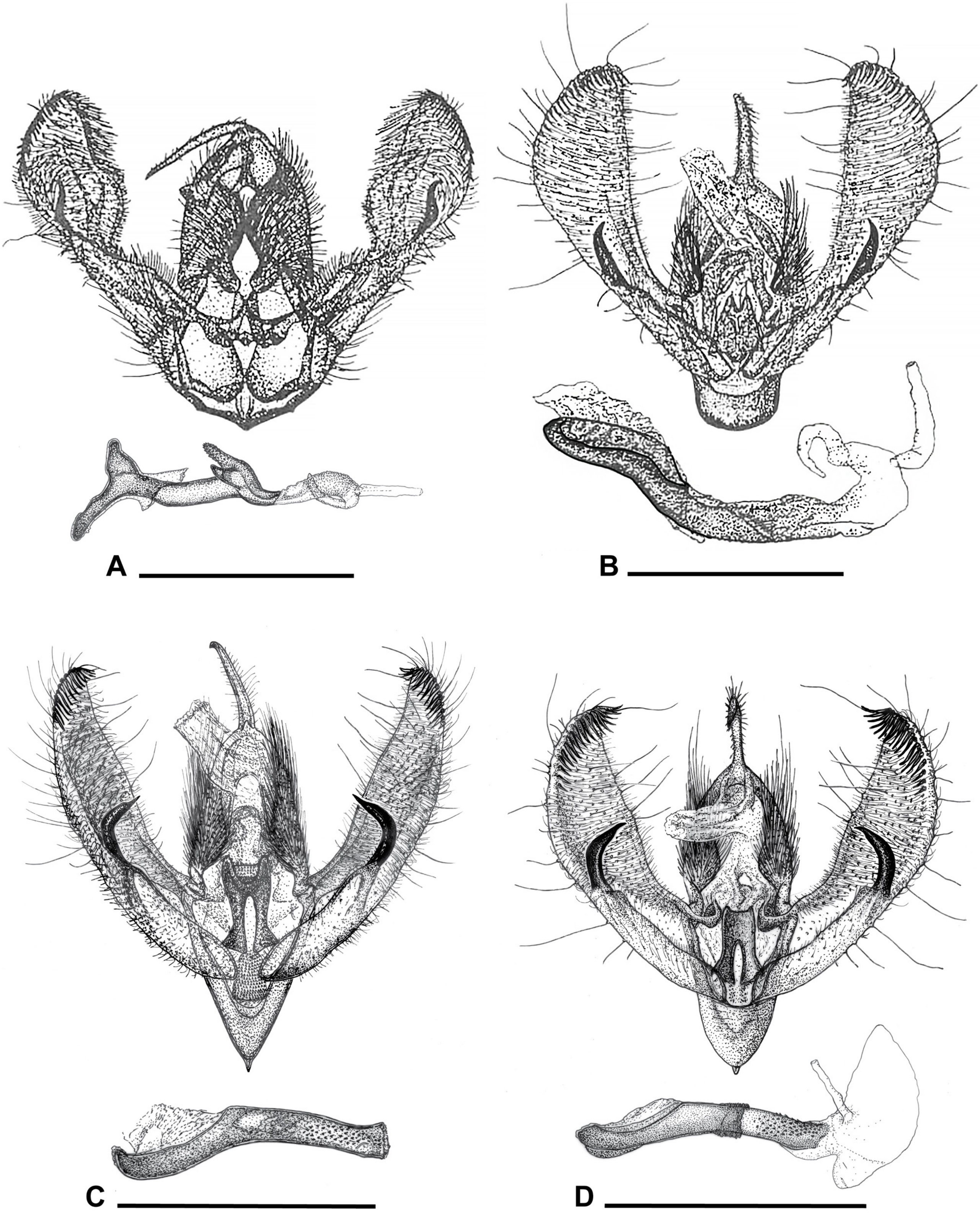

Figure 23. Male genitalia of Australian Agaristinae: (A) *Idalima aethrias*; (B) *Idalima leonora*; (C) *Coenotoca unimacula*; (D) *Coenotoca subaspersa*. Scale bars = 2.0 mm.

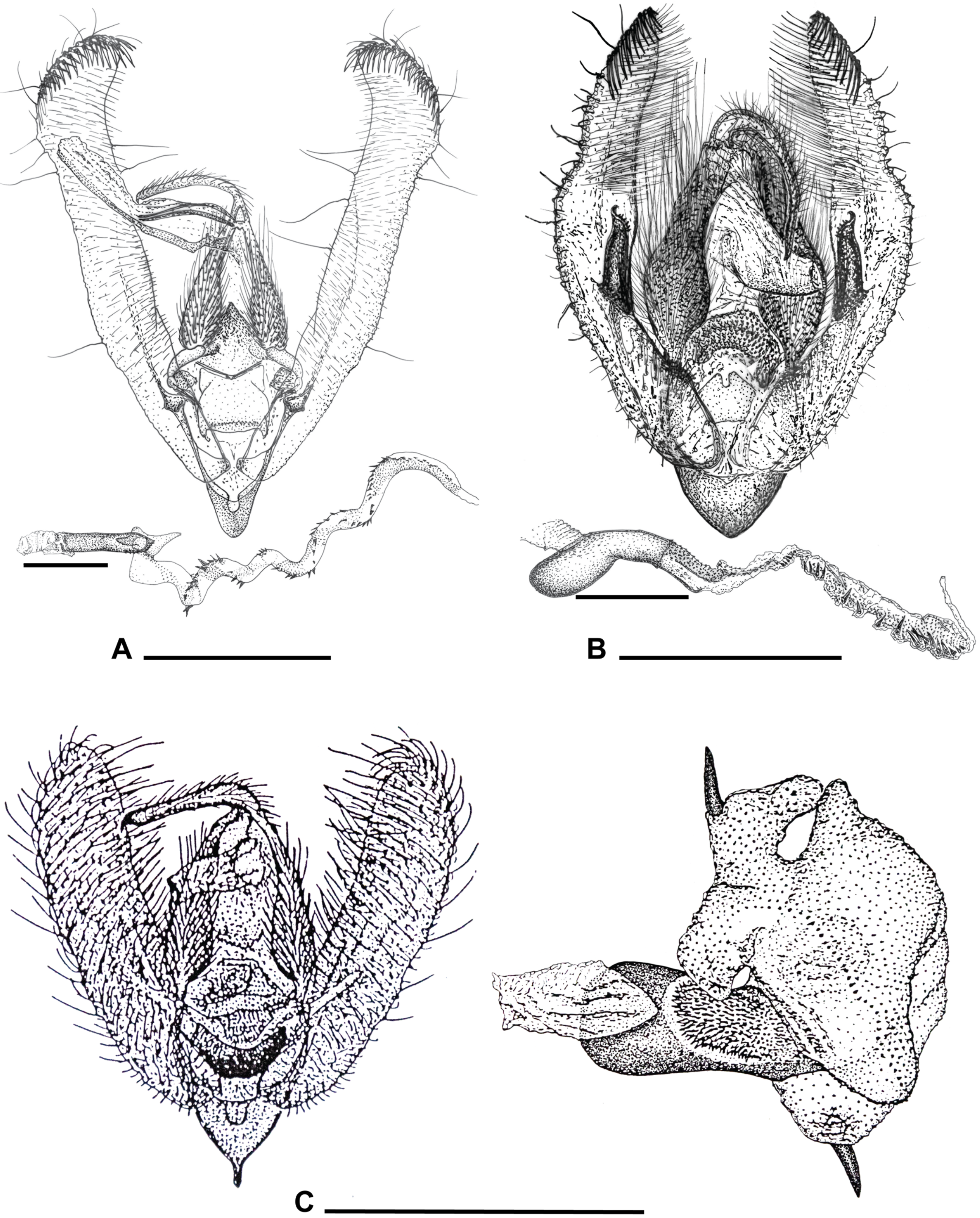

Figure 24. Male genitalia of outgroups: (A) *Heliocoverpa punctigera* (Heliothinae); (B) *Proteuxoa sanguinipuncta* (Amphipyrinae); (C) *Cremnophora angasii.* Scale bars = 2.0 mm.

Interestingly, both Hampson (1910) and Jordan (1912) also placed *hemiphragma* in the genus *Idalima*. Turner (1920) noted that *Periscepta* differed from *Phalaenoides* by the shape of the antenna and labial palp but he did not compare it with *Idalima*. Although *Idalima* emerged as possibly polyphyletic in our phylogenetic analysis, the two species previously assigned to *Periscepta* (Edwards 1996) showed a close relationship to the clade *I. affinis* + *I. metasticta*. This clade of four species (Figs 22A–D) was defined by four synapomorphies: ductus ejaculatorius narrow or narrower than width of phallus [character 10, state 1]; apex of harpe blunt [13, 1]; antemedial markings of forewing comprising a row of spots [31, 3]; and medial markings of forewing forming an uneven row of three discrete spots [32, 3]. In addition, the four species share several other traits, including: length of phallus shorter than four times its width [8, 1]; phallus straight without ventral curve [9, 0]; valva with a medial bulge, apex produced [19, 3]; ground colour of wings black [27, 1]; and subterminal markings of forewing comprising one or two rows of spots [34, 5]. While further work is needed to resolve the phylogenetic position of the three other species currently assigned to *Idalima*, most notably the closely related pair *I. leonora* and *I. tasso*, we recommend that *Periscepta* should not continue to be recognised. Thus, we provisionally place the following seven species in *Idalima* pending further systematic investigation of this group:

Idalima affinis (Boisduval, 1832)
= *Agarista vindex* Butler, 1884

Idalima metasticta Hampson, 1910

Idalima polysticta (Butler, 1875) **comb. nov.**

Idalima butleri (Swinhoe, 1892) **comb. nov.**
= *Cruria hemiphragma* Lower, 1903

Idalima aethrias (Turner, 1908)
= *Idalima cyanobasis* Hampson, 1910

Idalima leonora (Doubleday, 1846)

Idalima tasso (Jordan, 1912)

Discussion

Our phylogeny of the Australian Agaristinae is insufficiently resolved to confirm or refute Kiriakoff's (1977) classification of subgroups of the Australian genera based on male genitalia. However, we did find evidence of a close relationship between *Burgena* and *Cruria*, which supports his subgroup IIIb. The inclusion of additional characters from the vesica and external morphological characters of the adult strongly suggests that Kiriakoff's subgroup VI of seven genera (i.e., *Argyrolepidia*, *Agarista*, *Eutrichopidia*, *Periscepta*, *Apina*, *Agaristodes*, *Phalaenoides*) is polyphyletic. Furthermore, Kiriakoff (1977) placed *Comocrus* together with *Cruriopsis* Jordan, 1912 and *Crinocula* Jordan, 1896 from Asia in a separate group (subgroup IV), but we found that this taxon is synonymous with *Phalaenoides*.

Although our phylogeny was only partially resolved, three patterns were apparent (Table 2), which differs from the systematic list presented by Edwards (1996). First, *Leucogonia* and *Zalissa* are closely related and these genera, together with *Sarbanissa* Walker, 1865, possibly comprise the sister group to the rest of the Australian agaristines. All members of this group, which are nocturnal and cryptically patterned, have a simple, tubular vesica, a plesiomorphic trait compared with the diurnal and brightly coloured species, which have more elaborate vesica shapes, usually with curved diverticula. Second, several genera (*Hecatesia*, *Argyrolepidia*, *Coenotoca*, *Mimeusemia*, *Periopta*, *Ipanica*, *Apina*) comprise a 'three-barred' group in which most members have three bars (antemedial, medial, postmedial) on the forewing. The constituent species have an expanded or usually simple, tubular vesica, sometimes with a small, straight or spiralled diverticulum, and longitudinal thoracic markings. A large proportion of these species are nocturnal or crepuscular, and the forewing is usually drab or has a reddish-brown ground colour, some with iridescent markings. The remaining genera (*Radinocera*, *Agarista*, *Platagarista*, *Eutrichopidia*, *Burgena*, *Cruria*, *Idalima*) have the diverticula curved and sometimes the vesica also curved, or permanently everted and sclerotised (as in *Burgena* and *Cruria*). Nearly all of these species are diurnal and frequently brightly coloured. *Phalaenoides* share features with both of these latter divisions, and its phylogenetic placement requires further investigation.

Despite examining a large number of potential morphological characters, few appeared to be phylogenetically informative and although many multi-state complexes were recognised, the total number of morphological characters used barely exceeded the number of ingroup taxa, which partly explains the lack of deep resolution in our phylogeny. Characters of the everted vesica, previously unavailable to past workers, were informative and their use has improved estimates of species and species group relationships, as was found for the Heliothinae by Matthews (1999). However, many genitalic characters (including vesica shape and valva shape) exhibit continuous variation, and autapomorphies could not be satisfactorily categorised due to homoplasy. Additional morphological characters should be examined in future studies, including features of the mid and hind tibia, larval and pupal stages. Molecular phylogenetic analysis based on genetic and/or genomic data should be undertaken and compared as an independent dataset to our morphological-based study.

Further work is needed to resolve the taxonomic status and monophyly of the genera *Leucogonia* (and *Zalissa*), *Argyrolepidia* and *Idalima*. Both *Leucogonia* and *Argyrolepidia* extend into New Guinea and/or South-East Asia (Indonesia); hence, inclusion of the Papuan and Asian species is a requisite for determining the monophyly of these genera and may provide information on the affiliations of these groups. The taxonomic status and distribution of *Mimeusemia simplex* are not clear and require investigation—it is known only from the holotype male from Queensland, but the exact location from which the specimen was collected remains a mystery. Jordan (1912) considered *M. simplex* to be polytypic, containing five other subspecies from Maluku and mainland New Guinea and adjacent islands, and while most of these clearly belong to *Mimeusemia*, examination of Lucas' holotype of *Agarista simplex* T.P. Lucas, 1891 in the South Australian Museum indicates that *M. simplex* may well be specifically distinct from some of these Indonesian/New Guinea taxa.

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Appendix 1. List of material examined for morphological characters for cladistic analysis in the ANIC. Species are listed in alphabetical order for both ingroup and outgroup taxa.

INGROUP TAXA

Agarista agricola

New South Wales: 1♂ "Grafton, 5.ix.1954, F.S. Paul", "genitalia slide N1508, 27.ix.1985, M.J. Lewis"; 1♂ "Sydney, 15.ii.1952, L.H. Mosse-Robinson", "genitalia slide N1509, 27.ix.1985, M.J. Lewis". **Queensland:** 1♂ "Bunya Mountains, i.1932", "genitalia slide 16548, viii.1998, S.A. Wragg". Illustration and description in Kiriakoff (1977, fig. 24, p. 123).

Agaristodes feisthamelii

Australian Capital Territory: 1♀ "5 km N of Lees Spring 1220m, 28.xi.1972", "genitalia slide 16529, viii.1998, S.A. Wragg". **New South Wales:** 1♂ "63.23S 148.39E 1km S.W. Sawpit Creek Visitor's Centre Kosciusko N.P. 1260m, 14.xii.1986, E.D. Edwards", "genitalia slide 16528, viii.1989, S.A. Wragg". **Victoria:** 1♂ "Mt. Tamboritha, 14.xii.1975, J. Brooks", "genitalia slide1512, 22-28.ix.1985, M.J. Lewis". Illustration and description in Kiriakoff (1977, fig. 27, p. 129).

Apina callisto

Australian Capital Territory: 1♂ "Red Hill, 1929, M. Fuller", "genitalia slide 16531, viii.1998, S.A. Wragg". **South Australia:** 1♀ "Clare, 21.iv.1924, J.O. Wilson", "genitalia slide 16530, vii.1998, S.A. Wragg". Illustration and description in Kiriakoff (1977, fig. 25, p. 126).

Argyrolepidia aequalis

Queensland: 1♂ "Mt. Bartle, Frere, (East Base), 80 ft, 24.iv.1955, I.F.B. Common", "genitalia slide 16518, viii.1998, S.A Wragg".

Argyrolepidia fracta

Queensland: 1♂ "Shute Harbour, 21.iv.1964, I.F.B. Common & M.S. Upton", "genitalia slide N 1510, 28.ix.1985, M.J. Lewis"; 1♂ "Jardine R., 14.x.1979, Robinson & Apice", "genitalia slide N 1511, 28.ix.1985, M.J. Lewis"; 1 ♂ "Byfield, 29.i.1964, I.F.B. Common & M.S. Upton", "genitalia slide 16517, viii.1998, S.A. Wragg".

Argyrolepidia thoracophora

Queensland: 1♂ "Iron range, 12.iv.1964, I.F.B. Common and M.S. Upton", "genitalia slide N 401, 1978, E.D. Edwards"; 1♂ "Claudie R. Cape York Pen., 26.v.1974, A. & J. d'Apice", "genitalia slide N 1585, 1998, E.D. Edwards"; 1♂ "Claudie R. Cape York Pen., 25.v.1974, A. & J. d'Apice", "genitalia slide 16512, viii.1998, S.A. Wragg".

Burgena varia

Queensland: 1♂ "Waterview Ck. c.2000ft. 22 miles S.W. Ingham, 10.v.1961, R. Straatman", "genitalia slide 16506, viii. 1998, S.A. Wragg". Illustration and description in Kiriakoff (1977, fig. 14, p. 80).

Coenotoca subaspersa

New South Wales: 1♂ "Narara, 26.ix.1945, Mosse-Robinson", "genitalia slides 16519, viii.1998, S.A Wragg". **Queensland:** 1♂ "Mt. Mistake 87 km S.S.W. of Laidley, 11.ii.1976, S.R. Monteith", "genitalia slide N 1588, 1998, E.D. Edwards". Illustration and description in Kiriakoff (1977, fig. 34, p. 145).

Coenotoca unimacula

Queensland: 1♂ "3mls N. of Kuranda, 25.iv.1955, I.F.B. Common", "genitalia slide 1589, 1998, E.D. Edwards".

Comocrus behri

Australian Capital Territory: 1♂ "Black Mountain ANIC (light trap), 14.i.1964, I.F.B. Common", "genitalia slide 16507, viii.1998, S.A. Wragg". **South Australia:** 1♂ "Cradock, M.W. Mules", "genitalia slide 16546, ix.1998, S.A. Wragg". Illustration and description in Kiriakoff (1977, fig. 17, p. 95).

Cruria donowani

Queensland: 1♂ "Bunya Mt, 3500 ft. 4.x.1919", "genitalia slide 16508, iiiv.1998, S.A. Wragg". Illustration and description in Kiriakoff (1977, fig. 15, p. 86).

Cruria kochii

Queensland: 1♂ "Mt. Mulligan", "genitalia slide 16510, viii.1998, S.A. Wragg".

Cruria synopla

New South Wales: 1♂ "Dorrigo, 28.xi.1928, V.J. Robinson", "genitalia slide 16509, viii.1998, S.A. Wragg".

Eutrichopidia latina

Victoria: 1♂ "Moe, 4.i.1955, C.G.L. Gooding", "genitalia slide 16511, viii.1998, S.A. Wragg". **Australian Capital Territory:** 1♂ "Black Mountain, 27.i.1958, I.F.B. Common", "genitalia slide N1501, 27.ix.1985, M.J. Lewis". **New South Wales:** 1♂ "Wilton, CSIRO Experimental Farm, 20.xii.1971, V.J. Robinson", "genitalia slide N1500, 27.ix.1985, M.J. Lewis".

Hecatesia exultans

Victoria: 1♂ "Kinta, 31.x.1954, F.R. Wilson", "genitalia slide 1590, 1998, E.D. Edwards". **Western Australia:** 1♂ "Nr Lancelin, 6.vii.1976, W.J. Bailey", "genitalia slide 1591, 1998, E.D. Edwards".

Hecatesia fenestrata

Victoria: 1♂ "Drouiti, 11.xi.1957, C.G.L. Gooding", "genitalia slide 16520, viii.1998, S.A Wragg". Illustration and description in Kiriakoff (1977, fig. 21, p. 102).

Hecatesia thyridion

Western Australia: 1♂ "Albany, 18.i.1935, K. R. Norris", "genitalia slide 16521, viii.1998, S.A Wragg".

Idalima aethrias

Queensland: 1♂ "Bald Hills Homestead, 30 km N. of Cooktown, 14.ii.1982, M.S.& B.J. Moulds", "genitalia slide 16538 viii.1998, S.A Wragg".

Idalima affinis

New South Wales: 1♂ "Grafton, 27.ix.1952, F.S. Paul", "genitalia slide 16545, viii.1998, S.A Wragg". Illustration and description in Kiriakoff (1977, fig. 36, p. 151).

Idalima leonora

Northern Territory: 1♂ "12.17S 133.20E Cooper Creek, 11km S. by W of Nimbawah Rock, 1.xii.1972, I.F.B. Common & E.D. Edwards", "genitalia slide 16537 viii.1998, S.A Wragg"; 1♂ "12.48S 132.42E Nourlangia Ck, 8km N. of Mt. Cahill, 21.v.1973, E.D. Edwards & M.S. Upton", "genitalia slide 1577, 1988, E.D. Edwards".

Idalima metasticta

Northern Territory: 1♂ "Point Darwin, 8.x.1902, F.P. Dodd", "genitalia slide 16547, ix.1998, S.A Wragg"; 1♂ "Fort Dandus, Melville Is, 3.x.1933, T.G. Campbell", "genitalia slide 16542, viii.1998, S.A Wragg"; 1♀ "11.07S 132 08E, Smith Point, Coburg Pen., 8.ii.1977, R. Lewis", "genitalia slide 16523, viii.1998, S.A Wragg".

Ipanica cornigera

Queensland: 1♂ "Silver Plains Homestead, Cape York Pen., 21.xii.1965 J.L. Wassell", "genitalia slide 16532, viii.1998, S.A Wragg". Illustration and description in Kiriakoff (1977, fig. 20, p. 100).

Leucogonia cosmopis

Northern Territory: 1♂ "11.09S 132.07E, Black Point, Coburg Pen, 28.i.1977, E.D. Edwards", "genitalia slide 16536, viii.1998, S.A Wragg"; 1♂ "12.52S 132.50E, Koongarra, 15km E of Mt. Cahill, 8.iii.1973, M.S. Upton", "genitalia slide N 1578, 1988, E.D. Edwards".

Leucogonia ekeikei

Queensland: 1♂ "Mission Beach nr Tully, 5-23.xi.1967, R. Dobson", "genitalia slide 16544, viii.1998, S.A. Wragg"; 1♂ "Mission Beach nr Tully, 24-28.xi.1967, R. Dobson", "genitalia slide 1581, 1988, E.D. Edwards".

Mimeusemia centralis

Queensland: 1♂ "8km N. of Daintree River ferry, 6.ii.1980, B. Hacobian & N. Goodman", "genitalia slide, 16539, viii.1998, S.A Wragg"; 1♂ "13.53S 143.11E, 6km N.N.E. Coen, 13.i.1994, E.D. Edwards & P. Zborowski", "genitalia slide 16549, ix.1998, S.A Wragg".

Mimeusemia econia

Queensland: 1♂ "13.58S 143.11E Mt. White, Coen, GPS, 12.i.1994, E.D. Edwards & P. Zborowski", "genitalia slide 16540, viii.1998, S.A Wragg".

Periopta ardescens

Queensland: 1♂ "Claudie R., 16.xii.1913, J.A.", "genitalia slide 16524, viii.1998, S.A Wragg". Illustration and description in Kiriakoff (1977, fig. 35, p. 148).

Periopta diversa

Northern Territory: 1♂ "Borroloola, 26.i.1912, G.F.W.", "genitalia slide 16525, viii.1998, S.A Wragg".

Periscepta butleri

Western Australia: 1♂ "Bunbury, 30.ix.1967, K.M. Le Souef", "genitalia slide 16516, viii.1998, S.A Wragg"; 1♂ "Freemantle district, 20-21.x.1904, L.H. Mosse-Robinson", "genitalia slide N1587, 1988, E.D. Edwards".

Periscepta polysticta

Victoria: 1♂ "Moe, 10.i.1919, C.G.L. Gooding", "genitalia slide 16515, viii.1998, S.A Wragg"; 1♂ "Moe, 10.xii.1919, C.G.L. Gooding", "genitalia slide N1507, 28-28.ix.1985, M.J. Lewis". Illustration and description in Kiriakoff (1977, fig. 28, p. 131).

Phalaenoides glycinae

New South Wales: 1♂ "Narara, 11.iv.1951, L.H. Mosse-Robinson", "genitalia slide 16498, viii.1998, S.A Wragg"; 1♂ "Narara, 24.iii.1951, L.H. Mosse-Robinson", "genitalia slide 16502, viii.1998, S.A Wragg"; 1♂ "Wollongong, 12.xii.1965, V.J. Robinson", "genitalia slide 16503, viii.1998, S.A Wragg". 2♀ "Narara, 15.iv.1951, L.H. Mosse-Robinson", "genitalia slide 16497, 16499, viii.1998, S.A Wragg"; 1♀ "Narara, 7.iv.1951, L.H. Mosse-Robinson", "genitalia slide 16501, viii.1998, S.A Wragg"; **South Australia:** 1♂ "Glenelg, 7.vi.1958, J.O. Wilson", "genitalia slides 16504, 16505, viii.1998, S.A Wragg"; 1♀ "Glenelg, ii.1958, J.O. Wilson", "genitalia slide 16500, viii.1998, S.A Wragg". Illustration and description in Kiriakoff (1977, fig. 23, p. 120).

Phalaenoides tristifica

Australian Capital Territory: 1♂ "Canberra, 2500ft., 1.iii.1932", "genitalia slide 16513, viii.1998, S.A Wragg"; 1♂ "Mt. Gingera, 5,500ft, 16.ii.1961, M.S. Upton", "genitalia slide N1582, 1988, E.D Edwards". **Queensland:** 1♀ "Killorny", "genitalia slide 16514, viii.1998, S.A Wragg".

Platagarista macleayi

Victoria: 1♂ "Mallacoota, 9.xii.1966, C. Hill", "genitalia slide 16541, viii.1998, S.A Wragg". **New South Wales:** 1♀ "Bateman's Bay, 22.i.1963, I.F.B. Common, & M.S. Upton", "genitalia slide 16522, viii.1998, S.A Wragg". Illustration and description in Kiriakoff (1977, fig. 32, p. 141).

Radinocera maculosa

Queensland: 1♂ "Clermont, 15.x.194, E.J.D.", "genitalia slide 16527, viii.1998, S.A Wragg". Illustration and description in Kiriakoff (1977, fig. 33, p. 142).

Radinocera vagata

Queensland: 1♂ "Humpty Doo (light trap), 15.xii.1959, E.B. Boerema", "genitalia slide 16526, viii.1998, S.A Wragg". **Northern Territory:** 1♂ "Kimberly Research Station, Wyndham, 6.xii.1986, E.C.B. Langfield", "genitalia slide N 402, 1978, E.D. Edwards".

Zalissa catocalina

Queensland: 1♂ "St. Bernard's, Mt. Tamborine, (at light) 7.i.1962, C.W. Frazer", "genitalia slide 16534, viii.1998, S.A Wragg"; 1♂ "Brisbane, 30.iii.1903", "genitalia slide N 160, 1956, I.F.B. Common"; 1♂ "Mt. Tamborine, 4.xi.1961, I.F.B. Common & M.S. Upton", "genitalia slide 1579, 1988, E.D. Edwards".

Zalissa pratti

Queensland: 1♂ “19.00S 146.12E, Paluma, 900m, 29.i.1979, D.W. Frith”, “genitalia slide 16535, viii.1998, S.A Wragg”. Illustration and description in Kiriakoff (1977, fig. 39, p. 169).

Zalissa stichograpta

New South Wales: 1♂ “Upper Allyn R. 15,00ft., 10.xi.1960, I.F.B. Common & M.S. Upton”, “genitalia slide 16543, viii.1998, S.A Wragg”. **Queensland:** 1♂ “Mt. Tambourine, 4.xi.1961, I.F.B. Common & M.S. Upton”, “genitalia slide N 1580, 1988, E.D. Edwards”.

OUTGROUP TAXA

Cremnophora angasii

South Australia: 1♂ “29 mls S.W. of Whyalla, 10.v.1970, I.F.B. Common”, “genitalia slide N 1584, 1988, E.D. Edwards”. **Western Australia:** 1♂ “31.07S 121.24E 29 km S.E. by E of Coolgardie, 5.v.1983, E.S. Nielsen & E.D. Edwards”, “genitalia slide 16533, viii.1998, S.A Wragg”.

Heliothis punctifera (Heliothinae)

Queensland: 1♂ “3 mls N. Barrington, 31.viii.1968, M.J. Matthews”, “genitalia slide 13336, Euparal, M.J. Matthews”. **South Australia:** 1♂ “14 km N.N.W. Yalata, Mission, M.J. Matthews”, “genitalia slide 13339, Euparal, M.J. Matthews”. **Western Australia:** 1♂ “Point Sampson, 1.v.1995, M.J. Matthews”, “genitalia slide 13337, Euparal, M.J. Matthews”; 1♂ “54 km W of Marble Bar, 21-22.iv.1995, M.J. Matthews”, “genitalia slide 13338, Euparal, M.J. Matthews”.

Helicoverpa punctigera (Heliothinae)

Australian Capital Territory: 1♂ “Black Mountain, 18.x.1995, M.J. Matthews”, “genitalia slide 13383, Euparal, M.J. Matthews”. **Queensland:** 1♂ “9km S Normanton, 23.iii.1995, M.J. Matthews”, “genitalia slide 13378, Euparal, M.J. Matthews”; 1♂ “Toowoomba, 12.i.1995, M.J. Matthews”, “genitalia slide 13385, Euparal, M.J. Matthews”. **Western Australia:** 1♂ “50 km W. of Marble Bar, 26-27.iv.1995, M.J. Matthews”, “genitalia slide 13376, Euparal, M.J. Matthews”. **Northern Territory:** 1♂ “28 km W Timber Ck, 23.iii.1995, M.J. Matthews”, “genitalia slide 13381, Euparal, M.J. Matthews”.

Neumichtis saliaris (Amphipyrinae)

Victoria: 1♂ “Moe, 30.ix.1921, expupa, C.G.L. Gooding”, “genitalia slide N441, 1984, E.D. Edwards”. **Tasmania:** 1♂ “Mt. Wellington, 1929, G.H. Hardy”, “genitalia slide N 442, 1984, E.D. Edwards”.

Proteuxoa sanguinipuncta (Amphipyrinae)

New South Wales: 1♂ “Uralla, 7.ii.1968, R. Dobson”, “genitalia slide 3114, 1988, E.D. Edwards”.

Appendix 2. Characters and character states of the 39 characters assessed for the male genitalia and adult stage of Australian Agaristinae and four outgroups of Amphipyrinae and Heliothinae (Noctuidae).

1. Vesica type (see Fig. 4)
   [0] tubular, extending posteriorly;
   [1] tubular, extending posteriorly, small broadening medially;
   [2] tubular, extending posteriorly, large broadening laterally;
   [3] tubular, extending posteriorly, broadening distally;
   [4] permanently everted with a single, sclerotised process enclosing ductus seminalis;
   [5] tubular or "C" shaped, recurved anteriorly or laterally;
   [6] expanded anteriorly, ovoid or anvil shaped.

Note, this character falls into a number of relatively distinct, discrete character states; however, *Leucogonia ekeikei, Argyrolepidia aequalis* and *Coenotoca subaspersa* display autapomorphic vesica types which have been coded as state [6] due to superficial similarity and may not represent true synapomorphy.

2. Position of apical diverticulum
   [0] absent;
   [1] extends ventrally;
   [2] extends dorsally;
   [3] extends laterally.

Note, diverticula may have evolved independently in different lineages. Specific shape of the diverticula was useful for estimating relationships in some taxa (e.g., coiled in *Phalaenoides* and *Comocrus*).

3. Length of apical diverticulum
   [0] small, basal width less than ductus ejaculatorius;
   [1] large, basal width greater than ductus ejaculatorius.

Note, in characters 3 and 4, absent diverticula were scored as "?" to prevent multiple scoring.

4. Shape of apical diverticulum (see Fig. 5)
   [0] straight;
   [1] weakly curved apically;
   [2] tightly curved apically;
   [3] spiralled;
   [4] "C"-shaped.

5. Cornuti of vesica
   [0] absent;
   [1] with catinae;
   [2] with a small patch of dentate cornutus;
   [3] partially covered with long, slender cornutus.

6. Width of ductus ejaculatorius and presence of cornutus
   [0] narrow, cornutus absent;
   [1] almost as broad as phallus, cornutus present.

7. Position of gonopore
   [0] distal, posterior to diverticula (if the latter present);
   [1] medial, anterior to diverticula (if the latter present).

8. Length: width ratio of phallus
   [0] longer than four times width;
   [1] as short or shorter than four times width;
   [2] longer than five times width.

9. Shape of phallus (see Fig. 6)
   [0] straight;
   [1] anteriorly curved ventrally <45º;
   [2] anteriorly curved ventrally >45º;
   [3] weakly anteriorly and posteriorly curved ventrally;
   [4] posteriorly curved dorsally, anteriorly curved ventrally;
   [5] anteriorly strongly curved ventrally with dorso-posterior lobe.

10. Insertion point of ductus ejaculatorius into phallus
   [0] wider than width of phallus;
   [1] as narrow or narrower than width of phallus.

11. Sclerotised extensions of phallus into vesica (see Fig. 7)
   [0] with a spined ridge;
   [1] with two lateral, weakly sclerotised extensions into vesica;
   [2] with a strongly sclerotised, evenly ending, cylindrical extension into vesica;
   [3] with constricting lateral extensions resulting in invagination of vesica;
   [4] with a long, flat sclerotised plate extending into vesica.

12. Length of sacculus
   [0] reduced or absent;
   [1] terminates in proximal valva;
   [2] terminates in middle or distal valva.

13. Apex of harpe
   [0] sharp;
   [1] blunt.

14. Length of harpe
   [0] less than one-third length of tegumen;
   [1] between one-third and half length of tegumen;
   [2] more than half length of tegumen.

15. Sclerotization of anal tube
   [0] partially or weakly sclerotised;
   [1] scaphium strongly sclerotised, not spined;
   [2] scaphium strongly sclerotised, spined.

Note, the sclerotization probably acts to support the anal tube and is usually, but not exclusively, associated with a long anal tube, valva, and uncus.

16. Shape of juxta (see Fig. 8)
   [0] flat, square, or "M"-shaped;
   [1] triangular and flat-topped or indented dorsally;
   [2] narrowly triangular, tapering sharply dorsally;
   [3] pillar-shaped.

Note, the shape of the juxta appeared to be variable within specimens of the same species, and some apomorphies were difficult to categorise and were lumped in generalised states. However, preliminary character analysis revealed this to be a useful character for linking species groups.

17. Spinules on juxta
   [0] absent;
   [1] present.

18. Sclerotization of central juxta
   [0] absent;
   [1] present.

19. Width and shape of valvae (see Fig. 9)
   [0] narrow, apex sharply pointed, inner margin straight, angularly inward-curved at apex;
   [1] narrow, apex sharp, inner margin straight, outer margin angularly inward-curved at median;

[2] apex rounded, more than twice as broad distally than proximally;
[3] with a medial bulge, apex sharp or produced;
[4] width consistent, less than vinculum, margins straight, apex squarish or gently rounded;
[5] slender, "crescent" shaped, both margins strongly curved medially, apex pointed.

Note, this character was difficult to score satisfactorily. Many groupings are probably homoplasious; others were lumped into one character state due to the difficulty in objectively separating them.

20. Length of uncus
[0] up to half length of tegumen;
[1] greater than half but less than full-length of tegumen;
[2] equal to or greater than length of tegumen.

Note, long unci are often associated with long valvae and a long anal tube. Valvae shape across species groups is often highly divergent, and this character may be homoplasious across some groups.

21. Length of saccus
[0] greater than width of proximal valva;
[1] less than width of proximal valva.

Note, *Radinocera* species have very similarly-shaped genitalia, but the saccus of *R. maculosa* is slightly longer and is scored [0], whereas *R. vagata* is scored [1].

22. Male antennae
[0] bipectinate;
[1] serrate;
[2] filiform;
[3] filiform, dilated medially and distally ("clubbed").

23. Shape of frontal tubercle
[0] small rounded prominence;
[1] truncate conical process;
[2] elongate, spatulate.

Note, a range of frons shapes were scored as a truncate conical process. The frons of *Apina callisto* and *Ipanica cornigera* are very large, and of a distinctive spatula shape.

24. Markings of thorax (see Fig. 10)
[0] predominantly longitudinal bands;
[1] predominantly transverse bands;
[2] predominantly faint markings;
[3] predominantly large spots.

Note, the thoracic markings of the outgroup taxa and three ingroup taxa could not be unambiguously categorised and were scored as "?"

25. Lateral abdominal hair tufts in male
[0] absent;
[1] present.

Note, characters 25 and 26 were present only in *Hecatesia*.

26. Stridulatory organ of forewing in male
[0] absent;
[1] present.

27. Ground-colour of wings
[0] brown;
[1] black or greyish.

28. Intravenous red-colouration of forewing
[0] absent;
[l] present.

29. Silvery-blue iridescence on forewing
[0] absent;
[1] present.

Note, a consistent, very specific pattern of inter-venous iridescence is present in a number of species, and therefore highly likely to be synapomorphic.

30. White scales on forewing
[0] absent;
[1] coarse white scales, widely scattered;
[2] fine white scales, along tegmen;
[3] white bar of scales along posterior margin.

31. Antemedial markings of forewing (see Fig. 11A)
[0] absent;
[1] faint or cryptic;
[2] bar or line;
[3] row of spots.

Note, scoring wing patterns for *Argyrolepidia thoracophora* was problematic because this species belongs to a group of mimetic species superficially resembling *Vitessa* Moore [1860] (Pyralidae: Pyralinae) (Edwards 1996). The antemedial, medial and postmedial bars of *A. thoracophora* were scored because they were thought to contain phylogenetic information. These bars are not present in most *Vitessa* species; instead, a solid area of colour marks the corresponding regions of forewing. *Argyrolepidia thoracophora* was scored "?" for terminal markings because the parallel lines marking the veins resemble those of *Vitessa* and are obviously convergent to those of *Comocrus* and *Phalaenoides*, and "?" for thoracic markings, in which it also resembles *Vitessa* more closely than the ingroup.

32. Medial markings of forewing (see Fig. 11B)
[0] absent;
[1] faint or cryptic;
[2] rectangular sub-costal bar, with posterior marginal marking present or absent;
[3] uneven row of three discrete spots (costal, sub-costal and posterio-marginal);
[4] row of spots, separated by dark venation;
[5] widely separated, oblique subcostal and one, two or three posterio-marginal spots, separated by dark venation;
[6] aligned row of dots, fused dots or straight line.

33. Postmedial markings of forewing (see Fig. 11C)
[0] absent;
[1] faint or cryptic;
[2] bar, width variable;
[3] uneven row of discrete spots (costal, sub-costal and posterio-marginal);
[4] row of spots, separated by dark venation;
[5] two markings of elongate, paired spots;
[6] aligned row of spots, fused spots or straight line.

34. Terminal and subterminal markings of forewing (see Fig. 11D)
[0] absent;
[1] faint or cryptic;
[2] row of terminal spots;
[3] parallel row of lines along veins;
[4] large spot on wing apex and posterior margin;
[5] one or two rows of subterminal spots or lines.

35. Colour of forewing markings
[0] predominantly brown;

[1] white, cream or yellow;
[2] with blue.

36. Hindwing markings
[0] absent, or fringe markings only;
[1] central patch;
[2] median spot;
[3] median bar;
[4] two bars;
[5] two spots;
[6] terminal shade.

37. Colour of hindwing markings
[0] brown or black;
[1] amber or yellow;
[2] white or cream;
[3] with blue.

38. Hindwing scalloping
[0] not scalloped;
[1] indented at vein CuA_2.

39. Bar along proximal cubital vein
[0] absent;
[1] present.

Appendix 3. Morphological data matrix of the Australian Agaristinae for the 42 taxa (38 ingroups, 4 outgroups) and 39 characters assessed. File is available on Figshare: https://figshare.com/s/4c066e68c7ec715d3cc6