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Systematics, biogeography and host associations of the lace bug genus *Inoma* (Hemiptera: Heteroptera: Tingidae)

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Abstract. The lace bug genus *Inoma* Hacker, 1927 is revised, including a redescription of the genus and the type species, *I. multispinosa* Hacker, 1927. Eight species are described as new to science, as follows: *I. arrernte* sp. nov., *I. breviseta* sp. nov., *I. fuscata* sp. nov., *I. innamincka* sp. nov., *I. kalbarri* sp. nov., *I. silveirae* sp. nov., *I. solusa* sp. nov. and *I. stysi* sp. nov. A key to species is provided, and diagnostic characters are illustrated. *Inoma angusta* Drake, 1942 is not congeneric with the above species, based on the given redescription, and is posited as *incertae sedis. Inoma* is endemic to Australia, with a mostly arid distribution, with up to three species recorded from a single locality. Host plants of *Inoma* are recorded for the first time, predominantly from the angiosperm plant families, Lamiaceae and Myoporaceae, and most commonly from species of the ubiquitous genera *Eremophila* and *Dicrastylis*.

Keywords. Heteroptera, Tingidae, *Inoma*, systematics, biogeography, host plants, new species, Australia

Introduction

The Australian Heteroptera are diverse, highly endemic, and remain poorly documented (Cassis & Gross 1995, 2002; Cassis et al. 2007). Arguably the two families with the greatest taxonomic impediment are the plant bugs (Miridae) and lace bugs (Tingidae). Over the past 12 years, one of us [GC], in collaboration with Randall T. Schuh of the American Museum of Natural History, has lead an intensive and systematic survey of Australia, particularly of the temperate and arid regions, with emphasis on documenting host plant associations. Outcomes of this field work identified the taxonomic impediment, and the collections serve as a baseline for documenting Australia's true bugs.

Of the Australian lace bugs, the nominotypical subfamily is one of the most neglected family-groups, with only one new species described over the past 40 years (Cassis & Gross 1995). The Australian lace bugs comprises 57 genera and 152 species, with two of three lace bug subfamilies represented (Cantacaderinae and Tinginae; Neotropical Viannaidae is not represented).

The majority of lacebug species have been described by Herbert Hacker and Carl J. Drake (see Cassis & Gross (1995) for references). Only six species have been described since Drake's last work on Australian tingids (Drake 1964): five species and one new genus in the Cantacaderinae (Lis 1997, 2000a,b, 2001) and one species in the Tinginae (Péricart 1992).

The Australian endemic genus *Inoma* Hacker, 1927 has not been studied for over 60 years. *Inoma* was first described as a monotypic genus, based on ***I. multispinosa*** Hacker, 1927 from southeast Queensland. A second species, *Inoma angusta* Drake, 1942 was described from northeast New South Wales.

The aims of this paper were to revise *Inoma*, provide an analysis of the relationship of the species, and assess their biogeography and host plant relationships.

We dedicate this work to our colleague, Professor Pavel Štys, who will always be regarded as a giant in the study of true bugs. We name a new species, *Inoma stysi* sp. nov., after him. He has had a long interest in Australian heteropterology, and spent an extended sabbatical with one of us [GC] at the Australian Museum in the early 1990s. We wish him well on his 75th birthday and demand from him many more years of scholarship, unravelling the complexity of true bugs!

Materials and methods

Material examined. This study involved an investigation of 534 specimens of *Inoma*, most of which were collected over the past 12 years (Cassis et al. 2007). All specimens were given matrix codes, and as such a unique specimen identifier (USI) is permanently attached to each specimen. These data are recorded in the Planetary Biodiversity Inventory (PBI) locality database and are given in full in the 'Material Examined' or the type data sections. Specimen information (including specimen, locality and host plant information and images) can be viewed by searching the locality database through the PBI website (http://www.research.amnh.org/pbi/databases/locality_database.html).

Acronyms for museum collections are as follows:

AM	Australian Museum (Sydney);
AMNH	American Museum of Natural History (New York);
SAMA	South Australian Museum (Adelaide);
QM	Queensland Museum (Brisbane);
USNM	United States National Museum (Washington, D.C.).

Host plants were identified predominantly by botanists at the Western Australian Herbarium (Perth) and the Royal Botanic Gardens (Sydney). In each of these depositories, host plant voucher specimens, with unique identifying codes, are lodged.

Morphometric characters. Ten morphometric characters were quantified using a Leica MZ12.5 steromicroscope and digital micrometer. The measurements recorded in millimetres

are as follows: body length (BL); head length (HL); head width (HW); pronotal length (PL); pronotal width (PW); interocular distance (IOD); length of first, second, third, and fourth antennal segment (AI, AII, AIII, AIV).

Homology and terminology. Much of the terminology in lace bugs is specific to the family, particularly in relation to structures of the dorsum. Although this in part hampers establishment of homologies more broadly across the Cimicomorpha, we have maintained the idiosyncratic terminology, as summarised by Drake & Davis (1960), and also Lee (1969) for larval characters. The diagnostic characters and associated terminology are demonstrated in Figures 4 and 10.

To adequately and clearly describe the complex and variable vestiture of the *Inoma* species we have designated the following setal types:

1) Major setiferous tubercles**.** These structures comprise a tuberculate base, which is short to elongate, most often moderately elongate, cylindrical, and 'spine-like'. Each tubercle has a terminal, robust, and straight bristle-like seta; setal lengths vary, from being shorter, subequal or occasionally longer in length than the tuberculate base (e.g., Figs. 5a-e, 7a-e, 8a-f, 9a-e). These are distributed on the lateral and ventral margins of the paranota, the longitudinal carinae of the pronotum (including median carinae extending to collum), anterior margin of the collum, posteroventral margin of proepimeron, and the costal margins and carinate discoidal margins of the hemelytra. They are often in regular rows, either as a single row (e.g., longitudinal pronotal carinae, Fig. 5d), or in two rows, where the setiferous tubercles can be opposing or alternate (e.g., lateral margins of paranota, see Fig. 9d). The major setiferous tubercles are found in the following *Inoma* species: ***I. breviseta*** sp. nov., ***I. fuscata*** sp. nov., ***I. kalbarri*** sp. nov., ***I. multispinosa***, ***I. silveirae*** sp. nov., ***I. solusa*** sp. nov. and ***I. stysi*** sp. nov.

2) Minor setiferous tubercles**.** These structures comprise a short tuberculate base, which is rounded, with each tubercle bearing a terminal seta that is much longer than the tubercle. The seta can be arcuate (e.g., hemelytral margins in Fig. 4e) or straight (e.g., antenna in Fig. 9a). Generally these setae are not robust or bristle-like, having a softer appearance. Minor setiferous tubercles are found in the same position as the major setiferous tubercles, as in the following *Inoma* species: ***I. arrernte*** sp. nov. and ***I. innamincka*** sp. nov. As with the major setiferous tubercles, this setal type can also exist in single or multiple rows. In addition, minor setiferous tubercles are also found on the antennae and cephalic spines of all *Inoma* species, aside from ***I. multispinosa***. Many species also have minor setiferous tubercles with more elongate terminal setae, which are generally more straight and bristle-like on the femora and tibiae (e.g., Fig. 9h).

3) Woolly setae**.** These setae are simple and curly, sometimes weakly flattened, and mostly elongate. They are often densely distributed on the dorsum, particularly on the head and pronotum, and less so on the hemelytra (never on sutural area) (e.g., Fig. 5a-e). Woolly setae are also found on the thoracic pleura, sometimes densely. These setae are found in most *Inoma* species, except ***I. breviseta*** sp. nov. and ***I. multispinosa***.

4) Scale-like setae**.** These setae are flattened, more so than the woolly setae, are mostly adpressed to the body, and mostly short (occasionally elongate on abdominal venter). They are found on the dorsum of one *Inoma* species, ***I. breviseta*** sp. nov., but mostly found on the abdominal venter, in the following *Inoma* species: ***I. arrernte*** sp. nov., ***I. breviseta*** sp. nov., ***I. fuscata*** sp. nov., and ***I. innamincka*** sp. nov.

5) Hair-like setae**.** These setae are simple and tapered distally (e.g., Fig. 7f). They are never thickened or flattened. They are found either on the abdominal venter, legs, or the antennal segments. Hair-like setae are present on the abdominal venter of the following *Inoma* species: *I. kalbarri* sp. nov., *I. silveirae* sp. nov., *I. solusa* sp. nov. and *I. stysi* sp. nov.

Setiferous tubercles have been for the most part referred to as spines, in previous treatments of *Inoma* (Hacker 1927, Drake 1942) and *Lasiacantha* Stål, 1873 (Drake 1942b). These structures are not considered spines, lacking an articulated base; the setal descriptions above provide an enhanced definition of the vestiture, and are aligned with the views of Péricart (1992).

Imaging. Habitus photographs are provided for all taxa and were taken using a Visionary Digital system (http://www.visionarydigital.com/), inclusive of an Infinity K-2 macroscope and Canon 40D SLR camera. Multiple images of the same specimen were taken and composited using Helicon Focus software (Kozub et al. 2008).

Salient characters were examined by light and scanning electron microscopy, and SEMs are provided for characters of six of the nine *Inoma* species.

Illustrations of male and female genitalia were prepared using a Leica DMB compound microscope. Illustrations of male and female genitalia are provided to show infrageneric variation, but also to establish generic benchmarks for future studies of Australian lace bugs.

Mapping. Precise latitude and longitude data were obtained in the field using Global Positioning System devices. For historical collections, Geoscience Australia's (2006) online gazetteer was used to estimate coordinates.

Distribution maps were prepared using Map Maker Pro (Dudley 2008), on a transverse Mercator projection.

Phylogenetic analysis. Character data was compiled using the Nexus Data Editor (Page 2001) and parsimony analysis conducted using TNT (Goloboff et al. 2001). Most parsimonious trees were sought heuristically using 1000 random stepwise addition replicates with tree bisection-reconnection (TBR) branch swapping. Assessment of branch support was calculated as both decay indices (Bremer 1994) and bootstrap values (Felsenstein 1985), the latter calculated from 1000 bootstrap replicates using 1000 random addition replicates and TBR branch swapping. All 34 characters were unweighted and multistate characters were unordered. Characters were optimised on the resulting phylogeny using MacClade 4.0.8 (Maddison & Maddison 2005).

Multiple outgroups were designated in accordance with criteria established by Nixon & Carpenter (1993). The rationale for outgroup selection was based on putative close relationships between them and *Inoma*. The outgroups selected were: 1) two undetermined Australian species of *Lasiacantha*; 2) two determined Australian species of *Tingis* Fabricius, 1803 – *T. drakei* Hacker, 1929 and *T. perkensi* Drake, 1947; 3) an undetermined Australian species of *Ulonemia* Drake & Poor, 1937; and, 4) *Inoma angusta* incertae sedis, which herein is removed from *Inoma* (see remarks within generic description below). The tree was rooted at *Ulonemia* sp.

Taxonomy

Inoma Hacker, 1927

Inoma Hacker, 1927: 25 (gen. nov.).

Inoma: Drake & Ruhoff (1960): 62 (list); Drake & Ruhoff (1965): 249 (catalogue); Cassis & Gross (1995): 417 (catalogue).

Type species. *Inoma multispinosa* Hacker, 1927, by monotypy.

Diagnosis. *Inoma* is recognised by the following combination of characters: small to medium size, males (BL 1.81-2.96), females (BL 1.9-2.94); brachypterous and macropterous morphs; ovoid body; mottled or variegated colouration; with or without woolly or scale-like, pale setae, often densely distributed; all species with setiferous tubercles on anterior margin and crest of collum, pronotal carinae, margins of paranota and hemelytra, and carinate margins of discoidal area; antennae slender, elongate, AI subequal to AII; head with five elongate, porrect spines, paired frontal and occipital spines, medial spine sometimes forked; pronotum tricarinate, carinae uniseriate, subequal in height and not highly elevated; pronotal collum small to moderately enlarged, subtriangular, dorsally keeled; paranota and costal areas well developed, uniseriate or biseriate; legs slender, elongate; and, male aedeagus with a well developed, heavily sclerotised, distal U-shaped endosomal sclerite.

Redescription. COLOURATION. Varying from cream, yellow brown, to orange and red brown, to dark brown (Figs. 1, 2). Often with mottled or patterned colour pattern on dorsum, more so on hemelytra. Head and callar region of pronotum predominantly darkened, with posterior lobe of pronotum lighter. AIV and tarsi dark brown, almost black. Venter generally darker and more uniform in colouration than dorsum.

VESTITURE. Most species with covering of silvery to golden, woolly or scale-like setae, intermixed either with elongate, curly, woolly setae, or short, flattened, lanceolate, scale-like setae; sometimes with setiferous tubercles only. All species with setiferous tubercles in single or multiple (alternating or opposing) rows, mutiple rows most often along lateral paranotal and costal margins; either major (e.g., Fig. 5a-e), or minor setiferous tubercles (e.g., Fig. 4a-e). Head: setae when present, woolly or scale-like, dense and adpressed (e.g., Fig. 4a-c); minor setiferous tubercles present around base or on cephalic spines (e.g., Figs. 4a, 5a). Antennae: AI and AII glabrous or with setae as on head and in a single ring around segment (e.g., Figs. 4a, 5a); AIII glabrous or with minor setiferous tubercles (with an elongate, erect terminal seta – straight or recurved), and short, bristle-like setae (e.g., Fig. 7b); AIV always with both short and elongate bristle-like simple setae. Pronotum: setae when present, woolly or scale-like, most dense on pronotal callar region, less dense on collum, paranota, pronotal longitudinal carinae and posterior lobe (e.g., Fig. 4d); minor or major setiferous tubercles always present along lateral margins of paranota, margins of carinae, anterior margin and dorsal keel of collum (e.g., Fig 5d), also present along ventral margin of paranota (e.g., Fig. 5c). Thoracic pleura and sterna: setae when present, woolly or scale-like, generally denser on pleura, sparser on supracoxal lobes and sterna; posteroventral margin of proepimeron with a few minor or major setiferous tubercles (e.g., Fig. 6c); sternal carinae with one or two rows of setae, type

variable, rarely with minor setiferous tubercles. Legs: femora and tibiae with minor setiferous tubercles, setae when present, elongate and bristle-like with very small tuberculate base (as in antennae) (e.g., Figs. 7b, 8b, 9h). Hemelytra: (e.g., Figs. 4e-f, 5e) setae when present, woolly, less dense than on pronotal callar region, moderately distributed over discoidal and subcostal areas, very sparse on costal area; minor or major setiferous tubercles present along margin of costal area, on carinate R+M and cubitus veins bounding discoidal and sutural areas, on veins tubercles often recurved, terminal setae generally more elongate than on costal margins and paranota. Abdomen: setae when present, with either scale-like setae (e.g. Figs. 4h, 5h) or hair-like setae (e.g., Figs. 7f, 9h), short or elongate, densely distributed.

STRUCTURE. Macropterous and brachypterous forms. Head: five spines present, spines mostly as long and often longer than AI (e.g., Fig. 5a), rarely shorter than AI (e.g., Fig. 4a), semi-erect to erect; frontal spines inserted behind antennal bases, either slightly divergent, parallel or slightly convergent, not contiguous or crossing; medial spine straight or apex forked; occipital spines strongly arcuate laterally, or sometimes straight and slightly divergent apically; bucculae prominent, extending slightly beyond head, closed in front, broadly rounded anteriorly laterally (Fig. 4b). Labium: usually extending to mesocoxae; sometimes extending onto abdomen. Antennae: elongate; AI cylindrical, short, of greater diameter than other segments; AII equal to or at least 2/3 length of AI; AIII elongate; AIV short but longer than AI+AII, clavate, base sometimes elongate. Pronotum: (e.g., Figs. 4d, 5d) broad, lateral margins rounded, callar region flattened or convex (lateral views in Figs. 1 & 2), closely punctate, posterior lobe subequal to anterior portion, pointed and reticulated; collum weakly to moderately elevated and sub-triangular in shape, strongly keeled medially, truncate anteriorly, covering half of head; pronotum tricarinate, carinae elevated, but not highly so, uniseriate, areolae subquadrate and small or large, straight over most of length but lateral carinae slightly convergent at posterior end and terminating anteriorly at calli, median carina percurrent to collum, lateral carinae of equal height to median carina; paranota narrow and linear, obliquely extended or upright, uniseriate or biseriate, areolae subquadrate and small or large. Thoracic sterna: prosternal carinae barely visible, meso and metasternal carinae strongly elevated, parallel (or very slightly rounded) and of equal width. Metathoracic gland: orifice obsolete. Legs: slender, elongate, tibiae longer than femora. Hemelytra: macropters (e.g., Fig. 5e, 8f), brachypters (e.g., Fig. 4e-f, 8e); cubitus and R+M veins carinate; costal area uniseriate or biseriate, areolae large and subquadrate; subcostal area wide, at least half width of discoidal area, extending to just before forewing apex; discoidal area large, lanceolate in shape, junction of cubitus and R+M veins medially located on hemelytra; sutural area small, areole size generally large, areolae small in brachypters; hypocosta as wide as costal area or narrow. Male genitalia: pygophore subquadrate, ventral margin of opening expanded posteriorly with a concave or sinuous margin (e.g., Fig. 4g); parameres simple, sickle-shaped (e.g., Fig. 10a-b, d-e, h-i), with short bristle-like setae on entire inner margin and sometimes also on outer margin of apophysis, mostly with a few more elongate setae on sensory lobe, sometimes also with minute setae on dorsal surface (Fig. 10h-i), sensory lobe rounded (Fig. 10d-e, h-i) or sometimes slightly angular (Fig. 10a-b), apophysis elongate and acuminate with a rounded apex, tubular in cross section with rounded margins; aedeagus with a large, curved, inverted U-shaped sclerite in apical tubular portion of endosoma (Fig. 10c,f,g), heavily sclerotised,

some subtle variation in size and shape of cleft and length of the basal branches of sclerite; sometimes also with small, paired endosomal sclerites positioned basally near dorsal plate (e.g., Fig. 10c,f), small with shape varying from elongate-ovate (Fig. 10f,k), sub-triangular (Fig. 10c,m) and semi-circular (Fig. 10j,l) ; medial portion of phallotheca mostly entire dorsally, rarely divided (Fig. 10g); dorsal plate of aedeagus simple, broadly U-shaped with rounded distal margin (e.g., Fig. 10c,f).

Females: minor sexual dimorphism; differing from males as follows: eyes smaller; AIII less pilose with only elongate minor setiferous tubercles, lacking short simple setae; hemelytra slightly shorter and broader (both brachypters and macropters); sometimes slight colour variation. Female genitalia: membraneous, with paired pseudospermathecae, basally derived at junction of lateral oviducts, each with short duct and distal capitate seminal sac (Fig. 11).

Biology and host plant relationships. *Inoma* is found mostly on plant species of the angiosperm order Asterales, often belonging to the families Myoporaceae and Lamiaceae.

Distribution. *Inoma* is comprised of nine species, and is largely found in arid Australia, except for *I. multispinosa* which is known from temperate Australia, in the southeastern corner.

Remarks. *Inoma* has been redefined, with a detailed definition of characters, for inclusion of new species described herein. Characters which are now more broadly defined and show infrageneric variation include: 1) condition of setiferous tubercles (formerly referred to as spines by Hacker (1927)); 2) setal characters of pilose species; 3) paranota and costal areas, now either biseriate or uniseriate; 4) body colouration, including variation in patterning; 5) orientation of frontal cephalic spines, which may be weakly divergent, parallel or slightly converging; 6) elevation of collum, which although consistently keeled is not always sharply elevated, as indicated in the original description, with some species having only a weakly elevated collum; and, 7) elevation of pronotal callar region, which is not always convex, but sometimes almost flat or very slightly raised.

Inoma is aligned with the speciose genus *Tingis*, and putatively closely related to and possibly synonymous to *Lasiacantha*, the latter a diverse taxon, with species in Europe, Africa, India, southeast Asia and Australia. Morphological similarities between *Inoma* and *Lasiacantha* include: 1) shape and form of hemelytra; 2) elongate cephalic spines with laterally arcuate occipital spines; 3) sometimes bifurcate medial spine; 4) outline of head and bucculae; 6) mostly elevated pronotal collum; 7) marginal setiferous tubercles; 8) often dense vestiture; and, 9) slender legs and antennae.

Nonetheless, we have found a number of characters of *Inoma* which distinguish it from *Lasiacantha*, with the most critical being: 1) strongly keeled pronotal collum, subtriangular in shape, more moderately elevated; 2) setiferous tubercles along medial keel and anterior margin of the collum; 3) pronotal carinae distinctly elevated, but not greatly enlarged, 4) medial pronotal carina always same height as lateral carinae; 5) linear, narrow paranota, equal width throughout and at most two areolae wide; and, 6) costal area at most two areolae rows wide; and, 7) lack of very fine, hook-like setae on dorsum, as found in *Lasiacantha*.

Hacker (1927) noted an affinity of *Inoma* with *Urentius* Distant, 1903, but apart from superficial similarities, with the marginal setiferous tubercles and general body shape, this genus is possibly more distantly related.

Inoma angusta Drake, 1942, is considered here as species *incertae sedis*, because it lacks the aforementioned diagnostic characters, including the dorsally rounded collum, dorsal crest and setiferous tubercles on anterior margin and dorsal surface. In addition, *I. angusta* has incomplete and very narrow paranota, and has a rather elongate linear, narrow form rather than being either elongate-ovoid to ovoid. We have refrained from treating this species any further in this work, pending a more thorough examination of genus-group boundaries in Australian lace bugs, but here remove it from *Inoma*.

Checklist of species of *Inoma*

arrernte sp. nov.	Northern Territory
breviseta sp. nov.	Northern Territory, South Australia
fuscata sp. nov.	Northern Territory, Queensland
innamincka sp. nov.	South Australia
kalbarri sp. nov.	Western Australia
multispinosa Hacker, 1927	Australian Capital Territory, South Australia, Queensland,
silveirae sp. nov.	Northern Territory, Queensland, South Australia, Western Australia
solusa sp. nov.	Northern Territory
stysi sp. nov.	Northern Territory, Western Australia

Key to species of *Inoma*

1. Dorsum with major setiferous tubercles only, each tubercle with minute seta, barely evident; cream and red-brown colour banding pattern (Fig. 2). .... ***I. multispinosa*** Hacker, 1927
- Dorsum with setiferous tubercles intermixed with woolly or scale-like setae (e.g., Figs. 1-2); minor or major setiferous tubercles, if major then setae evident; without colour banding (e.g., Figs. 1-2). 2
2. Body with short, flattened, scale-like setae, thick, lanceolate-shaped, sparsely distributed on head and pronotum, absent from hemelytra (Fig. 1); paranota biseriate (Fig. 1); costal area uniseriate (Fig. 1); medial cephalic spine forked at apex. ..... ***I. breviseta* sp. nov.**
- Body with elongate, woolly setae (Fig. 1); setae not strongly flattened, at most very slightly flattened, densely distributed on head and pronotum, always present on hemelytra, even if only very sparsely so; costal area either uniseriate or biseriate; medial cephalic spine undivided apically. 3
3. Paranotal (e.g., Fig. 7d) and costal areas uniseriate (e.g., Fig. 7e). 4
- Paranotal (e.g., Fig. 5d) and costal areas biseriate (e.g., Fig. 5e). 7
4. Minor setiferous tubercles present on pronotum and hemelytra, setae much longer than tuberculate base and recurved (e.g., Figs. 4, 6). 5
- Major setiferous tubercles present on pronotum and hemelytra moderately elongate; setae as long or longer than spine base and usually straight (e.g., Figs. 5, 7-9). 6

5. Setae short, arcuate (Fig. 6d); labium short, reaching mesocoxae; abdominal venter dark brown with short, clavate, scale-like setae (Fig. 6f). ..... ***I. innamincka* sp. nov.**
- Setae elongate, curly (Fig. 4d); labium elongate, reaching abdomen; abdominal venter light brown with elongate, straight, hair-like setae (Fig. 4h). ..... ***I. arrernte* sp. nov.**
6. Small size (< 2.5 mm); pronotal callar region of medium brown colour (Fig. 2); costal area uniformly uniseriate, cells large and subquadrate (Figs. 8e,f). .... ***I. silveirae* sp. nov.**
- Medium size (mostly > 2.5 mm); pronotal callar region of dark brown colour (Fig. 1); costal area mostly uniseriate (Fig. 7e), biseriate sub-distally, adjacent to junction of hypocostal and cubital veins, cells large but more irregular in shape (Fig. 7e). .... ***I. kalbarri* sp. nov.**
7. Cephalic spines moderately elongate, with stout base (Fig. 9a); frontal cephalic spine at most a little longer than AI (Fig. 9a); occipital cephalic spines outwardly curved, not reaching lateral margin of eyes (Fig. 9a); setiferous tubercles on hemelytral veins elongate (longer than on costal margins), with fine setae longer than spine base, folded inwardly (Fig. 9e). ..... ***I. stysi* sp. nov.**
- Cephalic spines greatly elongate, with slender base (e.g., Fig. 5a); frontal spines elongate (Fig. 5a), subequal in length to AI + AII; occipital spines strongly curved outwardly, reaching lateral margins of eyes (e.g., Fig. 5a). 8
8. Setiferous tubercles on pronotal carinae very short, densely distributed in opposing rows, shorter than those on paranota (Fig. 2); abdominal venter with elongate, pale, straight, hair-like setae. ..... ***I. solusa* sp. nov.**
- Setiferous tubercles on pronotal carinae moderately elongate, sparsely distributed in a single row, same length as those on paranota (Fig. 5d); abdominal venter with short, clavate, scale-like setae (Fig. 5h). ..... ***I. fuscata* sp. nov.**

Inoma arrernte sp. nov.

(Figs. 1, 3-4, 10j, 13a)

Type material. Holotype: ♂, **AUSTRALIA: Northern Territory:** ~ 75 km E of Stuart Hwy on Ernest Giles Road, 24.56668°S 132.5324°E, 511 m, 30 Oct 2001, Cassis, Schuh, Schwartz, Silveira, Wall (AMNH_PBI 00016098) (AM).

Paratypes: **AUSTRALIA: Northern Territory:** 33 km E of Alice Springs on Ross Hwy, 23.73335°S 134.1536°E, 555 m, 25 Oct 2001, Cassis, Schuh, Schwartz, Silveira, Wall, ex. *Anemocarpa saxatilis* (Asteraceae; det. NSW Herbarium NSW658341), 3 ♂♂ (AMNH_PBI 00010201, AMNH_PBI 00013131, AMNH_PBI 00013657), 6 ♀♀ (AMNH_PBI 00013132-AMNH_PBI 00013136, AMNH_PBI 00013658) (AM); 74.2 km NW of Bond Springs on Tanami Rd, 23.41668°S 133.2307°E, 671 m, 22 Oct 2001, Cassis, Schuh, Schwartz, Silveira, Wall, *Rutidosis helichrysoides* (Asteraceae; det. field ID NSW 658290), 1 ♀ (AMNH_PBI 00016097) (AM); ~ 44 km E of Stuart Hwy on Ernest Giles Rd, 24.56668°S 132.6815°E, 494 m, 30 Oct 2001, Cassis, Schuh, Schwartz, Silveira, Wall, *Solanum ellipticum* (Solanaceae; det. NSW Herbarium NSW666249), 1 ♀ (AMNH_PBI 00010202) (AM); ~ 75 km E of Stuart Hwy on Ernest Giles Road, 24.56668°S 132.5324°E, 511 m, 30 Oct 2001, Cassis, Schuh, Schwartz, Silveira, Wall, 21 ♂♂ (AMNH_PBI 00016099-AMNH_PBI 00016101, AMNH_PBI 00016103-AMNH_PBI 00016120), 1 ♀ (AMNH_PBI 00016102) (AM).

Additional material examined. AUSTRALIA: Northern Territory: 33 km E of Alice Springs on Ross Hwy, 23.73335°S 134.1536°E, 555 m, 25 Oct 2001, Cassis, Schuh, Schwartz, Silveira, Wall, ex. *Anemocarpa saxatilis* (Asteraceae; det. NSW Herbarium NSW658341), 8 larvae (AMNH_PBI 00013670, AMNH_PBI 00013672-AMNH_PBI 00013677, AMNH_PBI 00230072).

Diagnosis. *Inoma arrernte* sp. nov. is recognised by the following combination of characters: small size (Fig. 1); body mostly stramineous (Fig. 1); body covered with elongate, silvery, woolly setae (Figs. 1, 4), densely distributed on dorsum; setae on abdominal venter shorter, scale-like and thickened (Fig. 4h); pronotum and hemelytra with dense distribution of minor setiferous tubercles with elongate recurved terminal seta (Figs. 1, 4d-f); cephalic spines of moderate length, as long as AI (Fig. 4a); occipital spines straight, weakly divergent (Fig. 4a); paranota and costal areas uniseriate (Fig. 4d); paranota obliquely extended (Fig. 4d); brachypters with large areolae in costal area, small in remainder.

Description of adult. Small size, macropterous (male 2.34, female 2.43) and brachypterous (males 1.75-1.93, females 1.79-2.01) forms (Fig. 1).

COLOURATION. Dorsum mostly stramineous (Fig. 1); venter brown. Head: light brown; spines yellow-brown; bucculae stramineous. Labium: mostly dark brown. Antennae: mostly yellow-brown; AIV dark brown. Pronotum: mostly stramineous, light brown anteriorly with a light brown spot in middle of median carina. Thoracic pleura and sterna: light brown with stramineous margins; sternal carinae stramineous. Legs: femora with basal half to two-thirds medium brown, remainder and tibiae lighter yellow-brown; tarsi dark brown. Hemelytra: stramineous, with two light brown patches on R+M vein; light brown markings in costal area on horizontal margins of areolae. Abdomen: venter light brown.

VESTITURE. Elongate, curly, fine, woolly setae present on head, dorsum and thoracic pleura; minor setiferous tubercles densely distributed on pronotum and hemelytra, very short, with elongate recurved terminal seta (Fig. 4a-f). Head: minor setiferous tubercles covering entire cephalic spines (Fig. 4a,c). Antennae: AIII with minor setiferous tubercles, with elongate terminal seta, tapered apically. Pronotum: minor setiferous tubercles in two opposing rows on posterior half of paranota, single rows on rest of pronotum. Thoracic pleura and sterna: densely distributed elongate, woolly setae; posteroventral margin of proepimeron with a few minor setiferous tubercles; sternal carinae with two rows of hair-like, recurved, terminal seta. Legs: femora with minor setiferous tubercles, terminal seta curly, slightly thickened; tibiae with minor setiferous setae, with longer bristle-like, semi-erect, terminal seta. Hemelytra: woolly setae densely distributed; minor setiferous tubercles in two opposing rows on costal margin, extending to forewing apex; elsewhere in one row (Fig. 4e-f). Abdomen: venter with moderately dense distribution of shorter, thickened, scale-like setae (Fig. 4h).

STRUCTURE. Head (Figs. 4a-d): spines moderate length, subequal to AI length (Figs. 4a-c); frontal spines parallel (Fig. 4a); medial spine straight (Fig. 4a), occipital spines weakly diverging (Fig. 4a). Labium: elongate, extending to abdomen. Antennae: AIV compact, without cylindrical base. Pronotum: callar region slightly convex in macropters (Fig 1) or flat in brachypters (Figs. 1, 4e-f); collum very weakly enlarged (Fig. 3d), slightly rounded apex; paranota uniseriate (Figs. 1, 4d), obliquely extended; carinae areolae small. Hemelytra: Macropters (Figs. 1, 4f): costal area uniseriate, areolae large; subcostal and discoidal areas with smaller areolae; sutural area with large areolae; hypocosta wide, as wide as costal area (Fig. 1). Brachypters (Figs. 1, 4e): reduced sutural and costal areas; acutely rounded posteriorly; convex laterally; costal area, areolae large and sometimes rectangular and elongate rather than quadrate; remainder of forewing with small areolae. Male genitalia: pygophore (Fig. 4g); parameres with rounded sensory lobe, sensory lobe with elongate setae, inner margin of parameres with short setae, dorsal surface of parameres with broad distribution of minute

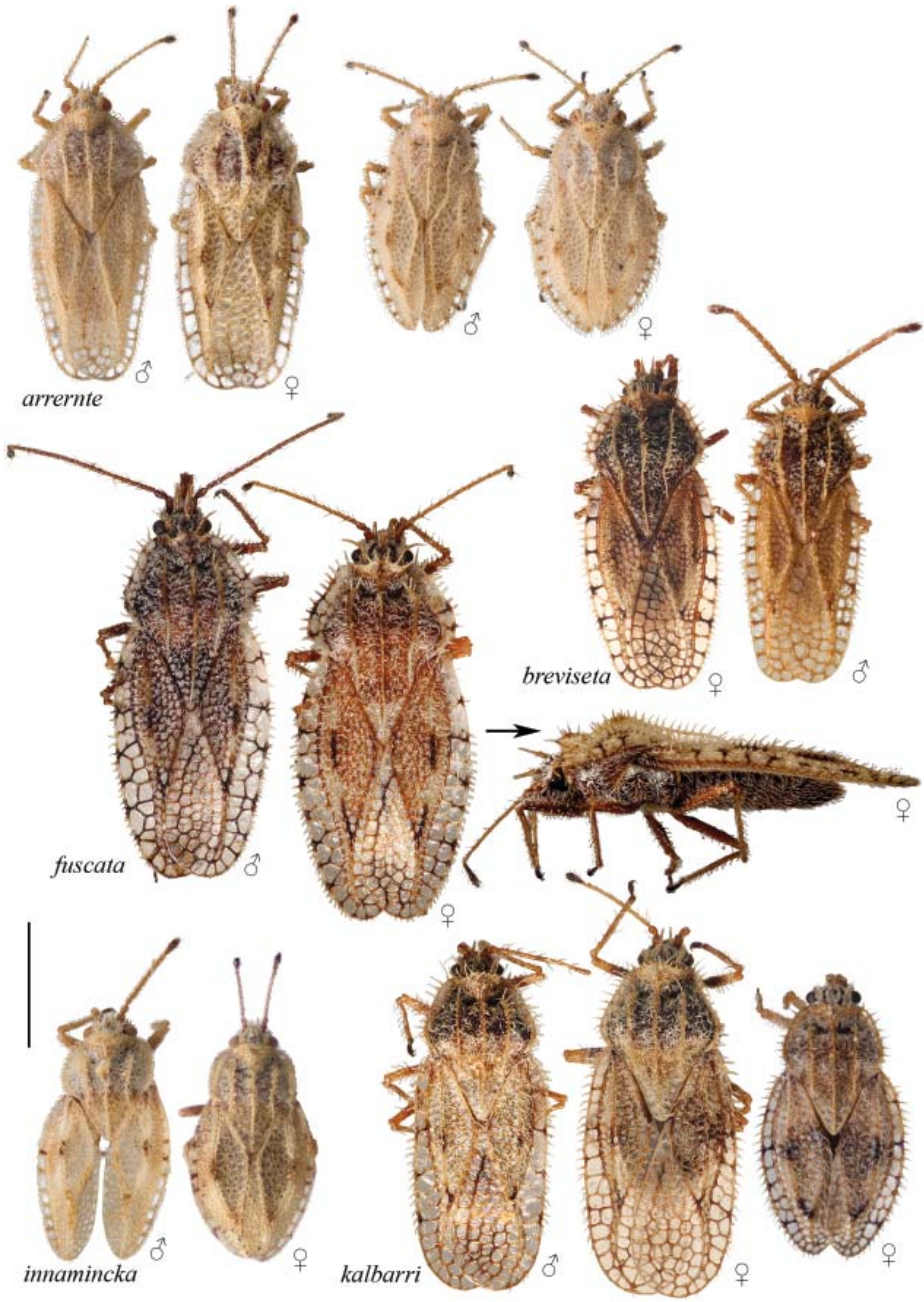

Fig. 1. Habitus photographs of *Inoma* species: *I. arrernte* sp. nov. (macropters and brachypters), *I. breviseta* sp. nov., *I. fuscata* sp. nov. (also lateral view), *I. innamincka* sp. nov. and *I. kalbarri* sp. nov. (macropters and female brachypter). Scale = 1 mm.

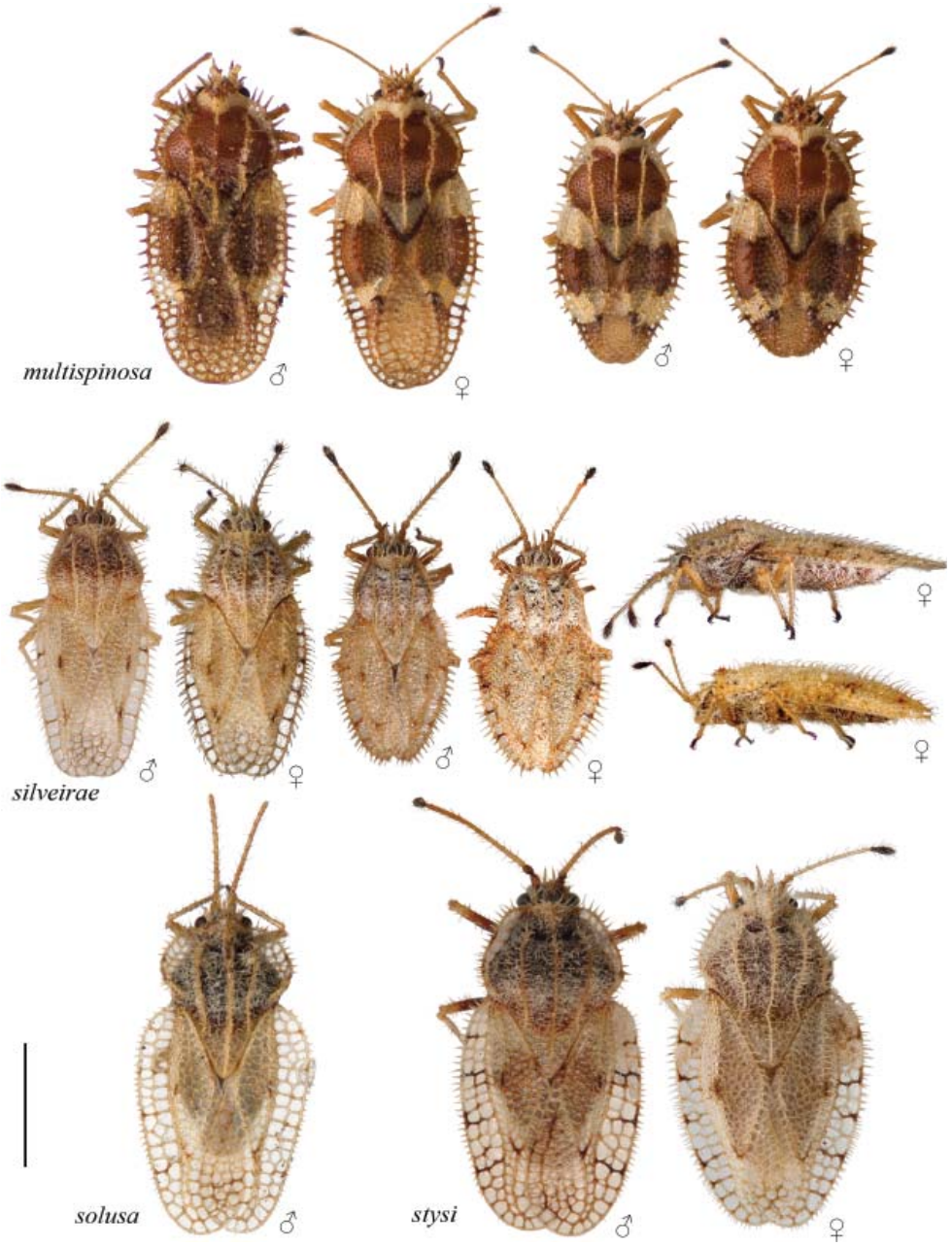

Fig. 2. Habitus photographs of *Inoma* species: *I. multispinosa* Hacker, 1927 (macropters and brachypters), *I. silveirae* sp. nov. (macropters and brachypters, also in lateral view), *I. solusa* sp. nov. and *I. stysi* sp. nov. Scale = 1 mm.

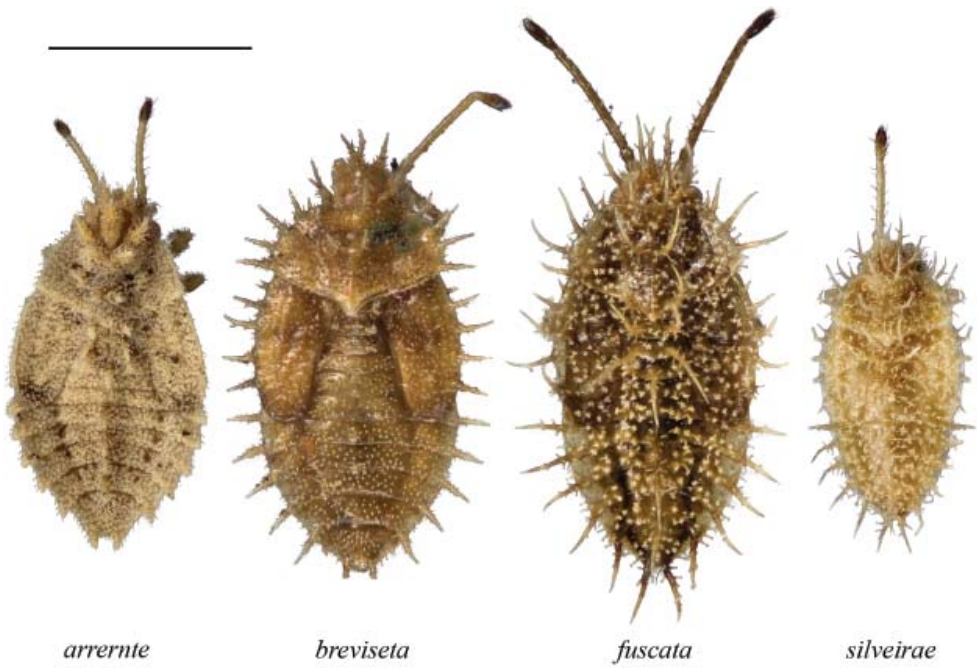

Fig. 3. 5th instar larval habitus photographs of *Inoma* species: *I. arrernte* sp. nov., *I. breviseta* sp. nov., *I. fuscata* sp. nov. and *I. silveirae* sp. nov. Scale = 1 mm.

setae; distal U-shaped endosomal sclerite with shallow, rounded cleft, long basal branches, straight distal margin; paired, semi-circular, basal endosomal sclerites, surface tuberculate (Fig. 10j). Female genitalia: subtriangular subgenital plate (Fig. 4h).

MEASUREMENTS. Measures of 1 ♂ and 1 ♀ macropters and ranges of 10 ♂♂ and 10 ♀♀ brachyters given in Table 1.

Description of fifth instar larva (Fig. 3). COLOURATION. Stramineous, with darker areas of light to mid-brown on pronotal carinae, tip of hemelytral lobes, medially across abdominal tergites, and spotted sub-laterally on abdominal sternites; AIV, labium, femora and tarsi embrowned.

VESTITURE AND STRUCTURE. Dorsum with dense distribution of pale, stellate-shaped cuticular outgrowths, short and not strongly elevated, distally with four short sub-quadrate tips; same cuticular outgrowths also present sublaterally on abdominal sternites, on thoracic pleura and laterally on head below eye; pronotum with pairs of elongate, medial processes; mesonotum, metanotum and abdominal tergite I with elongate, paired medial processes; abdominal tergites II and V-VIII with single, elongate, medial process; posterolateral corners of abdominal tergites IV-IX with single, short process, lateral margins of pronotum and hemelytral lobes without any processes; minor setiferous tubercles with short, clavate, terminal

seta, covering all processes, cephalic spines, lateral and posterior margins of pronotum, and intermixed sparsely with cuticular outgrowths on hemelytral lobes and abdominal tergites.

Differential diagnosis. This species is similar to *I. innamincka* sp. nov., but differs from it by the following character states: 1) slightly smaller body; 2) longer recurved terminal setae on minor setiferous tubercles; 3) denser covering of woolly setae on dorsum, which are longer and more curled; 4) lighter brown abdominal venter, with elongate scale-like setae; and 5) more elongate labium, reaching the abdomen. This species is also similar to *I. silveirae* sp. nov., but can be distinguished from it by the possession of minor setiferous tubercles (cf. major setiferous tubercles of *I. silveirae* sp. nov.), a slightly more elevated collum, and being more stramineous or cream in colouration (cf. lighter brown colour of *I. silveirae* sp. nov.).

Etymology. This species is named after the Aboriginal people of the region of central Australia, on whose traditional lands it was collected, the Arrernte (UH-rrahn-da) people. Noun in apposition.

Biology. *Inoma arrernte* sp. nov. is found on a broad range of plant species, commonly on *Anemocarpa saxatilis* (Asteraceae), on which both adults and larvae have been found, and *Halgania cyanea* (Boraginaceae). It has been recorded singly on *Rutidosis helichrysoides* (Asteraceae) and *Solanum ellipticum* (Solanaceae).

Distribution. *Inoma arrernte* sp. nov. is known only from four localities in central Australia, in the Alice Springs region of the Northern Territory (Fig. 13a). It has only been collected from mid-elevations (> ca. 500 m).

Inoma breviseta sp. nov.

(Figs. 1, 3, 12c-d, 13b)

Type material. Holotype: ♂, **AUSTRALIA: South Australia:** 8 km S of Martins Well, 31.40001°S 139.0753°E, 187 m, 08 Nov 2001, Cassis, Schuh, Schwartz, ex. *Eremophila* sp. (Myoporaceae; det. Field ID NSW666362) (AMNH_PBI 00013162) (AM).

Paratypes: **AUSTRALIA: Northern Territory:** 184 km E of Stuart Hwy on Lasseter Hwy, 25.23334°S 131.5703°E, 510 m, 31 Oct 2001, Cassis, Schuh, Schwartz, Silveira, Wall, ex, *Eremophila gilesii* F. Muell. (Myoporaceae; det. NSW Herbarium NSW666275), 1 ♀ (AMNH_PBI 00013656) (AM); 25.3 km NW of Bond Springs on Tanami Rd, 23.51668°S 133.6212°E, 746 m, 21 Oct 2001, Cassis, Schuh, Schwartz, Silveira, Wall, ex. *Eremophila gilesii* F. Muell. (Myoporaceae; det. NSW Herbarium NSW658289), 1 ♂ (AMNH_PBI 00010116), 1 ♀ (AMNH_PBI 00010119) (AM).

Additional material examined. AUSTRALIA: Northern Territory: 25.3 km NW of Bond Springs on Tanami Rd, 23.51668°S 133.6212°E, 746 m, 21 Oct 2001, Cassis, Schuh, Schwartz, Silveira, Wall, ex. *Eremophila gilesii* F. Muell. (Myoporaceae; det. NSW Herbarium NSW658289), 1 larva (AMNH_PBI 00010102) (AM).

Diagnosis. This species is recognised by the following combination of characters: medium size; mostly dark brown, with variegated colouration pattern (Fig. 1); head, pronotum and venter covered with moderately dense distribution of short, adpressed, thickened, scale-like setae (Fig. 1), absent from hemelytra; pronotum and hemelytra with major setiferous tubercles, with tuberculate base longer than seta (Fig. 1); cephalic spines moderately elongate (Fig. 1); occipital spines laterally arcuate (Fig. 1); medial spine apically bifurcate (Fig. 1); paranota biseriate, obliquely upturned (Fig. 1); longitudinal carinae narrow (Fig. 1); costal area uniseriate (Fig. 1); hemelytra with large areolae in costal and sutural areas, small areolae in subcostal and discoidal areas (Fig. 1).

Description of adult. Relatively small size, macropterous form (males 2.34-2.35, females 2.40-2.53) (Fig. 1).

COLOURATION. Body mostly dark brown with paler markings (Fig. 1). Head: dark brown to black; spines orange-brown; basal half of bucculae dark brown, rest orange-brown. Labium: dark brown. Antennae: AI and AII orange-brown; AIII-AIV missing. Pronotum: dark brown to black, posterolateral margins paler; collum orange-brown; paranota orange-brown and stramineous; carinae stramineous, median carina with a dark brown marking medially. Thoracic pleura and sterna: dark brown; sternal carinae lighter, orange-brown. Legs: mostly orange-brown; tarsi dark brown. Hemelytra: mottled colouration, stramineous, orange-brown to dark brown; sutural area dark brown. Abdomen: venter dark brown.

VESTITURE. Body with moderately dense distribution of short, lanceolate, adpressed, silvery, scale-like setae (Fig. 1); major setiferous tubercles present on pronotum and hemelytra, elongate base, seta shorter than tuberculate base. Head: minor setiferous tubercles present at base of cephalic spines. Antennae: AIII with minor setiferous tubercles, terminal seta with rounded apex. Pronotum: moderately dense distribution of scale-like setae, sparser posteriorly; major setiferous tubercles mostly in single rows, in two opposing rows on posterior half of paranotal margin. Thoracic pleura and sterna: scale-like setae dense, more sparse on supracoxal lobes and sterna; posteroventral margin of proepimeron with a few major setiferous tubercles, seta equal to tubercluate base; sternal carinae with single row of recurved, scale-like setae. Legs: femora and tibiae with rows of minor setiferous tubercles, terminal seta elongate, pale, erect, bristle-like. Hemelytra: without setae; major setiferous tubercles in two opposing rows along costal margin, extending to forewing apex. Abdomen: venter with moderately dense distribution of short, silvery, adpressed, scale-like setae.

STRUCTURE. Head: spines elongate; frontal spines diverging slightly; medial spine shorter, apex forked; occipital spines curved outward. Labium: short, not extending past mesosternum. Pronotum: disc convex, tumid; collum slightly enlarged; paranota biseriate, obliquely extended, inner row of areolae very small. Hemelytra: costal area uniseriate, areolae large; subcostal and discoidal areas with small areolae; sutural area with large areolae; hypocosta very narrow. Male genitalia: not examined.

MEASUREMENTS. Ranges of 2 ♂♂ and 2 ♀♀ given in Table 1.

Description of fifth instar larva (Fig. 3). COLOURATION. Dorsum orange-brown, with darker red-brown areas at base and apices of hemelytral lobes, abdominal venter, AIV, and tarsi.

VESTITURE AND STRUCTURE. Dorsum with moderate distribution of short, spine-like, pale cuticular outgrowths; pronotum with two pairs of elongate, medial processes; mesonotum, metanotum and abdominal tergite I with paired medial processes, elongate on mesonotum, short on metanotum and abdominal tergite I; abdominal tergites II, V, VI and VIII with single, elongate, medial process; lateral margins of pronotum and hemelytral lobes, and posterolateral corners of abdominal tergites with elongate processes projected laterally; processes covered with minor setiferous tubercles, terminal seta short, spine-like; medial cephalic spine bifurcate.

Differential diagnosis. This species can be distinguished by its short, adpressed, scale-like setae and the absence of any setae on the hemelytra. This species is similar to *I. fuscata* sp. nov. but differs by the setal characters above and also by being slightly smaller, in addition to having a bifurcate medial cephalic spine and a uniseriate costal area.

Etymology. Named for the short scale-like setae on the head, pronotum and venter of this species. Noun in apposition.

Biology. *Inoma breviseta* sp. nov. has been collected on *Eremophila gilesii* (Myoporaceae) in the Northern Territory (Fig. 12d), and an unidentified *Eremophila* species in South Australia.

Distribution. *Inoma breviseta* sp. nov. is known from three localities in central Australia (Fig. 13b), two in the Alice Springs region, and a disjunct location in the Flinders Ranges of South Australia. It is known from low to mid elevations (ca. 175-800 m). This species has been collected at the same locality as *Inoma fuscata* sp. nov. and *I. silveirae* sp. nov. (Fig. 12c).

Inoma fuscata sp. nov.

(Figs. 1, 3, 5, 10d-f & k, 11, 12c-d, 13a)

Type material. Holotype: ♂, **AUSTRALIA: Northern Territory:** 184 km E of Stuart Hwy on Lasseter Hwy, 25.23334°S 131.5703°E, 510 m, 31 Oct 2001, Cassis, Schuh, Schwartz, Silveira, Wall, ex. *Eremophila gilesii* F. Muell. (Myoporaceae; det. NSW Herbarium NSW666275) (AMNH_PBI 00010124) (AM).

Paratypes: **AUSTRALIA: Northern Territory:** 184 km E of Stuart Hwy on Lasseter Hwy, 25.23334°S 131.5703°E, 510 m, 31 Oct 2001, Cassis, Schuh, Schwartz, Silveira, Wall, ex. *Eremophila gilesii* F. Muell. (Myoporaceae; det. NSW Herbarium NSW666275), 6 ♂♂ (AMNH_PBI 00010123, AMNH_PBI 00010127, AMNH_PBI 00010129, AMNH_PBI 00010134, AMNH_PBI 00010138-AMNH_PBI 00010139), 12 ♀♀ (AMNH_PBI 00010121-AMNH_PBI 00010122, AMNH_PBI 00010126, AMNH_PBI 00010128, AMNH_PBI 00010130-AMNH_PBI 00010133, AMNH_PBI 00010135-AMNH_PBI 00010137, AMNH_PBI 00010141) (AM), 29 ♂♂ (AMNH_PBI 00179560-AMNH_PBI 00179562, AMNH_PBI 00179568-AMNH_PBI 00179593), 31 ♀♀ (AMNH_PBI 00179871-AMNH_PBI 00179901) (AMNH); 25.3 km NW of Bond Springs on Tanami Rd, 23.51668°S 133.6212°E, 746 m, 21 Oct 2001, Cassis, Schuh, Schwartz, Silveira, Wall, ex. *Eremophila gilesii* F. Muell. (Myoporaceae; det. NSW Herbarium NSW658289), 7 ♂♂ (AMNH_PBI 00010105, AMNH_PBI 00010108-AMNH_PBI 00010110, AMNH_PBI 00010112-AMNH_PBI 00010113, AMNH_PBI 00010118), 8 ♀♀ (AMNH_PBI 00010103-AMNH_PBI 00010104, AMNH_PBI 00010106-AMNH_PBI 00010107, AMNH_PBI 00010111, AMNH_PBI 00010114-AMNH_PBI 00010115, AMNH_PBI 00010117) (AM), 5 ♂♂ (AMNH_PBI 00179514-AMNH_PBI 00179517, AMNH_PBI 00179529), 10 ♀♀ (AMNH_PBI 00023899, AMNH_PBI 00179762-AMNH_PBI 00179767, AMNH_PBI 00179771-AMNH_PBI 00179773) (AMNH); 26.8 km W of Tanami Rd on Mt Wedge Station Rd, 22.50001°S 132.179°E, 589 m, 23 Oct 2001, Cassis, Schuh, Schwartz, Silveira, Wall, ex. *Eremophila gilesii* F. Muell. (Myoporaceae, det. NSW Herbarium, NSW658313), 1 ♀ (AMNH_PBI 00010120) (AM), 4 ♂♂ (AMNH_PBI 00023900-AMNH_PBI 00023902, AMNH_PBI 00179690), 3 ♀♀ (AMNH_PBI 00179977-AMNH_PBI 00179979) (AMNH); 71.6 km NE of Kings Canyon Resort, 23.80002°S 131.6635°E, 743 m, 03 Nov 2001, Cassis, Schuh, Schwartz, Silveira, Wall, ex. *Eremophila gilesii* F. Muell. (Myoporaceae, det. NSW Herbarium, NSW666317), 4 ♂♂ (AMNH_PBI 00179683-AMNH_PBI 00179686) (AMNH). **Queensland:** 14.2 km E of Charleville, 26.42171°S 146.3756°E, 375 m, 31 Oct 1998, Schuh, Cassis, Silveira, ex. *Eremophila freelingii* F. Muell. (Myoporaceae; det. NSW Herbarium NSW427507), 4 ♂♂ (AMNH_PBI 00010143-AMNH_PBI 00010144, AMNH_PBI 00010146, AMNH_PBI 00013643), 2 ♀♀ (AMNH_PBI 00010142, AMNH_PBI 00010145) (AM), 8 ♂♂ (AMNH_PBI 00179505-AMNH_PBI 00179508, AMNH_PBI 00179510-AMNH_PBI 00179513), 9 ♀♀ (AMNH_PBI 00179753-AMNH_PBI 00179761) (AMNH); 16 km W of Adavale, 25.9545°S 144.7206°E, 380 m, 01 Nov 1998, Schuh, Cassis, Silveira, ex. *Aristida jerichoensis* var. *subopinulifera* (Domin) Henrard (Poaceae; det. NSW Herbarium), 3 ♂♂ (AMNH_PBI 00010150, AMNH_PBI 00010152-AMNH_PBI 00010153), 4 ♀♀ (AMNH_PBI 00010147-AMNH_PBI 00010149, AMNH_PBI 00010151) (AM); 8.2 km E of Mungallala, 26.46401°S 147.6248°E, 560 m, 31 Oct 1998, Schuh, Cassis, Silveira, ex. *Acacia*

sp. (Fabaceae; det. NSW Herbarium), 1 ♂ (AMNH_PBI 00010163) (AM); Cunnamulla, 28.071°S 145.685°E, Oct 1941, N. Geary, 1 adult – sex unknown (AMNH_PBI 00010140) (AM).

Additional material examined. AUSTRALIA: Northern Territory: 184 km E of Stuart Hwy on Lasseter Hwy, 25.23334°S 131.5703°E, 510 m, 31 Oct 2001, Cassis, Schuh, Schwartz, Silveira, Wall, ex. *Eremophila gilesii* F. Muell. (Myoporaceae; det. NSW Herbarium NSW666275), 1 larva (AMNH_PBI 00010125) (AM).

Diagnosis. This species is recognised by the following combination of characters: medium size, red-brown to dark brown, with dark brown and cream patches on hemelytra and paranota (Fig. 1); head and AI almost black (Fig. 1); cephalic spines and rest of antennae lighter brown (Fig. 1); body covered with silvery, elongate, somewhat curly, woolly setae (Figs. 1, 5d), with setae on abdominal venter short, clavate and scale-like (Fig. 5h); pronotum and hemelytra with moderately elongate major setiferous tubercles, terminal seta straight and equal length or shorter than tuberculate base (Fig. 5c-e); major setiferous tubercles in one row on pronotum and hemelytra veins, in two opposing rows along costal margin, continuing to forewing apex (Fig. 5c-e); cephalic spines elongate, occipital spines strongly arcuate laterally (Fig. 5a); paranota and costal area biseriate (Figs. 1, 5d-e); paranotal and costal areas biseriate (Figs. 1, 5d); hemelytra with large areolae in costal and sutural areas, and smaller areolae in discoidal and subcostal areas (Figs. 1, 5e).

Description of adult. Moderate size, macropterous form (males 2.55-3.19, females 2.66-3.13) (Fig. 1).

COLOURATION. Head: dark brown; spines stramineous; bucculae mostly orange-brown, margins paler. Labium: dark brown. Antennae: mostly orange-brown; AIV dark brown. Pronotum: dark brown, medially orange-brown between carinae; collum cream and orange-brown along medial ridge and posteriorly; paranota mottled cream and dark brown; carinae cream and medially orange-brown. Thoracic pleura: mostly orange-brown, margins paler. Thoracic sterna: sternal carinae cream. Legs: mostly orange-brown; tarsi dark brown. Hemelytra: orange-brown with contrasting cream and dark brown markings on the costal area, sutural area and veins of the discoidal area. Abdomen: venter uniformly orange-brown.

VESTITURE. Woolly setae present on head, dorsum and thoracic pleura, moderately dense distribution, mostly elongate, silvery, curly, and slightly thickened (Fig. 5a-e). Major setiferous tubercles on pronotum and hemelytra elongate, terminal seta same length or shorter than tuberculate base (Fig. 5a-e). Head: minor setiferous tubercles present, on lower half of cephalic spines (Fig. 5a). Antennae: minor setiferous tubercles present on AIII, terminal seta elongate, apex rounded (Fig. 5b). Pronotum: major setiferous tubercles in single rows (Fig. 5d). Thoracic pleura and sterna: woolly setae on supracoxal lobes and sterna not as dense, shorter and thickener than pleural woolly setae; posteroventral margin of proepimeron with a few major setiferous tubercles; sternal carinae with single row of simple setae, rounded distally. Legs: femora with minor setiferous tubercles, terminal seta thickened, truncate apically, semi-erect, silvery, bristle-like; tibiae with rows of minor setiferous tubercles, terminal seta more elongate, pale and semi-erect. Hemelytra: major setiferous tubercles in two alternating rows along costal margin and extending to forewing apex (Fig. 5e). Abdomen: venter with moderately dense distribution of short, clavate, silvery, scale-like setae (Fig. 5h).

STRUCTURE. Head (Fig. 5a-c): spines greatly elongate (Fig. 5a); frontal spines parallel or converging slightly (Fig. 5a); medial spine straight (Fig. 5a); occipital spines strongly

curved outward (Fig. 5a). Labium: short, not extending past mesosternum. Antennae: AIV with elongate cylindrical base. Pronotum: disc convex (Fig. 1); collum moderately enlarged (Figs. 1, 5d); paranota obliquely extended, biseriate, areolae large (Figs. 1, 5d); carinae, areolae large (Figs. 1, 5d). Hemelytra: costal area biseriate, areolae large (Figs. 1, 5d); subcostal and discoidal areas with areolae smaller than costal area (Figs. 1, 5d); sutural area with large areolae (Figs. 1, 5d); hypocosta narrow (Fig. 5e). Legs: pretarsus (Fig. 5f). Male genitalia: pygophore (Fig. 5g); parameres with rounded sensory lobe, sensory lobe with greatly elongate setae, inner margin of parameres with short setae, dorsal surface of parameres smooth without minute setae (Fig. 10d-e); distal U-shaped endosomal sclerite with deep and rounded cleft, long basal branches, and a straight distal margin (Fig. 10f); with paired basal endosomal sclerites, elongate-ovate in shape (Fig. 10k). Female genitalia: subgenital plate subtriangular, not greatly elongate (Fig. 5h).

Description of fifth instar larva (Fig. 3). COLOURATION. Medium brown, with lighter yellow-brown areas along lateral portions of pronotum and abdominal tergites; apical portions of dorsal cuticular outgrowths, AIV and tarsi darkened.

VESTITURE AND STRUCTURE. Dorsum and thoracic pleura with moderate distribution of pale, stellate-shaped cuticular outgrowths, elongate and highly elevated above dorsum, apices with five short and rounded tips; pronotum with two pairs of medial processes; mesonotum, metanotum and abdominal tergite I with paired medial processes; abdominal tergites II, V, VI & VIII with single medial process; lateral margins of pronotum, forewing lobes and posterolateral corners of abdominal tergites with processes; all processes greatly elongate, projected dorsally and covered with minor setiferous tubercles; minor setiferous tubercles, terminal seta short with a broad cup-shaped apex.

MEASUREMENTS. Ranges of 10 ♂♂ and 10 ♀♀ given in Table 1.

Differential diagnosis. This species is uniformly darker than other *Inoma* species, with large dark-brown patches on the hemelytra and pronotum. It also has a dark-brown pronotal disc, head, and abdominal venter, but such colour patterning is common to other species of *Inoma*. There is some colour variation within populations from dark brown to almost black to medium red-brown. This species is similar in appearance to *I. breviseta* sp. nov., *I. kalbarri* sp. nov. and *I. stysi* sp. nov. In *I. fuscata* sp. nov., the dorsum has a moderately dense distribution of elongate, curly woolly setae and a straight medial spine; these characters clearly distinguish it from *I. breviseta* sp. nov. There are only two *Inoma* species (*I. fuscata* sp. nov. and *I. breviseta* sp. nov.) that possess distinctive short, clavate scale-like setae on the abdominal venter. *Inoma fuscata* sp. nov. can be distinguished from *I. stysi* sp. nov. by being larger, darker dorsally, and with a more linear and elongate body. *Inoma fuscata* sp. nov. can be distinguished from *I. kalbarri* sp. nov. by the biseriate paranota and costal area, and the entire costal area of the hemelytra with major setiferous tubercles. In addition, *I. fuscata* sp. nov. can be distinguished from both *I. kalbarri* sp. nov. and *I. stysi* sp. nov. by its greatly elongate cephalic spines, less dense distribution of woolly setae on head and pronotum, and the abdominal venter with short, clavate, scale-like, adpressed setae.

Etymology. This species is named for its fuscous colouration.

Biology. *Inoma fuscata* sp. nov. was collected on the emu bush species, *Eremophila gilesii* (Myoporaceae) in the Northern Territory (Fig. 12d) and *Eremophila freelingii* in Queensland. Single records from an *Acacia* sp. in Queensland and *Aristida jerichoensis* var. *subopinulifera*

(Poaceae) at Adavale in Queensland may represent 'sitting' records. These two *Eremophila* species are both small to medium shrubs, which are broadly sympatric in western Queensland, north-west New South Wales and southern Northern Territory, although ***E. gilesii*** is more broadly distributed longitudinally (Chinnock 2007). We have yet to establish if ***I. fuscata*** sp. nov. is found on both *Eremophila* species when they are locally sympatric.

Distribution. *Inoma fuscata* sp. nov. is known from eight localities in southwest Queensland and southern Northern Territory (Fig. 13a), with significant disjunction across the Simpson Desert. This species has been collected with ***I. breviseta*** sp. nov. and ***I. silveirae*** sp. nov. (Fig. 12c).

Inoma innamincka sp. nov.

(Figs. 1, 6, 10l, 13a)

Type material. Holotype: ♂, **AUSTRALIA: South Australia:** 17.6 km S of Innamincka, 27.88068°S 140.6712°E, 130 m, 06 Nov 1998, Schuh, Cassis, Silveira, ex. *Teucrium racemosum* R. Br. (Lamiaceae; det. NSW Herbarium NSW427991) (AMNH_PBI 00013139) (AM).

Paratypes: **AUSTRALIA: South Australia:** 17.6 km S of Innamincka, 27.88068°S 140.6712°E, 130 m, 06 Nov 1998, Schuh, Cassis, Silveira, ex. *Teucrium racemosum* R. Br. (Lamiaceae; det. NSW Herbarium NSW427991), 3 ♀♀ (AMNH_PBI 00013137-AMNH_PBI 00013138, AMNH_PBI 00013659) (AM).

Diagnosis. This species is recognised by the following combination of characters: small size (Fig. 1); ovoid body (Fig. 1); generally light-brown to stramineous colouration dorsally and dark brown venter (Fig. 1); body densely covered with short, curled, silvery, woolly setae (Figs. 1, 6a-f); minor setiferous tubercles densely distributed (Figs. 6a-e), terminal seta short and recurved, longer than tuberculate base (Figs. 6a-e); frontal cephalic spines elongate, medial and occipital spines stout (Fig. 6a); paranotal and costal areas uniseriate (Figs. 1, 6d-e); hemelytra of brachypters with large areolae in costal area, small in remainder (Figs. 1, 6e).

Description of adult. Small species, only brachypterous morph known (male 1.95, females 1.93-2.17) (Fig. 1).

COLOURATION. Head: medium brown, spines and bucculae stramineous. Labium: mostly dark brown. Antennae: mostly orange-brown, AIV dark brown. Pronotum: disc medium brown, remainder stramineous, light brown spot on apex of collum and middle of median carina. Thoracic pleura: red-brown with paler margins. Thoracic sterna: dark brown; sternal carinae stramineous. Legs: mostly orange-brown, slightly darker at base of femora; tarsi dark brown. Hemelytra: mostly patchy stramineous/cream and yellow-brown; darker orange brown patches medially on R+M vein, at junction of R+M and cubitus veins and on some horizontal areole margins in costal area. Abdomen: venter dark red-brown.

VESTITURE. Woolly setae present on head, dorsum and thoracic pleura, moderately dense distribution, setae short, curly, silvery, fine (Fig. 6a-e). Minor setiferous tubercles on pronotum and hemelytra with minute tuberculate base and short recurved seta, slightly longer than base; densely distributed (Fig. 6a-e). Head: minor setiferous tubercles present, covering entire cephalic spines (Fig. 6a). Antennae: minor setiferous tubercles present on AIII, terminal seta elongate with tapered apex. Pronotum: minor setiferous tubercles densely distributed, not in rows as such (Fig. 6d). Thoracic pleura and sterna: posteroventral margin of proepimeron with a few minor setiferous tubercles; sternal carinae with two rows of recurved scale-like setae. Legs: femora and tibiae with a dense distribution of short, weakly clavate, pale, scale-

like setae. Hemelytra: minor setiferous tubercles as on pronotum and extending to forewing apex (Fig. 6e). Abdomen: venter with moderately dense distribution of short, clavate, silvery, scale-like setae (Fig. 6f).

STRUCTURE. Head (Fig. 6a-d): frontal spines moderately elongate, converging slightly (Fig. 6a); medial spine stout, straight (Fig. 6a); occipital spines stout, parallel, directed forwards, straight (Fig. 6a). Labium: short, not extending past mesosternum. Antennae: AIV without elongate base. Pronotum: disc flat (brachypters); collum slightly enlarged, apex slightly rounded; paranota uniseriate, narrow, obliquely extended; carinae, areolae large (Fig. 6d). Hemelytra: brachypters (Fig. 6e); costal area uniseriate, areolae large (Fig. 6e); areolae small over remainder of hemelytra (Fig. 6e); hypocostal area wide, same width as costal area. Male genitalia: parameres with rounded sensory lobe, sensory lobe with elongate setae, inner margin of parameres with short setae, dorsal surface of parameres with broad distribution of minute setae; distal U-shaped endosomal sclerite moderately sclerotised, with shallow and rounded cleft, long basal branches, and a straight distal margin; paired basal endosomal sclerites present, semi-circular with small raised surface bumps (Fig. 10l). Female genitalia: subgenital plate triangular (Fig. 6f).

MEASUREMENTS. Ranges of 1 ♂ and 3 ♀♀ given in Table 1.

Differential diagnosis. *Inoma innamincka* sp. nov. is similar to *I. arrernte* sp. nov., but differs by the following character states: 1) slightly larger; 2) shorter and slightly less dense distribution of woolly setae; 3) very short curved terminal setae on minor setiferous tubercles; 4) darker brown abdomen, with short, clavate scale-like setae; and, 5) shorter labium, just reaching mesocoxae. This species is the only *Inoma* speices that is currently known from brachypterous specimens alone. Like *I. arrernte* sp. nov., it can be distinguished from *I. silveirae* sp. nov. by having minor setiferous tubercles, a slightly more elevated collum, and more stramineous or cream colouration.

Etymology. This species is named after the town of Innamincka, near the type locality. Noun in apposition.

Biology. *Inoma innamincka* sp. nov. is known only from the labiate species, *Teucrium racemosum* (Lamiaceae).

Distribution. This species is known only from the type locality, just south of Innamincka, South Australia (see Fig. 13a).

Inoma kalbarri sp. nov.

(Figs. 1, 7, 10g, 12e, 13b)

Type material. Holotype: ♂, **AUSTRALIA: Western Australia:** Kalbarri National Park, Z-Bend Road, 27.64166°S 114.4569°E, 450 m, 28 Oct 1996, Schuh and Cassis, ex. *Dicrastylis fulva* Harv. (Lamiaceae; det. WA Herbarium PERTH 05120500) (AMNH_PBI 00013655) (AM).

Paratypes: **AUSTRALIA: Western Australia:** Kalbarri National Park, Z-Bend Road, 27.64166°S 114.4569°E, 450 m, 28 Oct 1996, Schuh and Cassis, ex. *Dicrastylis fulva* Harv. (Lamiaceae, det. WA Herbarium PERTH 05120500), 2 ♂♂ (AMNH_PBI 00013129, AMNH_PBI 00013130), 6 ♀♀ (AMNH_PBI 00013124-AMNH_PBI 00013128, AMNH_PBI 00013654) (AM); 56.6 km W of Yalgoo, 28.42397°S 116.1233°E, 600 m, 27 Oct 1996, Schuh and Cassis, ex. *Dicrastylis fulva* forma *fulva* Harv. (Lamiaceae, det. WA Herbarium PERTH 05120632), 1 ♂ (AMNH_PBI 00013181) (AM); Moorine Rock, 11.7 km N of Great Eastern Hwy on Noongar Road, 31.22843°S 118.979°E, 345 m, 04 Dec 1997, Schuh, Cassis, Brailovsky, Asquith, ex. *Pityrodia teckiana* (F. Muell.) E. Pritz. (Lamiaceae, det. WA Herbarium, PERTH 05056004), 6 ♂♂ (AMNH_PBI 00179499-AMNH_PBI 00179504), 7 ♀♀ (AMNH_PBI 00179746-AMNH_PBI 00179752) (AMNH).

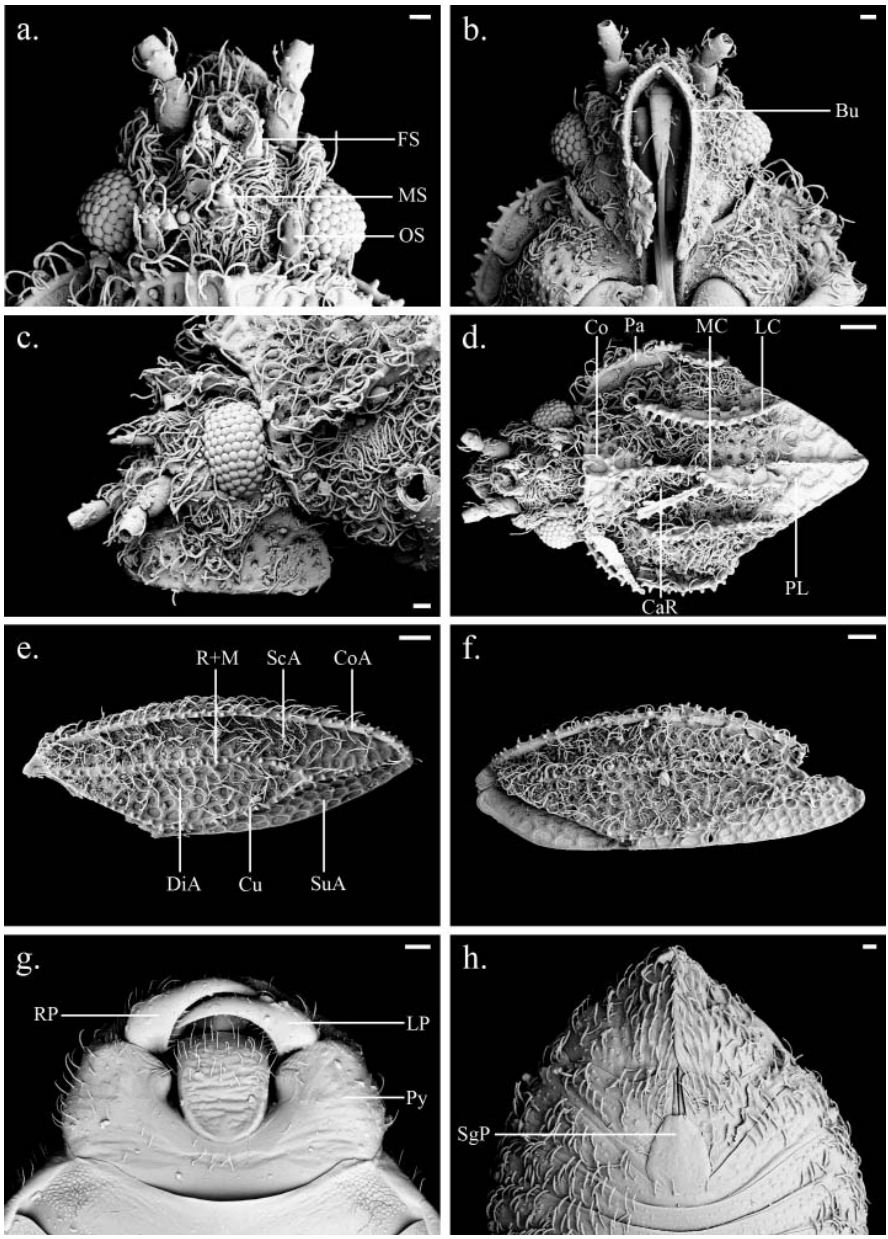

Fig. 4. *Inoma arrernte* sp. nov. a – head dorsal (♀, 30 μm); b – head ventral (♀, 30 μm); c – head lateral (♀, 30 μm); d – pronotum dorsal (♀, 100 μm); e – hemelytra (♂, 100 μm); f – hemelytra (♀, 100 μm); g – pygophore dorsal (♂, 30 μm); h – abdomen ventral (♀, 30 μm). Scales in brackets, measured in μm. FS, frontal spine; MS, medial spine; OS, occipital spine; Bu, bucculae; CaR, callar region; Co, collum; Pa, paranota; MC, median carina; LC, lateral carina; PL, posterior lobe; R+M, radius and media vein; Cu, cubitus vein; CoA, costal area; ScA, subcostal area; SuA, sutural area; DiA, discoidal area; RP, right paramere; LP, left paramere; Py, Pygophore; SgP, subgenital plate.

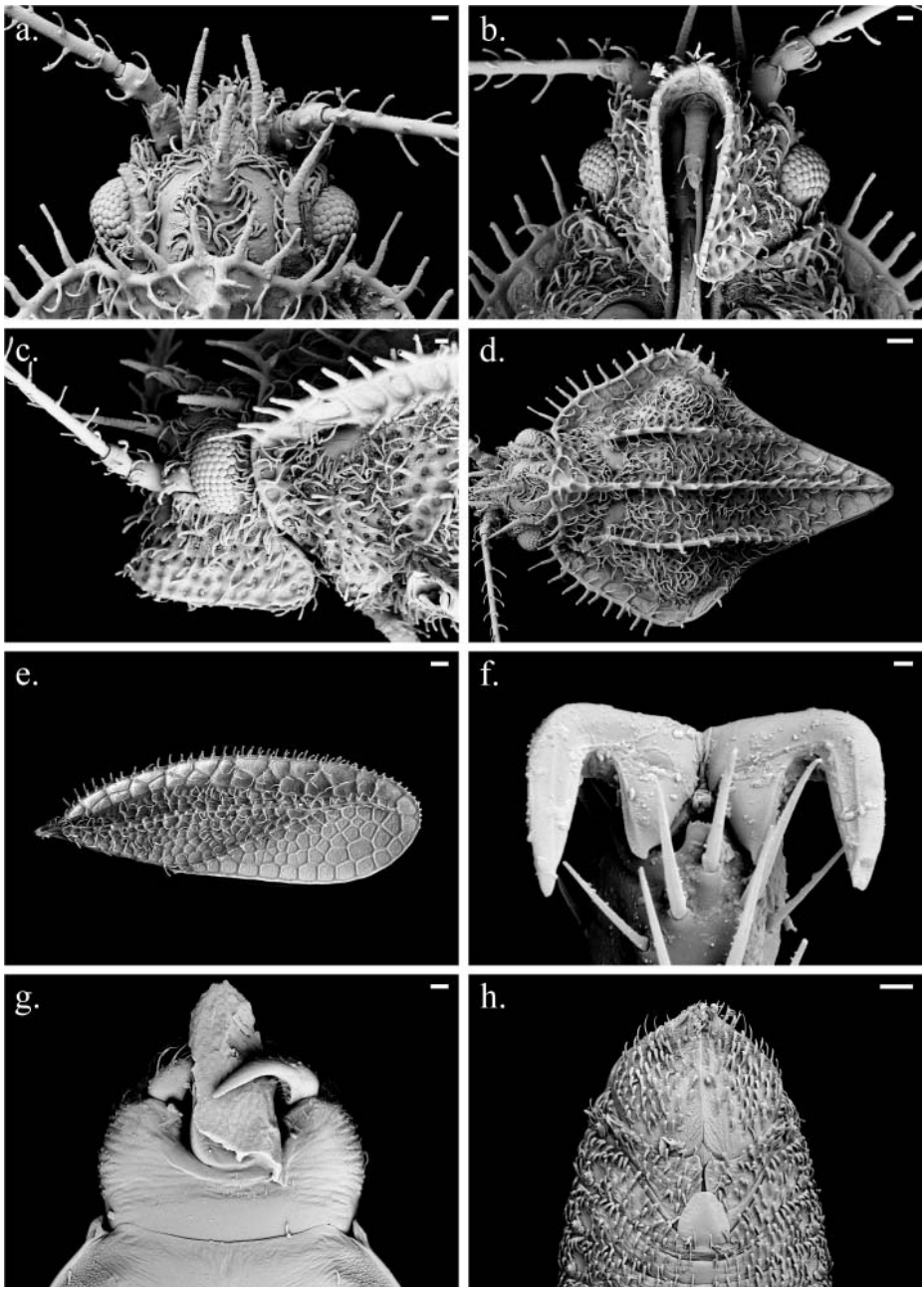

Fig. 5. *Inoma fuscata* sp. nov. a – head dorsal (♀, 30 µm); b – head ventral (♀, 30 µm); c – head lateral (♀, 30 µm); d – pronotum dorsal (♀, 100 µm); e – hemelytra (♀, 100 µm); f – tarsal claw (♀, 3 µm); g – pygophore dorsal (♂, 30 µm); h – abdomen ventral (♀, 100 µm). Scales in brackets, measured in µm.

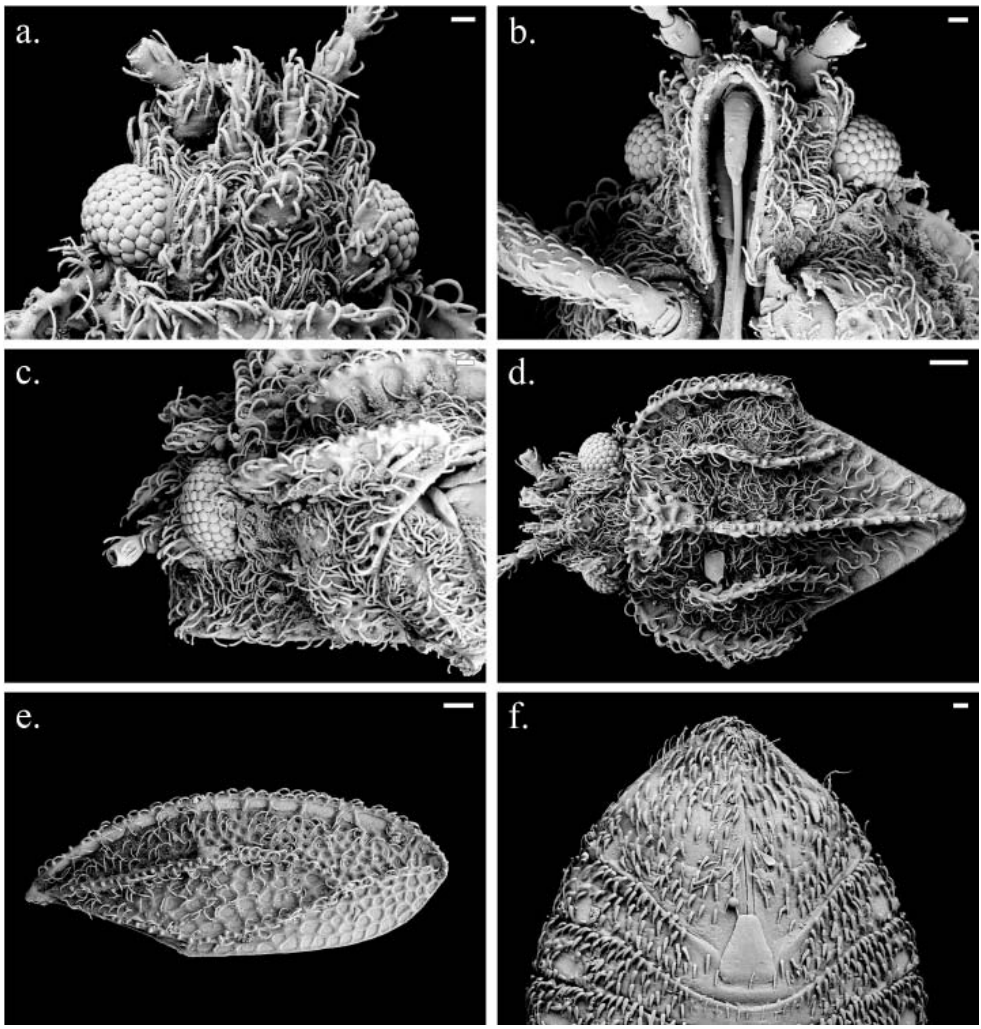

Fig. 6. *Inoma innamincka* sp. nov. a – head dorsal (♀, 30 μm); b – head ventral (♀, 30 μm); c – head lateral (♀, 30 μm); d – pronotum dorsal (♀, 100 μm); e – hemelytra (♀, 100 μm); f – genital segment of abdomen ventral (♀, 30 μm). Scales in brackets, measured in μm.

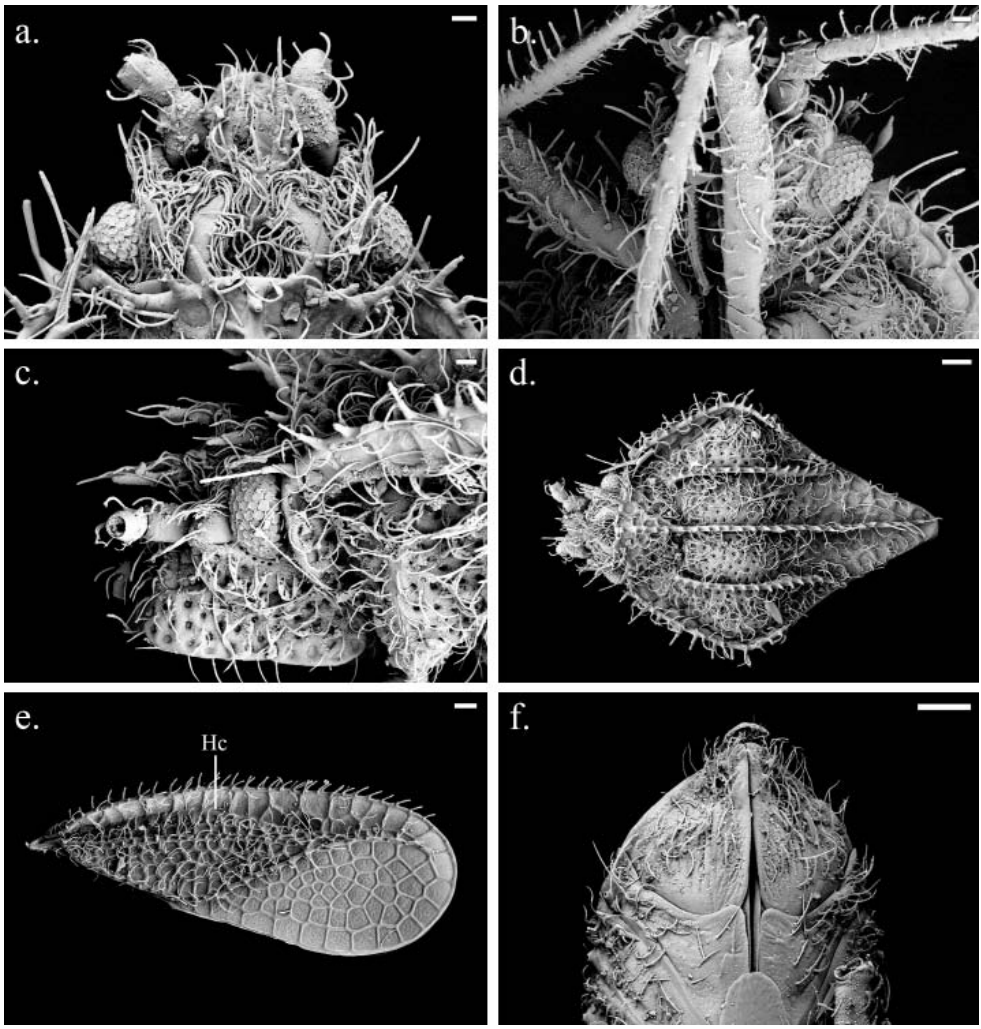

Fig. 7. *Inoma kalbarri* sp. nov. a – head dorsal (♀, 30 µm); b – head ventral (♂, 30 µm); c – head lateral (♀, 30 µm); d – pronotum dorsal (♀, 100 µm); e – hemelytra (♀, 100 µm); f – genital segment of abdomen ventral (♀, 100 µm). Scales in brackets, measured in µm. Hc, hypocostal vein.

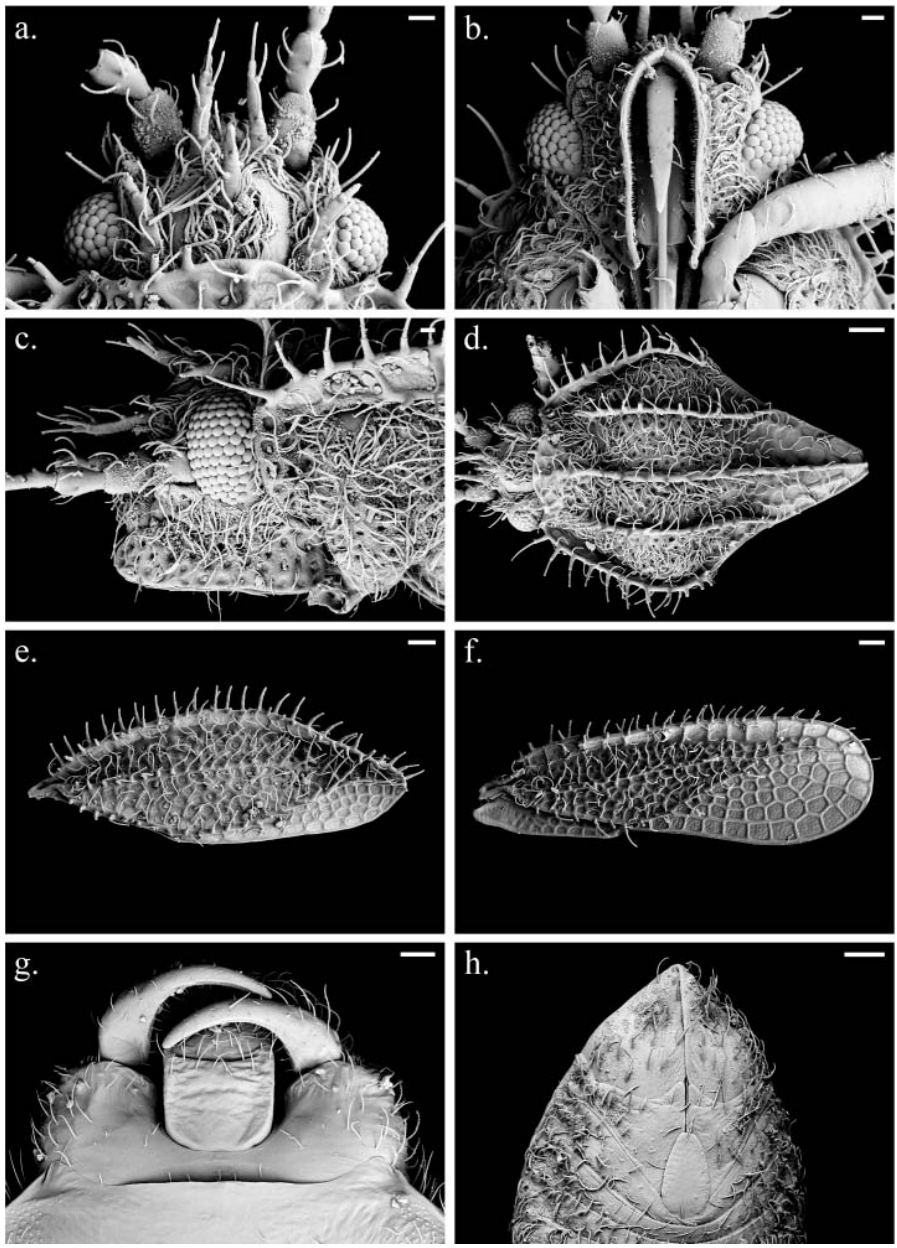

Fig. 8. *Inoma silveirae* sp. nov. a – head dorsal (♀, 30 μm); b – head ventral (♀, 30 μm); c – head lateral (♀, 20 μm); d – pronotum dorsal (♀, 100 μm); e – macropterous hemelytra (♂, 100 μm); f – brachypterous hemelytra (♀, 100 μm); g – pygophore dorsal (♂, 30 μm); h – genital segment of abdomen ventral (♀, 100 μm). Scales in brackets, measured in μm.

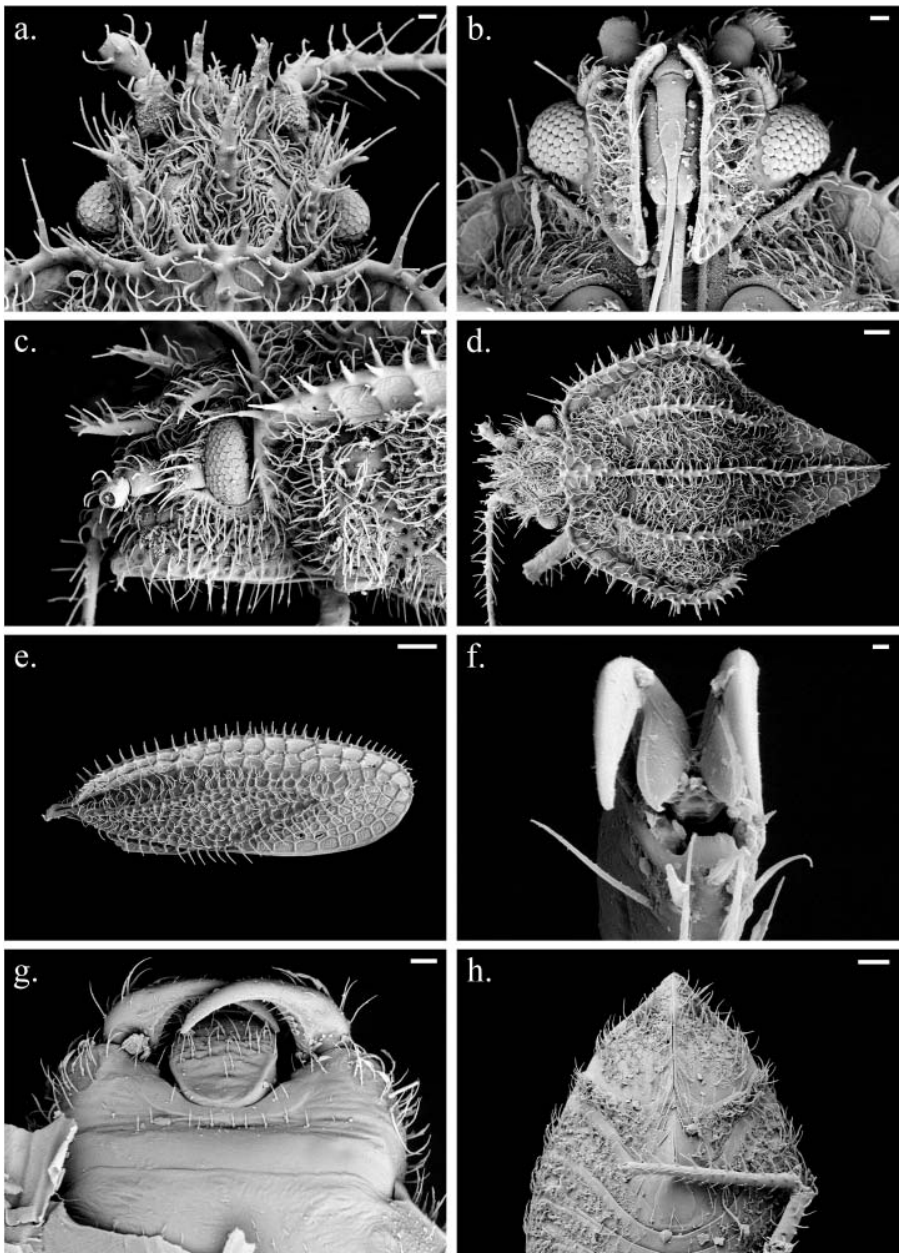

Fig. 9. *Inoma stysi* sp. nov. a – head dorsal (♀, 30 μm); b – head ventral (♂, 30 μm); c – head lateral (♀, 30 μm); d – pronotum dorsal (♀, 100 μm); e – hemelytra (♀, 200 μm); f – tarsal claw (♀, 3 μm); g – pygophore dorsal (♂, 30 μm); h – abdomen ventral (♀, 100 μm). Scales in brackets, measured in μm.

Diagnosis. *Inoma kalbarri* sp. nov. is recognised by the following combination of characters: medium size (Fig. 1); head and pronotum dark, with hemelytra more light brown with smaller dark brown patches (Fig. 1); body covered with elongate, curly, silvery woolly setae (Figs. 1, 7); elongate, semi-erect, hair-like setae on abdominal venter (Fig. 7f); pronotum and hemelytra with elongate major setiferous tubercles, terminal seta as long as tuberculate base (Figs. 1, 7d-e); cephalic spines elongate, occipital spines arcuate laterally (Fig. 7a); paranota upturned (Figs. 1, 7d); paranotal and costal area uniseriate (Figs. 1, 7d-e); hemelytra with large areolae in costal and sutural areas and smaller areolae in subcostal and discoidal areas (Figs. 1, 7d-e).

Description of adult. Moderate size, macropterous (males 2.38-2.56, females 2.58-2.77) and brachypterous (only one female examined) morphs (Fig. 1).

COLOURATION. Head: black; spines stramineous; bucculae, basal half medium brown, distal half paler orange-brown. Labium: dark brown. Antennae: mostly light brown; AIV dark brown, almost black. Pronotum: dark brown to black anterior half to humeral angle, posterior 1/2 mostly stramineous, orange-brown around median carina; collum, paranota and carinae stramineous. Thoracic pleura: dark brown with paler margins. Thoracic sterna: sternal carinae cream. Legs: mostly orange-brown; basal third to two-thirds of femora darker red-brown; tarsi dark brown to black. Hemelytra: mostly orange-brown with stramineous and dark-brown patches. Abdomen: venter uniformly dark brown, almost black.

VESTITURE. Woolly setae present on head, dorsum and thoracic pleura, moderately dense distribution, setae elongate, silvery, curly and fine (Fig. 7a-e). Major setiferous tubercles on pronotum and hemelytra elongate, terminal seta as long as or longer than tuberculate base (Fig. 7a-e). Head: minor setiferous tubercles present, covering entire cephalic spines (Fig. 7a). Antennae: minor setiferous tubercles present on AIII, terminal seta elongate with tapered apex. Pronotum: major setiferous tubercles in two opposing rows on posterior half of paranota, and in a single straight row on anterior half of paranota and entire carinae (Fig. 7d); terminal setae elongate on tubercles on anterior half of pronotum. Thoracic pleura and sterna: woolly setae as on dorsum; posteroventral margin of proepimeron without setiferous tubercles; sternal carinae with single row of hair-like setae. Legs: femora and tibiae with elongate bristle-like setae (Fig. 7b). Hemelytra: major setiferous tubercles in two opposing rows along costal margin, terminating before forewing apex (Fig. 7e). Abdomen: venter with moderately dense distribution of elongate, silvery, semi-erect, hair-like setae (Fig. 7f).

STRUCTURE. Head (Fig. 7a-c): cephalic spines moderately elongate (Fig. 7a); frontal spines converging slightly or parallel (Fig. 7a); medial spine straight (Fig. 7a); occipital spines weakly curved laterally (Fig. 7a). Labium: elongate, extending to abdomen. Pronotum: disc slightly tumid; collum slightly enlarged, paranota uniseriate, narrow, upturned; carinae areolae small (Fig. 7d). Hemelytra: Macropters (Fig. 1, 7e): costal area mostly uniseriate, biseriate distally where hypocostal vein bends near junction of R+M and cubitus veins (see Fig. 7e), areolae large; subcostal and discoidal areas with smaller areolae; sutural area with large areolae; hypocosta narrow. Brachypter: reduced sutural and costal areas; acutely rounded posteriorly; convex lateral margin; sutural area with small areolae; all other characters as above. Male genitalia: parameres with rounded sensory lobe, sensory lobe with elongate setae, inner margin of parameres with short setae, dorsal surface of parameres with a few

minute setae on sensory lobe, near paramere base; distal U-shaped endosomal sclerite with shallow and rounded cleft, short basal branches, and a sinuate distal margin; without paired basal endosomal sclerites; medial portion of phallotheca divided dorsally (Fig. 10g). Female genitalia: subgenital plate large, subtriangular (Fig. 7f).

MEASUREMENTS. Ranges of 3 ♂♂ and 6 ♀♀ given in Table 1.

Differential diagnosis. *Inoma kalbarri* sp. nov. is similar to *I. fuscata* sp. nov., and can be differentiated from it by the following characters: 1) shorter body length; 2) lighter hemelytra; 3) finer, slightly curlier, and longer woolly setae, more densely distributed; 4) shorter cephalic spines; 5) longer hair-like setae on abdominal venter; 6) uniseriate paranotal and costal areas; 7) incomplete margin of setiferous tubercles on the hemelytra (ending before forewing apex); 8) more rounded hemelytra; and, 9) hemelytral sutural area broader. *Inoma kalbarri* sp. nov. is similar to *I. silveirae* sp. nov. in having a flatter body (lateral view), and uniseriate upturned paranotal and costal areas. *Inoma kalbarri* sp. nov. is also distinguished from *I. silveirae* sp. nov. by the broader hemelytra, as well as being significantly larger and also darker, especially on the pronotum.

Etymology. This species is named after the type locality. Noun in apposition.

Biology. *Inoma kalbarri* sp. nov. is known from the two labiate species, *Dicrastylis fulva* (Lamiaceae) (Fig. 12e) and *Pityrodia teckiana* (Lamiaceae).

Distribution. *Inoma kalbarri* sp. nov. is known from three localities in southwest Western Australia, one on the coast in the Kalbarri National Park, a second further inland near Yalgoo, and the third even further inland and further south at Moorine Rock (Fig. 13b).

Inoma multispinosa Hacker, 1927

(Figs. 2, 10a-c,m, 13a)

Inoma multispinosa Hacker, 1927: 25, pl. ix (sp. nov., habitus).

Inoma multispinosa: Drake & Ruhoff (1965: 249, pl. 42) (catalogue, habitus); Cassis & Gross (1995: 417) (catalogue; lectotype designation)

Type material. Lectotype: ♂, **AUSTRALIA: Queensland:** Brisbane, 27.46666°S 153.01666°E, 27 Aug 1911, H. Hacker (label data: holotype He3170 Brisbane H. Hacker 21/8/11; on a card with a paralectotype female specimen), (AMNH_PBI 00201268) (QM).

Paralectotypes: ♀, **AUSTRALIA: Queensland:** Brisbane, 27.46666°S 153.01666°E, 27 Aug 1911, H. Hacker (label data: holotype He3170 Brisbane H. Hacker 21/8/11; on a card with lectotype male specimen), (AMNH_PBI 00201268) (QM); 2 ♀♀, Sunnybank, 27.56666°S 153.05°E, 12 Sep 1926, H. Hacker (label data: He3170 3; brachypterous females on same card), (AMNH_PBI 00201267) (QM). Types seen.

Additional material examined. **AUSTRALIA: Australian Capital Territory:** Canberra, 35.33333°S 149.16666°E, 26 Aug 1990, T. J. Henry, *Dillwynia retorta* (Fabaceae: Faboideae), 7 ♂♂ (AMNH_PBI 00191263-AMNH_PBI 00191269), 26 ♀♀ (AMNH_PBI 00191261, AMNH_PBI 00191262, AMNH_PBI 00191270-AMNH_PBI 00191293) (USNM). **Queensland:** Sunnybank, 27.579°S 153.059°E, 12 Aug 1928, H. Hacker, 1 ♀ (AMNH_PBI 00037150) (QM). **South Australia:** Mount Lofty, 34.974°S 138.709°E, 12 Mar 1964, G. F. Gross, 11 ♂♂ (AMNH_PBI 00016128-AMNH_PBI 00016138), 3 ♀♀ (AMNH_PBI 00016125-AMNH_PBI 00016127) (SAMA).

Diagnosis. *Inoma multispinosa* is recognised by the following combination of characters: small size (Fig. 2); brachypterous or macropterous (Fig. 2); distinctive light cream and red-brown banding colouration on hemelytra (Fig. 2); pronotum and hemelytra with elongate major setiferous tubercles, sparsely distributed, with minute, barely visible terminal seta (Fig. 2); head, dorsal surface of pronotum and hemelytra, thoracic pleura and abdominal venter glabrous (Fig. 2); cephalic spines elongate, occipital spines laterally curved, medial spine

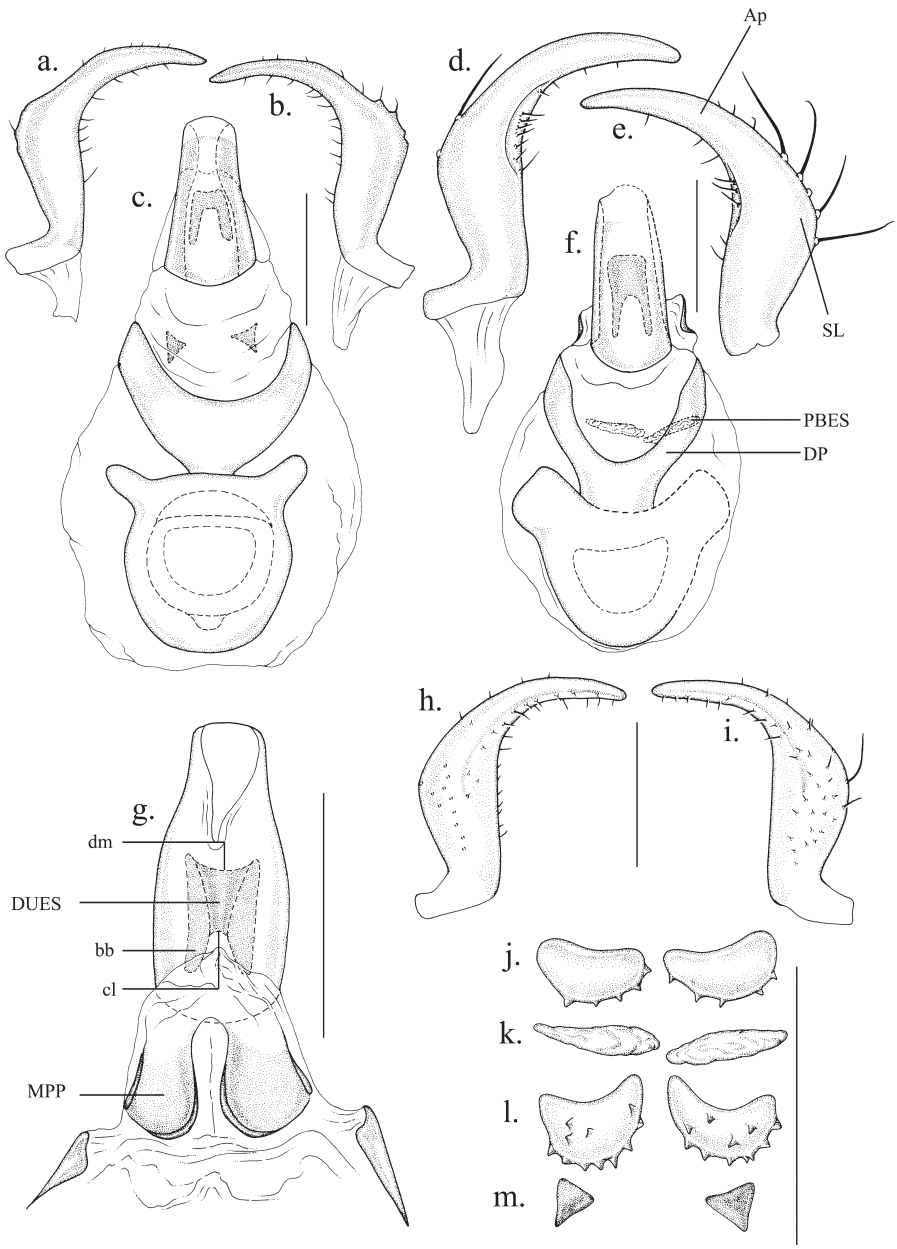

Fig. 10. Male genitalia of *Inoma* species. a-c, m – *I. multispinosa* Hacker, 1927; d-f, k – *I. fuscata* sp. nov.; g – *I. kalbarri* sp. nov.; h-i – *I. silveirae* sp. nov.; j – *I. arrernte* sp. nov.; l – *I. innamincka* sp. nov. a, d, h – right paramere, dorsal view; b, e, i – left paramere, dorsal view; c, f – aedeagus, dorsal view; g – aedeagus, ventral view; j-m – paired basal endosomal sclerites. Scale = 0.1 mm. Ap, apophysis; SL, sensory lobe; PBES, paired basal endosomal sclerites; DP, dorsal plate; DUES, dorsal U-shaped endosomal sclerite; dm, distal margin; bb, basal branch; cl, cleft; MPP, medial portion of phallotheca.

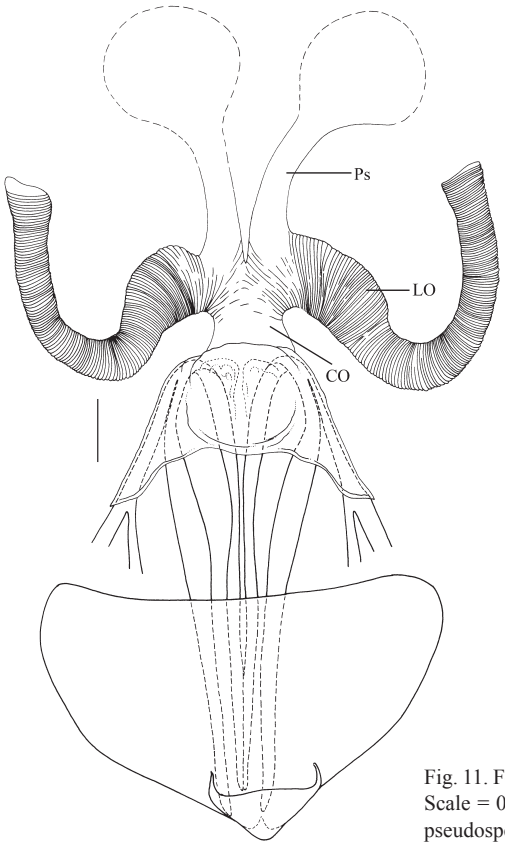

Fig. 11. Female genitalia of *Inoma fuscata* sp. nov. in dorsal view. Scale = 0.1 mm. CO, common oviduct; LO, lateral oviduct; Ps, pseudospermatheca.

forked (Fig. 2); paranotal and costal areas uniseriate and narrow (Fig. 2); paranota obliquely extended; hemelytra with large areolae in coastal area and remainder smaller (Fig. 2).

Redescription of adult. Small size, macropterous (males 2.22-2.40, females 2.36-2.46) and brachypterous (males 1.94-2.17, females 1.97-2.18) morphs (Fig. 2).

COLOURATION. Head: red-brown; bucculae stramineous posteriorly; cephalic spines stramineous in basal half, red-brown in distal half. Antennae: mostly orange-brown; AIV dark brown. Pronotum: disc red-brown; posterior lobe stramineous with dark brown margin; collum stramineous; paranota stramineous with red-brown margin. Thoracic pleura and sterna: pleura red-brown with paler margins; sternal carinae stramineous. Legs: mostly orange-brown; tarsi dark brown. Hemelytra: stramineous and red-brown horizontal broad banding; sutural area more orange-brown; junction of R+M and cubitus veins dark brown. Abdomen: venter uniformly very dark brown, almost black.

VESTITURE. Major setiferous tubercles present, elongate, terminal seta minute, barely visible, tubercles sparsely distributed, mostly in single rows on pronotum and hemelytra. Head, dorsum, thoracic pleura and abdominal venter without setae. Head: cephalic spines with minor setiferous tubercles present at base, terminal seta obsolete. Antennae: AIV with

simple, bristle-like setae, rest glabrous. Pronotum: major setiferous tubercles in single rows, absent from ventral margin of paranota. Thoracic pleura and sterna: posteroventral margin of proepimeron with a few major setiferous tubercles; sternal carinae with minor setiferous tubercles, terminal seta obsolete. Legs: femora and tibiae with a few minor setiferous tubercles, terminal seta obsolete. Hemelytra: major setiferous tubercles in two opposing rows on posterior half of costal area, in single rows elsewhere; major setiferous tubercles on costal margin not extending to forewing apex. Abdomen: venter glabrous.

STRUCTURE. Head: spines elongate; frontal spines slightly divergent, widely separated; medial spine forked; occipital spines outwardly curved, erect. Labium: elongate, extending to metacoxae. Antennae: AIV compact, with short base. Pronotum: callar region strongly convex, tumid, in both macropters and brachypters; collum moderately enlarged; paranota uniseriate, narrow, obliquely extended, areolae of carinae small. Hemelytra: Macropters: costal area uniseriate, areolae large; subcostal area broad, as wide as discoidal area; subcostal, discoidal and sutural areas with mostly small areolae; hypocosta broad, as wide as costal area. Brachypters: reduced sutural and costal areas; sutural area greatly reduced; all other characters as for macropters. Male genitalia: parameres with slightly angular sensory lobe, sensory lobe with short setae, inner margin and outer margin of apophysis with short setae, dorsal surface of paramere smooth, without minute setae (Fig. 10a-b); distal U-shaped endosomal sclerite with deep and squared cleft, long basal branches, and a sinuate distal margin (Fig. 10c); with paired basal endosomal sclerites, very small, sub-triangular in shape (Fig. 10m).

MEASUREMENTS. Ranges of 9 ♂♂ and 2 ♀♀ macropters and 7 ♂♂ and 10 ♀♀ brachypters given in Table 2.

Differential diagnosis. *Inoma multispinosa* is distinguished from all other *Inoma* species by the following characters: 1) lack of woolly or scale-like setae; 2) distinctive cream and reddish brown colour banding on hemelytra; 3) sparsely distributed, elongate setiferous tubercles with minute terminal seta; and, 4) deeply bifurcate, medial cephalic spine.

Biology. *Inoma multispinosa* was collected on the pea species, *Dillwynia retorta* (Fabaceae), in the Australian Capital Territory. No hosts were recorded for specimens collected in Queensland. The host plant for this species is found in heathlands and dry sclerophyll forests, and is generally limited to the east of the Great Dividing Range, from south-east Queensland south to Victoria (CHAH 2008; Australia's Virtual Herbarium).

Distribution. *Inoma multispinosa* is known from temperate to subtropical areas of the eastern seaboard of Australia, ranging from south-east Queensland to Canberra in the Australian Capital Territory (Fig. 13a). It is distinguished biogeographically from all other species of *Inoma*, which are known from arid Australia to the drier climes of coastal south-west Western Australia.

Inoma silveirae sp. nov.

(Figs. 2-3, 8, 10h-i, 12a-c,f, 13b)

Type material. Holotype: ♂, **AUSTRALIA: Northern Territory:** 8.8 km N of Mt Wedge Stn Rd junction on Tanami Rd, 22.63335°S 132.3525°E, 598 m, 23 Oct 2001, Cassis, Schuh, Schwartz, Silveira, Wall, (AMNH_PBI 00013151) (AM).

Paratypes: **AUSTRALIA: Northern Territory:** 184 km E of Stuart Hwy on Lasseter Hwy, 25.23334°S 131.5703°E, 510 m, 31 Oct 2001, Cassis, Schuh, Schwartz, Silveira, Wall, ex. *Dicrastylis beveridgei* var. *beveridgei* F. Muell. (Lamiaceae), 3 ♂♂ (AMNH_PBI 00013165-AMNH_PBI 00013167), 5 ♀♀ (AMNH_PBI 00010198-AMNH_PBI 00010200, AMNH_PBI 00013168-AMNH_PBI 00013169) (AM); 193 km E of Stuart Hwy on Lasse-

ter Hwy, 25.21667°S 131.4776°E, 519 m, 31 Oct 2001, Cassis, Schuh, Schwartz, Silveira, Wall, ex. *Dicrastylis beveridgei* F. Muell. (Lamiaceae, det. NSW Herbarium, NSW666267), 2 ♂♂ (AMNH_PBI 00179526-00179527), 2♀♀ (AMNH_PBI 00179774-179775), ex. *Alyogyne pinoniana* (Gaudich.) Fryxell (Malvaceae, det. NSW Herbarium, NSW666268), 1 ♂ (AMNH_PBI 00179528) (AMNH); 26.8 km W of Tanami Rd on Mt Wedge Station Rd, 22.50001°S 132.179°E, 589 m, 23 Oct 2001, Cassis, Schuh, Schwartz, Silveira, Wall, 1 ♀ (AMNH_PBI 00013170) (AM); 35.4 km W of Uluru at Kata Tjuta jct on Lasseter Hwy, 25.33334°S 130.6892°E, 592 m, 01 Nov 2001, Cassis, Schuh, Schwartz, Silveira, Wall, ex. *Dicrastylis gilesii* var. *gilesii* f. *densa* Munir (Lamiaceae; det. NSW Herbarium NSW666280), 2 ♀♀ (AMNH_PBI 00016121, AMNH_PBI 00016122) (AM); 8.8 km N of Mt Wedge Stn Rd jct on Tanami Rd, 22.63335°S 132.3525°E, 598 m, 23 Oct 2001, Cassis, Schuh, Schwartz, Silveira, Wall, *Dicrastylis lewellinii* (F. Muell.) F. Muell. (Lamiaceae; det. NSW Herbarium NSW658320), 13 ♂♂ (AMNH_PBI 00010164-AMNH_PBI 00010168, AMNH_PBI 00010181-AMNH_PBI 00010185, AMNH_PBI 00010203-AMNH_PBI 00010205), 16 ♀♀ (AMNH_PBI 00010169-AMNH_PBI 00010180, AMNH_PBI 00010186-AMNH_PBI 00010188, AMNH_PBI 00013644) (AM), 19 ♂♂ (AMNH_PBI 00179546-AMNH_PBI 00179559, AMNH_PBI 00179563-AMNH_PBI 00179567), 23 ♀♀ (AMNH_PBI 00179848-AMNH_PBI 00179870) (AMNH). **Queensland:** 75.7 km W of Windorah, 25.37703°S 141.9457°E, 250 m, 03 Nov 1998, Schuh, Cassis, Silveira, ex. *Newcastelia cephalantha* F. Muell. (Lamiaceae; det. NSW Herbarium NSW427984), 31 ♂♂ (AMNH_PBI 00010219, AMNH_PBI 00010225, AMNH_PBI 00010227, AMNH_PBI 00010230-AMNH_PBI 00010232, AMNH_PBI 00010234-AMNH_PBI 00010235, AMNH_PBI 00010239, AMNH_PBI 00010241-AMNH_PBI 00010244, AMNH_PBI 00010247, AMNH_PBI 00010252-AMNH_PBI 00010253, AMNH_PBI 00010256-AMNH_PBI 00010257, AMNH_PBI 00010261, AMNH_PBI 00010263-AMNH_PBI 00010265, AMNH_PBI 00010269, AMNH_PBI 00013140-AMNH_PBI 00013147), 29 ♀♀ (AMNH_PBI 00010220-AMNH_PBI 00010222, AMNH_PBI 00010226, AMNH_PBI 00010228-AMNH_PBI 00010229, AMNH_PBI 00010233, AMNH_PBI 00010236-AMNH_PBI 00010238, AMNH_PBI 00010240, AMNH_PBI 00010245-AMNH_PBI 00010246, AMNH_PBI 00010248-AMNH_PBI 00010251, AMNH_PBI 00010254-AMNH_PBI 00010255, AMNH_PBI 00010258-AMNH_PBI 00010260, AMNH_PBI 00010262, AMNH_PBI 00010266-AMNH_PBI 00010268, AMNH_PBI 00013148-AMNH_PBI 00013150), 1 adult – sex unknown (AMNH_PBI 00010223) (AM), ex. *Dicrastylis lewellinii* (F. Muell.) F. Muell. (Lamiaceae, det. Det: Royal Bot Gard. NSW NSW427989), 19 ♂♂ (AMNH_PBI 00179523-AMNH_PBI 00179525, AMNH_PBI 00179530-AMNH_PBI 00179545), 21 ♀♀ (AMNH_PBI 00179776-AMNH_PBI 00179791, AMNH_PBI 00179843-AMNH_PBI 00179847) (AMNH). **South Australia:** 18.8 km NW of Cordillo Downs Homestead, 26.64315°S 140.4723°E, 140 m, 05 Nov 1998, Schuh, Cassis, Silveira, ex. *Ptilotus obovatus* (Gaudich.) F. Muell. (Amaranthaceae; det. NSW Herbarium NSW427988), 1 ♂ (AMNH_PBI 00010196) (AM). **Western Australia:** 31.7 km W of Agnew toward Sandstone, 27.96227°S 120.4277°E, 800 m, 26 Oct 1996, Schuh and Cassis, ex. *Dicrastylis morrisonii* Munir (Lamiaceae; det. WA Herbarium PERTH 05095204), 3 ♂♂ (AMNH_PBI 00010195, AMNH_PBI 00013163-AMNH_PBI 00013164), 5 ♀♀ (AMNH_PBI 00010190-AMNH_PBI 00010194) (AM); 82.2 km W of Agnew toward Sandstone, 28.01057°S 119.9455°E, 650 m, 26 Oct 1996, Schuh and Cassis, 2 ♂♂ (AMNH_PBI 00016176, AMNH_PBI 00016177) (AM), 1 ♂ (AMNH_PBI 00179687) (AMNH).

Additional material examined. AUSTRALIA: Queensland: 75.7 km W of Windorah, 25.37703°S 141.9457°E, 250 m, 03 Nov 1998, Schuh, Cassis, Silveira, ex. *Newcastelia cephalantha* F. Muell. (Lamiaceae; det. NSW Herbarium NSW427984), 1 larva (AMNH_PBI 00010224) (AM); 82.2 km W of Agnew toward Sandstone, 28.01057°S 119.9455°E, 650 m, 26 Oct 1996, Schuh and Cassis, 1 larva (AMNH_PBI 00016178) (AM).

Diagnosis. *Inoma silveirae* sp. nov. is recognised by the following combination of characters: small size (Fig. 2); brachypterous or macropterous (Fig. 2); mostly cream or yellow-brown with some darker brown patches on paranota and forewings (Fig. 2); body covered with elongate, curly woolly setae (Figs. 2, 8), more silvery on head and pronotum, more golden on hemelytra; setae on abdominal venter elongate, fine and hair-like (Fig. 8h); pronotum and hemelytra with elongate major setiferous tubercles (Figs. 2, 8d-f), terminal seta as long or longer than tuberculate base; cephalic spines moderately elongate, occipital spines outcurved (Fig. 8a); paranota upturned (Figs. 2, 8d); paranota and longitudinal carinae narrow (Fig. 8d);

paranotal and coastal areas uniseriate (Fig. 8d); macropters with large areolae in coastal and sutural areas (Fig. 8f); and, brachypters with small areolae in discoidal and subcostal areas (Fig. 8e).

Description of adult. Small size, macropterous (males 2.08-2.37, females 2.14-2.39) and brachypterous (males 1.7-2.03, females 1.82-2.07) forms (Fig. 2).

COLOURATION. Head: dark brown (almost black); spines yellow-brown; bucculae yellow-brown. Labium: dark brown. Antennae: mostly yellow-brown; AIV dark brown (almost black). Pronotum: mostly medium brown, anteriorly dark brown to black and posteriorly paler yellow-brown; collum, paranota and carinae pale yellow-brown. Thoracic pleura: dark brown, with paler margins. Thoracic sterna: sternal carinae cream. Legs: mostly yellow-brown; tarsi dark brown to black. Hemelytra: mostly pale yellow-brown, sometimes with variegated appearance and dark brown markings on areole margins of costal and discoidal areas. Abdomen: venter uniformly light or dark brown.

VESTITURE. Woolly setae on head, dorsum and thoracic pleura, densely distributed, elongate, curly, more silvery on head and pronotal callar region, more golden elsewhere. Major setiferous tubercles on pronotum and hemelytra elongate, terminal seta as long or often longer than tuberculate base, sometimes slightly curved, not oriented regularly (Fig. 8a-f). Head: woolly setae silvery; minor setiferous tubercles covering entire cephalic spines (Fig. 8a). Antennae: minor setiferous tubercles present on AIII, terminal seta elongate with tapered apex. Pronotum: woolly setae silvery; major setiferous tubercles in two opposite rows on paranota, single rows on rest of pronotum (Fig. 8d). Thoracic pleura and sterna: woolly setae densely distributed; posteroventral margin of proepimeron with a few, very small, minor setiferous tubercles, terminal seta elongate; sternal carinae with single row of hair-like setae. Legs: femora and tibiae with elongate, pale hair-like setae in rows, shorter on ventral surface. Hemelytra: yellow-gold woolly setae similar to pronotum, same as on hemelytra; major setiferous tubercles in two opposing rows along costal margin and extending to forewing apex (Fig. 8e-f). Abdomen: venter with moderately dense distribution of elongate, silvery, semi-erect, hair-like setae (Fig. 8h).

STRUCTURE. Head (Fig. 8a-c): cephalic spines elongate (Fig. 8a); frontal spines parallel (Fig. 8a); medial spine straight (Fig. 8a); occipital spines, weakly curved outwards (Fig. 8a). Labium: elongate, extending to base of abdomen. Antennae: AIV compact, with short base. Pronotum: callar region slightly convex (macropters) or flat (brachypters) (see Fig. 2 – lateral views); collum slightly enlarged; paranota uniseriate, narrow, upturned; carinae, areolae small (Fig. 8d). Hemelytra: Macropters (Fig. 8f): costal area uniseriate, areolae large; subcostal and discoidal areas with smaller areolae; sutural area with large areolae; hypocosta wide, roughly equal width to costal area. Brachypters (Fig. 8e): reduced sutural and costal areas; acutely rounded posteriorly; convex lateral margin; sutural area with small areolae; all other characters as above (Fig. 8e). Male genitalia: pygophore (Fig. 8g); parameres with rounded sensory lobe, sensory lobe with elongate setae, margins of apophysis with short setae, dorsal surface of parameres with broad distribution of minute setae (Fig. 10h-i); distal U-shaped endosomal sclerite with deep and rounded cleft, elongate basal branches, and a straight distal margin; without paired basal endosomal sclerites. Female genitalia: subgenital plate elongate, subtriangular (Fig. 8h).

MEASUREMENTS. Ranges of 10 ♂♂ and 8 ♀♀ macropters and 10 ♂♂ and 10 ♀♀ brachypters given in Table 2.

Description of fifth instar larva (Fig. 3). COLOURATION: yellow to stramineous, with darkened areas on pretarsi, tip of abdomen, tip of labium, and AIV.

VESTITURE AND STRUCTURE: Dorsum with a moderate distribution of stellate-shaped cuticular outgrowths, elongate and greatly elevated above dorsum, apex with four rounded tips; pronotum with two pairs of medial processes; mesonotum, metanotum and abdominal tergite I with paired, medial processes; TII, V, VI & VIII with single, medial process; lateral margins of pronotum, hemelytral lobes, and posterolateral angles of abdominal tergites with processes; all processes greatly elongate, projected dorsally and covered with minor setiferous tubercles; setiferous tubercles, terminal seta short with a broad cup-shaped apex.

Differential diagnosis. This species is similar in size and colouration to *I. arrernte* sp. nov. and *I. innamincka* sp. nov., but is most readily recognised by its small size, stramineous colouration of the dorsum, and elongate major setiferous tubercles on the lateral margins of the pronotum and hemelytra.

Etymology. This species is named in honour of Rossana Silveira, one of the collectors who has greatly contributed to Australian true bug collections, between 1998-2003.

Biology. *Inoma silveirae* sp. nov. is found on a variety of host plants, including *Newcastelia cephelantha* (Lamiaceae) and *Dicrastylis lewellinii* (Lamiaceae) in Queensland, *Dicrastylis lewellinii, Dicrastylis gilesii* var.*gilesii* (Fig. 12b), *Dicrastylis beveridgei* var. *beveridgei* in Northern Territory and *Dicrastylis morrisonii* in Western Australia (Fig. 12f). In addition, single specimens were collected from *Ptilotus obovatus* (Amaranthaceae) in South Australia, and *Alyogyne pinoniana* (Malvaceae) in the Northern Territory, which may be sitting records.

Distribution. *Inoma silveirae* sp. nov. is widespread in semi-arid and arid Australia, from nine largely disjunct localities in four states, ranging across western Queensland to central Australia (including southern Northern Territory and northern South Australia), with a widely separated population in the south-central Western Australia (Fig. 13b). This species has been collected with *I. fuscata* sp. nov. and *I. breviseta* sp. nov. in the Northern Territory and *I. stysi* sp. nov. in Western Australia (Fig. 12c).

Inoma solusa sp. nov.

(Figs. 2, 13b)

Type material. HOLOTYPE: ♂, **AUSTRALIA: NORTHERN TERRITORY:** 10.4 km N of Ross Hwy on Arltunga Claraville Rd, 23.53334°S 134.509°E, 640 m, 26 Oct 2001, Cassis, Schuh, Schwartz, Silveira, Wall (AMNH_PBI 00016124) (AM).

Diagnosis. *Inoma solusa* sp. nov. is recognised by the following combination of characters: moderate size (Fig. 2); rather uniform light brown dorsal colouration, with dark brown head and pronotal callar region (Fig. 2); head and pronotum with dense elongate, curly, silvery woolly setae; hemelytra almost glabrous; abdominal venter with elongate, straight setae; pronotum and hemelytra with uniform distribution of short major setiferous tubercles; cephalic spines elongate, occipital spines outwardly curved; paranota biseriate with medial cells much smaller than lateral cells; costal area biseriate with moderately large areolae; subcostal, discoidal and sutural areas all with moderately sized areolae.

Table 1. Measurements of ten characters for *Inoma arrernte* sp. nov., *I. breviseta* sp. nov., *I. fuscata* sp. nov., *I. innamincka* sp. nov. and *I. kalbarri* sp. nov. See Materials and methods for character descriptions; n – number of specimens measured; Max – maximum measurement, Min – minimum measurement, and Std Dev. – standard deviation.

		BL	HL	HW	PL	PW	IOD	AI	AII	AIII	AIV
arrernte											
macropters											
male (n = 1)		2.34	0.20	0.97	0.41	0.87	0.23	0.09	0.10	0.56	0.15
female (n = 1)		2.43	0.19	1.06	0.42	0.89	0.26	0.09	0.09	0.51	0.12
brachypters											
male (n = 10)	Min:	1.75	0.14	0.68	0.37	0.51	0.19	0.04	0.06	0.54	0.10
	Mean:	1.82	0.20	0.74	0.39	0.56	0.21	0.09	0.08	0.56	0.15
	Max:	1.93	0.25	0.81	0.44	0.58	0.24	0.13	0.10	0.60	0.20
	Std Dev.:	0.06	0.04	0.04	0.02	0.02	0.02	0.02	0.01	0.02	0.03
female (n = 10)	Min:	1.79	0.16	0.77	0.39	0.57	0.18	0.07	0.07	0.38	0.11
	Mean:	1.90	0.48	1.06	0.42	0.63	0.23	0.09	0.09	0.47	0.15
	Max:	2.01	3.06	3.17	0.45	0.71	0.25	0.13	0.11	0.53	0.20
	Std Dev.:	0.06	0.91	0.74	0.02	0.05	0.02	0.02	0.01	0.05	0.03
breviseta											
male (n = 2)	Min:	2.34	0.13	1.07	0.42	0.71	0.25	0.09	0.10	0.72	0.15
	Mean:	2.35	0.14	1.08	0.43	0.74	0.25	0.09	0.11	0.76	0.19
	Max:	2.35	0.15	1.08	0.44	0.76	0.25	0.09	0.12	0.80	0.22
	Std Dev.:	0.01	0.02	0.00	0.01	0.03	0.00	0.00	0.01	0.06	0.05
female (n = 2)	Min:	2.40	0.17	1.07	0.42	0.73	0.26	0.07	0.07	0.58	0.12
	Mean:	2.46	0.18	1.11	0.43	0.77	0.26	0.07	0.08	0.58	0.12
	Max:	2.53	0.20	1.15	0.44	0.81	0.26	0.08	0.09	0.58	0.12
	Std Dev.:	0.09	0.02	0.06	0.02	0.05	0.00	0.01	0.01	–	–
fuscata											
male (n = 10)	Min:	2.55	0.13	1.14	0.43	0.77	0.23	0.08	0.08	0.93	0.24
	Mean:	2.96	0.19	1.34	0.48	0.89	0.26	0.11	0.10	1.02	0.27
	Max:	3.19	0.24	1.43	0.52	1.04	0.29	0.15	0.13	1.09	0.31
	Std Dev.:	0.19	0.03	0.10	0.03	0.08	0.02	0.02	0.01	0.06	0.03
female (n = 10)	Min:	2.66	0.18	1.25	0.43	0.80	0.25	0.07	0.08	0.72	0.15
	Mean:	2.94	0.21	1.37	0.47	0.89	0.27	0.11	0.09	0.84	0.19
	Max:	3.13	0.24	1.45	0.51	0.98	0.30	0.13	0.10	0.94	0.23
	Std Dev.:	0.17	0.02	0.08	0.02	0.06	0.02	0.02	0.01	0.08	0.03
innamincka											
male (n = 1)		1.95	0.19	0.85	0.42	0.66	0.22	0.10	0.08	0.53	0.18
female (n = 3)	Min:	1.93	0.20	0.86	0.41	0.65	0.22	0.07	0.06	0.43	0.16
	Mean:	2.07	0.21	0.91	0.44	0.69	0.24	0.09	0.07	0.44	0.17
	Max:	2.17	0.22	0.97	0.47	0.74	0.25	0.10	0.07	0.46	0.19
	Std Dev.:	0.13	0.01	0.06	0.03	0.04	0.02	0.02	0.01	0.02	0.02
kalbarri											
male (n = 3)	Min:	2.38	0.15	1.06	0.33	0.73	0.21	0.07	0.07	0.72	0.00
	Mean:	2.49	0.17	1.09	0.37	0.76	0.22	0.09	0.08	0.72	–
	Max:	2.56	0.19	1.12	0.40	0.80	0.22	0.10	0.08	0.72	0.00
	Std Dev.:	0.10	0.02	0.03	0.04	0.03	0.01	0.02	0.01	–	–
female (n = 6)	Min:	2.58	0.19	1.11	0.41	0.77	0.23	0.07	0.07	0.61	0.18
	Mean:	2.68	0.22	1.15	0.42	0.81	0.24	0.08	0.08	0.63	0.19
	Max:	2.77	0.26	1.22	0.45	0.84	0.25	0.10	0.09	0.65	0.20
	Std Dev.:	0.06	0.02	0.05	0.01	0.02	0.01	0.01	0.01	0.02	0.01

Table 2. Measurements of ten characters for *I. multispinosa* Hacker, 1927, *I. silveirae* sp. nov., *I. solusa* sp. nov. and *I. stysi* sp. nov. See Materials and methods for character descriptions; n – number of specimens measured; Max – maximum measurement, Min – minimum measurement, and Std Dev. – standard deviation.

		BL	HL	HW	PL	PW	IOD	AI	AII	AIII	AIV
multispinosa											
macropters	Min:	2.22	0.13	0.99	0.37	0.73	0.18	0.05	0.05	0.72	0.21
male (n = 9)	Mean:	2.32	0.18	1.03	0.39	0.78	0.22	0.07	0.07	0.78	0.21
	Max:	2.40	0.21	1.07	0.41	0.83	0.26	0.10	0.09	0.85	0.21
	Std Dev.:	0.06	0.02	0.03	0.01	0.03	0.03	0.01	0.01	0.09	–
female (n = 2)	Min:	2.36	0.15	1.10	0.40	0.85	0.20	0.06	0.05	0.57	0.14
	Mean:	2.41	0.17	1.10	0.40	0.86	0.22	0.07	0.05	0.60	0.17
	Max:	2.46	0.18	1.11	0.40	0.87	0.25	0.09	0.06	0.63	0.20
	Std Dev.:	0.07	0.02	0.01	0.00	0.02	0.03	0.02	0.00	0.04	0.04
brachypters											
male (n = 7)	Min:	1.94	0.18	0.94	0.37	0.70	0.18	0.05	0.06	0.60	0.14
	Mean:	2.03	0.20	0.99	0.39	0.73	0.21	0.07	0.07	0.65	0.17
	Max:	2.17	0.23	1.08	0.43	0.75	0.25	0.09	0.08	0.69	0.21
	Std Dev.:	0.08	0.02	0.05	0.02	0.02	0.02	0.01	0.01	0.03	0.02
female (n = 10)	Min:	1.97	0.19	0.97	0.37	0.73	0.19	0.05	0.06	0.51	0.17
	Mean:	2.07	0.21	1.06	0.40	0.77	0.23	0.69	0.07	0.58	0.19
	Max:	2.18	0.24	1.12	0.44	0.81	0.27	6.33	0.09	0.72	0.21
	Std Dev.:	0.07	0.02	0.05	0.02	0.03	0.02	1.98	0.01	0.06	0.01
silveirae											
macropters	Min:	2.08	0.08	0.91	0.38	0.62	0.18	0.06	0.08	0.53	0.17
male (n = 10)	Mean:	2.25	0.16	0.99	1.19	0.69	0.20	0.10	0.09	0.60	0.19
	Max:	2.37	0.20	1.11	8.27	0.78	0.24	0.12	0.11	0.67	0.23
	Std Dev.:	0.11	0.04	0.07	2.49	0.05	0.02	0.02	0.01	0.04	0.02
female (n = 8)	Min:	2.14	0.15	0.89	0.37	0.64	0.18	0.03	0.05	0.39	0.14
	Mean:	2.26	0.19	0.98	0.39	0.68	0.20	0.08	0.08	0.49	0.18
	Max:	2.39	0.21	1.07	0.40	0.71	0.23	0.12	0.10	0.61	0.21
	Std Dev.:	0.09	0.02	0.06	0.01	0.03	0.02	0.03	0.01	0.08	0.03
brachypters											
male (n = 10)	Min:	1.74	0.14	0.74	0.35	0.54	0.19	0.08	0.07	0.47	0.14
	Mean:	1.88	0.17	0.87	0.38	0.58	0.21	0.09	0.09	0.55	0.18
	Max:	2.03	0.23	0.96	0.41	0.63	0.23	0.14	0.11	0.68	0.23
	Std Dev.:	0.11	0.03	0.07	0.02	0.03	0.02	0.02	0.01	0.06	0.03
female (n = 10)	Min:	1.82	0.13	0.86	0.38	0.61	0.19	0.04	0.05	0.46	0.14
	Mean:	1.95	0.17	0.92	0.40	0.63	0.23	0.09	0.08	0.50	0.19
	Max:	2.07	0.20	0.97	0.41	0.68	0.25	0.14	0.10	0.56	0.22
	Std Dev.:	0.09	0.02	0.03	0.01	0.02	0.02	0.03	0.02	0.03	0.02
solusa											
male (n = 1)		2.48	0.19	1.11	0.42	0.81	0.23	0.07	0.09	0.73	2.48
stysi											
male (n = 5)	Min:	2.59	0.15	1.09	0.43	0.80	0.22	0.08	0.07	0.70	0.20
	Mean:	2.87	0.20	1.30	0.48	0.93	0.25	0.11	0.09	0.84	0.27
	Max:	3.27	0.24	1.39	0.52	1.02	0.29	0.13	0.10	0.94	0.33
	Std Dev.:	0.28	0.04	0.13	0.04	0.08	0.02	0.02	0.02	0.09	0.07
female (n = 9)	Min:	2.74	0.16	1.31	0.47	0.95	0.27	0.08	0.08	0.64	0.13
	Mean:	2.87	0.22	1.42	0.49	1.02	0.29	0.11	0.09	0.73	0.20
	Max:	3.00	0.28	1.48	0.50	1.10	0.31	0.14	0.12	0.80	0.24
	Std Dev.:	0.08	0.04	0.06	0.01	0.05	0.01	0.02	0.01	0.07	0.04

Description. Moderate size, macropterous form (male 2.48) (Fig. 2).

COLOURATION. Head: dark brown, almost black; cephalic spines yellow-brown; bucculae dark-brown with paler margins. Antennae: orange-brown (AIV missing). Pronotum: callar region dark brown, almost black; posterior lobe yellow-brown; paranota, pronotal longitudinal carinae and collum yellow to orange-brown with a few small red-brown spots on margins. Thoracic pleura and sterna: dark brown; sternal carinae yellow-brown. Legs: mostly orange-brown; tarsi dark brown, almost black. Hemelytra: mostly yellow to orange-brown, with a few red-brown patches on margins, and in sutural area. Abdomen: venter dark brown.

VESTITURE. Woolly setae on head, dorsum and thoracic pleura, moderately densely distributed, elongate, curly and silvery. Major setiferous tubercles on pronotum and hemelytra, short and densely distributed, terminal seta no longer than tuberculate base. Head: minor setiferous tubercles covering most of cephalic spines. Antennae: minor setiferous tubercles present on AIII, terminal seta elongate with tapered apex. Pronotum: major setiferous tubercles in opposing rows on paranota and paranotal carinae. Thoracic pleura and sterna: woolly setae straighter than on pronotum; posteroventral margin of proepimeron with a few major setiferous tubercles; sternal carinae with two rows of hair-like setae. Legs: femora and tibiae with minor setiferous tubercles, terminal seta mixed short and long, bristle-like and pale. Hemelytra: woolly setae almost absent; major setiferous tubercles in opposing rows on costal margins and veins, thinning apically on costal margin. Abdomen: venter with elongate, pale, straight, semi-erect, hair-like setae.

STRUCTURE. Head: spines elongate; frontal spines parallel; medial spine straight; occipital spines curved outwards. Labium: short; just reaching mesocoxae. Antennae: AIV unknown. Pronotum: callar region convex, tumid; collum moderately enlarged; paranota biseriate, obliquely extended, medial row of areolae small, large laterally; carinae areolae small. Hemelytra: costal area biseriate, areolae moderately large; subcostal, discoidal and sutural areas with moderately large areolae; hypocosta narrow. Male genitalia: not examined.

MEASUREMENTS. Measure of 1 ♂ given in Table 2.

Differential diagnosis. *Inoma solusa* sp. nov. is similar to *I. stysi* sp. nov., differing by the following characters: 1) uniform distribution of short setiferous tubercles; 2) hemelytra almost glabrous; and, 3) greatly elongate and strongly curved occipital cephalic spines, extending beyond lateral margins of eyes.

Etymology. This species name is inspired by the Latin adjective *solus*, *-a*, *-um*, meaning alone, as it is described from a single specimen, however, the word *solusa* is created as combination of letters; noun in apposition.

Biology. No host record with specimen. Possibly from *Eremophila*, but not confirmed.

Distribution. This species is known from central Australia, restricted to the Northern Territory (Fig. 13b).

Inoma stysi sp. nov.

(Figs. 2, 9, 12g, 13b)

Type material. Holotype: ♂, **AUSTRALIA: Western Australia:** 31.7 km W of Agnew toward Sandstone, 27.96227°S 120.4277°E, 800 m, 26 Oct 1996, Schuh and Cassis, ex. *Eremophila forrestii* F. Muell. (Myoporaceae; det. WA Herbarium PERTH 05054788) (AMNH_PBI 00013662) (AM).

Paratypes: **AUSTRALIA: Northern Territory:** 13.5 km E of Stuart Hwy on Horseshoe Bend Rd, 25.13334°S 133.2999°E, 464 m, 28 Oct 2001, Cassis, Schuh, Schwartz, Silveira, Wall, ex. *Eremophila macdonnellii* F. Muell.

(Myoporaceae, det. NSW Herbarium NSW658390), 3 ♂♂ (AMNH_PBI 00179738-AMNH_PBI 00179740) (AMNH). **Western Australia:** Great Northern Highway, 5km N of Munjina – Wittenoom Rd intersection, 3.5km W of rd, 22.205°S 118.74555°E, 31 May 2004, M. Bulbert & N. Tatarnic, 1 ♀ (AMNH_PBI 00016123) (AM); 31.7 km W of Agnew toward Sandstone, 27.96227°S 120.4277°E, 800 m, 26 Oct 1996, Schuh and Cassis, ex. *Eremophila forrestii* F. Muell. (Myoporaceae; det. WA Herbarium PERTH 05054788), 1 ♂ (AMNH_PBI 00013180), 8 ♀♀ (AMNH_PBI 00013171-AMNH_PBI 00013177, AMNH_PBI 00013663) (AM); 46.5 km W of Yalgoo, 28.41302°S 116.2151°E, 600 m, 27 Oct 1996, Schuh and Cassis, ex. *Eremophila forrestii* F. Muell. (Myoporaceae; det. WA Herbarium PERTH 05120705), 1 ♂ (AMNH_PBI 00013182), 2 ♀♀ (AMNH_PBI 00013178, AMNH_PBI 00013179) (AM); 82.2 km W of Agnew toward Sandstone, 28.01057°S 119.9455°E, 650 m, 26 Oct 1996, Schuh and Cassis, 1 ♂ (AMNH_PBI 00179689) (AMNH).

Diagnosis. This species is recognised by the following combination of characters: medium size (Fig. 2); minor sexual dimorphism, male with a very dark pronotal callar region and hemelytra markings, larger eyes and hemelytra, female paler, hemelytra slightly smaller in sutural area and less rounded apically, eyes very small (Fig. 2); body covered with elongate, silvery setae (Fig. 9a-e); setae on abdominal venter elongate and semi-erect (Fig. 9h); pronotum (Fig. 9d) and hemelytra (Fig. 9e) with moderately elongate major setiferous tubercles, terminal seta no longer than tuberculate base on pronotum and costal margins, much longer than base on hemelytral veins (Fig. 9e), with greatly elongate terminal seta anteriorly on paranota (Fig. 9a); cephalic spines elongate, occipital spines outcurved (Fig. 9a); paranota (Fig. 9d) and costal areas (Fig. 9e) biseriate, paranota obliquely extended; hemelytra with large areolae in costal area, rest generally small (Fig. 9e).

Description of adult. Moderate size, macropterous form (males 2.59-3.27, females 2.74-3.00) (Fig. 2).

COLOURATION. Head: dark brown, almost black; spines stramineous; bucculae mostly orange brown, margins paler. Labium: mostly dark brown. Antennae: AI and AII red/orange brown; AIII yellow-brown; AIV dark brown, almost black. Pronotum: callar region dark brown, almost black, lighter posteriorly; posterior lobe stramineous; collum, paranota and carinae stramineous with light to medium brown patches along margins. Thoracic pleura: mostly dark brown, supracoxal lobes lighter red (medium)-brown. Thoracic sterna: dark brown, almost black, sterna carinae stramineous. Legs: mostly yellow/orange-brown, basal two-thirds of femora sometimes darker red-brown; tarsi dark brown. Hemelytra: patchwork; stramineous, yellowy and orange-brown and dark-brown markings. Abdomen: venter uniformly dark brown. Female generally lighter; pronotal callar region red-brown; legs orange-brown; hemelytra more uniform yellow and orange brown with red-brown patches.

VESTITURE. Woolly setae present on head, dorsum and thoracic pleura, moderately dense distribution, elongate, curly, silvery and slightly thickened. Major setiferous tubercles on pronotum and hemelytra, moderately elongate, terminal seta mostly short, no longer than tuberculate base (Fig. 9a-e). Head: minor setiferous tubercles covering cephalic spines (Fig. 9a). Antennae: minor setiferous tubercles present on AIII, terminal seta elongate with tapered apex (Fig 9a). Pronotum: major setiferous tubercles in two opposing rows on collum, paranota and carinae (Fig. 9d); first anterior tubercle on paranota with greatly elongate straight terminal seta (Fig. 9a). Thoracic pleura and sterna: woolly setae straighter on pleura than pronotum; sternal carinae with two-rows of hair-like setae. Legs: femora and tibiae with minor setiferous tubercles, terminal seta elongate, erect, pale and bristle-like. Hemelytra: major setiferous tubercles in two opposing rows along costal margin, extending to forewing apex; major setiferous tubercles on hemelytra veins in single row, terminal seta greatly elongate,

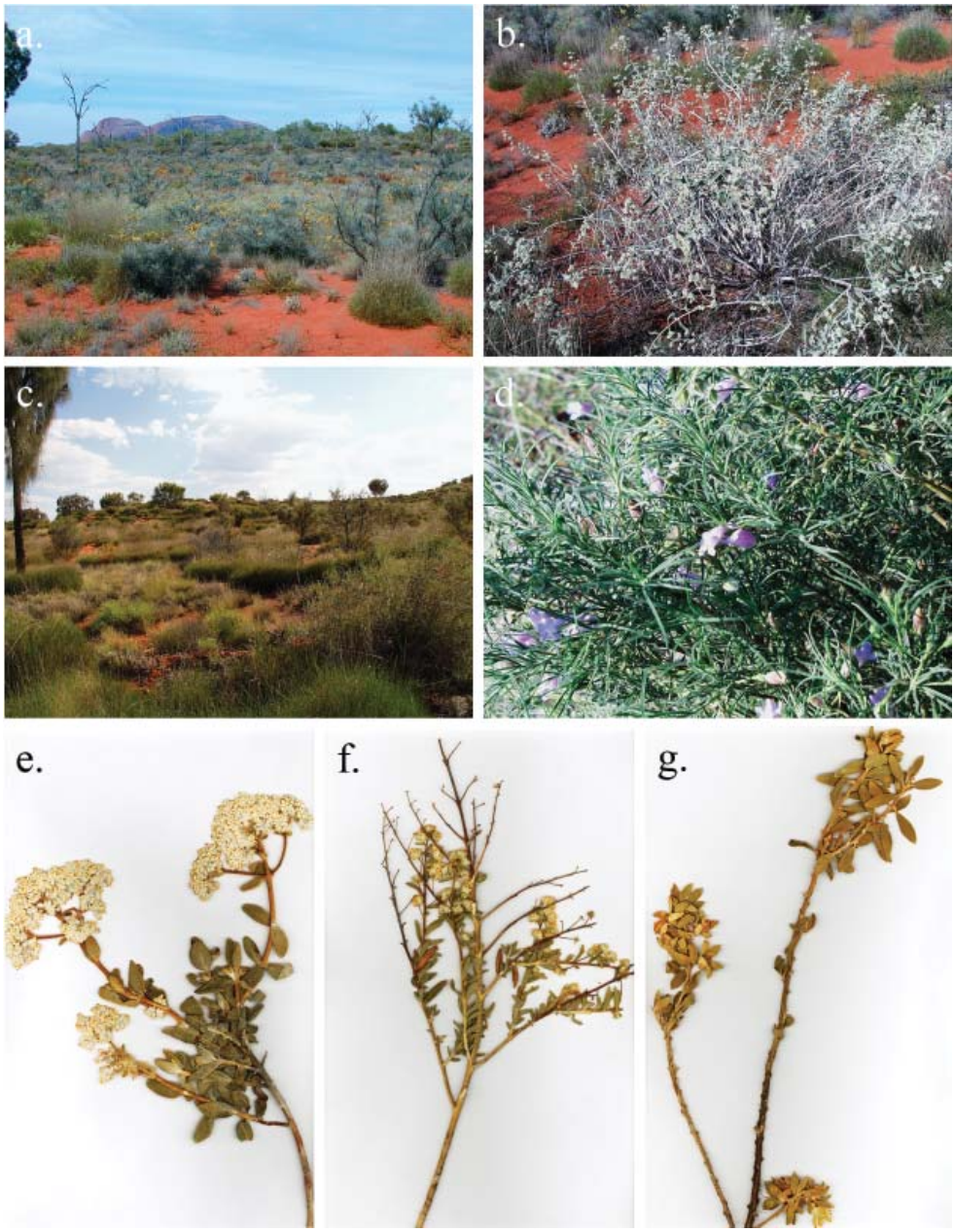

Fig. 12. a – locality for *Inoma silveirae* sp. nov.: Northern Territory, 35.4 km W of Uluru at Kata Tjuta junction on Lasseter Highway; b – *Dicrastylis gilesii* var. *gilesii*, host plant of *I. silveirae* sp. nov.; c – locality for *I. breviseta* sp. nov., *I. fuscata* sp. nov. and *I. silveirae* sp. nov.: Northern Territory, 184 km E of Stuart Hwy on Lasseter Hwy.; d – *Eremophila gilesii*, host plant of *I. breviseta* sp. nov. and *I. fuscata* sp. nov.; e – *Dicrastylis fulva*, host plant of *I. kalbarri* sp. nov.; f – *Dicrastylis morrisonii*, host plant of *I. silveirae* sp. nov.; g – *Eremophila forrestii*, host plant of *I. stysi* sp. nov.

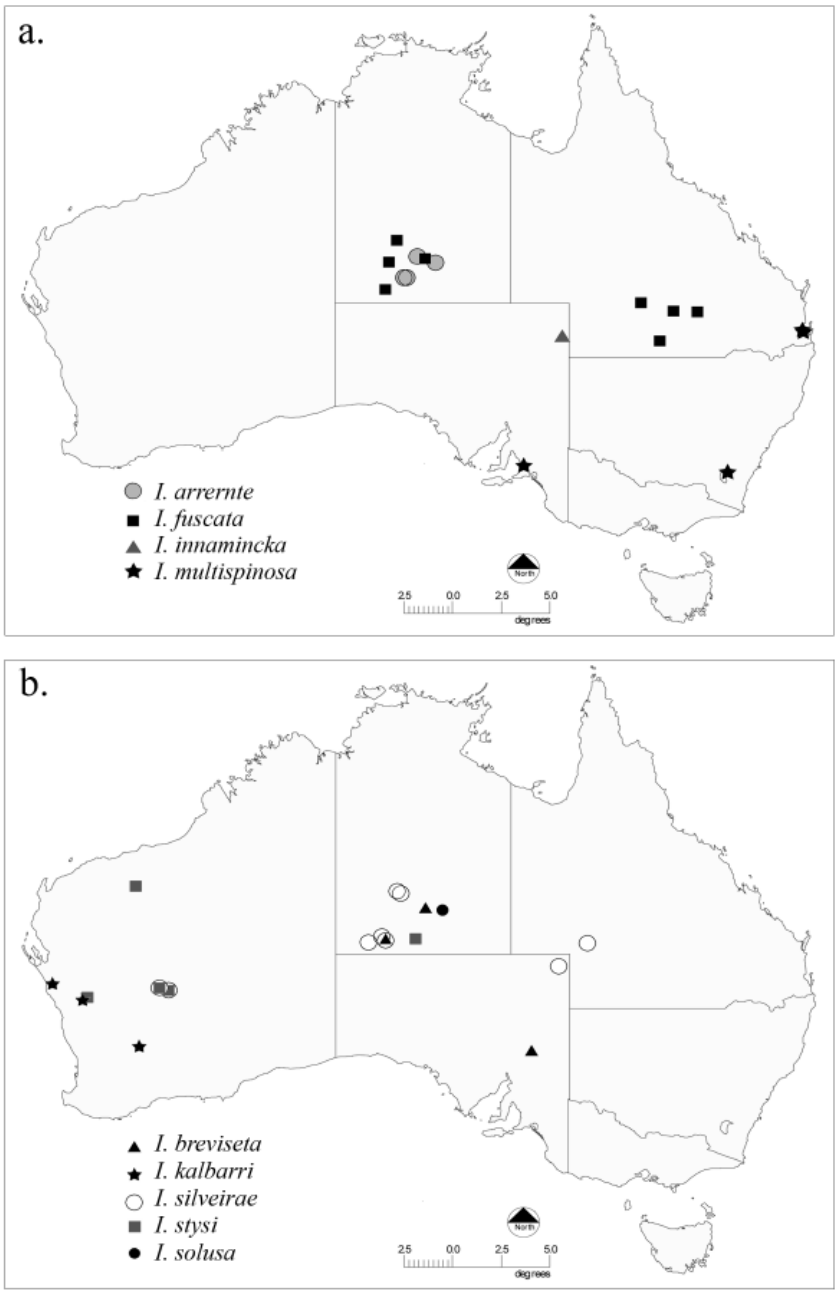

Fig. 13a-b. Localities of *Inoma* species.

straight (Fig. 9e). Abdomen: venter with dense distribution of elongate, erect, pale, straight, hair-like setae (Fig. 9h).

STRUCTURE. Head (Figs. 9a-d): cephalic spines elongate (Fig. 9a); frontal spines straight (Fig. 9ia); medial spine straight (Fig. 9a); occipital spines strongly curved outwards (Fig. 9a). Labium: elongate, extending to metacoxae. Antennae: AIV compact, with short base. Pronotum: callar region convex, slightly tumid; collum slightly enlarged; paranota biseriate, obliquely extended; carinae areolae small (Fig. 9d). Hemelytra: costal area biseriate; areolae large; subcostal, discoidal and most of sutural area with small areolae; hypocosta very narrow (Fig. 9e); female hemelytra slightly smaller with smaller/reduced sutural area. Legs: pretarsus (Fig. 9f). Male genitalia: pygophore (Fig. 9g); parameres with rounded sensory lobe, sensory lobe with a few elongate setae, inner margin with short setae, dorsal surface of parameres with broad distribution of minute setae; distal U-shaped endosomal sclerite with shallow and rounded cleft, long basal branches, and a straight distal margin; without paired basal endosomal sclerites. Female genitalia: sub-triangular subgenital plate, moderate size (Fig. 9h).

MEASUREMENTS. Ranges of 5 ♂♂ and 9 ♀♀ given in Table 2.

Differential diagnosis. *Inoma stysi* sp. nov. is similar to *I. solusa* sp. nov., but is distinguished from it by the following character states: 1) elongate major setiferous tubercles on pronotum and hemelytra, more so on forewings; and, 3) moderately dense distribution of woolly setae on the hemelytra (cf. to almost glabrous hemelytra in *I. solusa* sp. nov.).

Etymology. This species is named in honour of Professor Pavel Štys, in recognition of his contributions to heteropterology.

Biology. *Inoma stysi* sp. nov. has been collected on *Eremophila forrestii* (Myoporaceae), from a number of localities (Fig. 12g) in Western Australia and *Eremophila macdonnellii* in the Northern Territory. No host plant was recorded for the lone Pilbara specimen.

Distribution. *Inoma stysi* sp. nov. is known from three localities in south-central Western Australia and a single record from farther north in the Pilbara region (Fig. 13b). This species is also known from central Australia in the south of the Northern Territory.

Phylogeny

Phylogenetic analysis was based on 34 morphological characters for all *Inoma* species and six outgroup species. Male genitalic characters for *I. breviseta* sp. nov. and *I. solusa* sp. nov., were not coded, as insufficient male specimens were available for study. Characters and character states are given in Table 3 and the data matrix in Table 4. Two trees were produced from parsimony analysis (tree length = 55, consistency index (CI) = 0.7091, retention index (RI) = 0.8118, rescaled consistency index (RC) = 0.5756). The ingroup relationships of the two trees are identical, and the only difference between them is in the outgroup arrangement. Character optimization is given on tree 1, as shown in Figure 14, and the following discussion refers to character states at the nodes (numbered) of the ingroup, inclusive of the character definition of *Inoma*.

Node 1. *Inoma* is defined phylogenetically by a single synapomorphy, the presence of setiferous tubercles on the anterior margin and crest of the collum (13-1). It is supported

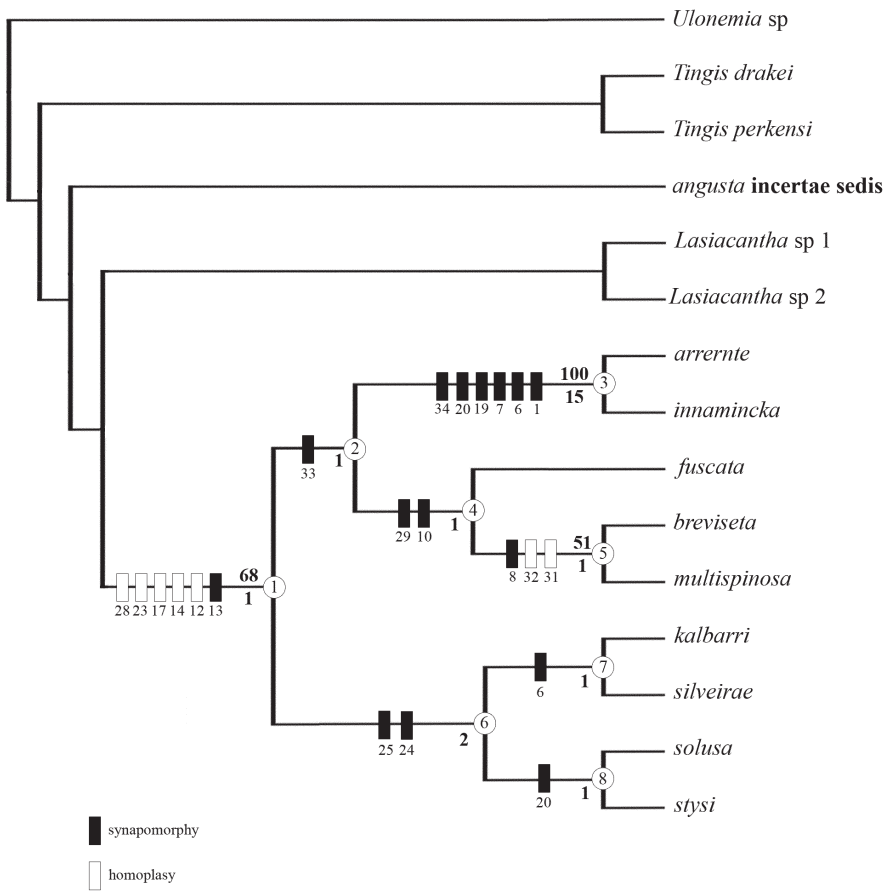

Fig. 14. Tree 1 of parsimony analysis inclusive of character optimisation (character state changes mapped at numbered nodes).

by five homoplasious characters, including the subtriangular collum (12-1), semi-circular paranota (14-1), presence of spines on the paranotal carinae (17-1), abdominal venter with elongate setae (23-1), and the male endosoma with a U-shaped sclerite (28-1). This node has a Bremer support of 1 and < 50% bootstrap support.

Node 2. *Inoma* is divided into two major subclades, with the most diverse including five species, which is further subdivided into three clades. This group is defined by a single synapomorphy, with paired basal endosomal sclerites (33-1). This character state exists more broadly in the Tinginae, but is phylogenetically informative within *Inoma*. This node has a Bremer support of 1 and < 50% bootstrap support.

Node 3. The sister-species relationship of *I. arrernte* sp. nov. + *I. innamincka* sp. nov. is the most strongly supported node, with 100% bootstrap and a Bremer support of 15. There are five synapomorphies, as follows: large body (1-1), elongate cephalic occipital spines (6-1),

Table 3. Characters and character states used in phylogenetic analysis of *Inoma* Hacker, 1927 species and related genera.

Character	0	1	2
1. General size:	very small;	medium to large.	
2. Cephalic spines – setiferous tubercles on/around base:	absent;	present.	
3. Frontal spines:	very short, adpressed;	elongate, porrect.	
4. Frontal spines – orientation:	not strongly convergent	strongly convergent;	
5. Occipital spines:	adpressed or just above head;	erect.	
6. Occipital spines – length:	very short;	long;	greatly elongate.
7. Occipital spines – orientation:	straight;	outcurved/arcuate.	
8. Medial spine – shape:	straight;	bifurcate.	
9. Antenna AIII – type of setae:	short, adpressed;	elongate, erect.	
10. Antenna AIII – shape of setae at apex:	rounded;	tapered.	
11. Collum – size:	slightly to moderately elevated;	greatly elevated.	
12. Collum – shape:	rounded;	sub-triangular;	cone-shaped.
13. Collum – setiferous tubercles:	absent;	on anterior margin and crest.	
14. Paranota – shape:	linear, narrow;	semi-circular, expanded;	wider anteriorly.
15. Paranota – areole no.:	one or two cells wide;	three or more cells wide.	
16. Pronotal carinae – height:	medial equal to lateral;	medial higher than lateral.	
17. Pronotal carinae – setiferous tubercles:	absent;	present.	
18. Paranota and costal margins – setiferous tubercles:	absent;	present.	
19. Setiferous tubercles – terminal seta shape:	straight;	recurved.	
20. Setiferous tubercles – tubercle type:	minor;	major.	
21. Vestiture:	without woolly or scale-like setae;	with woolly or scale-like setae.	
22. Vestiture – fine hook-like setal type on dorsum:	absent;	present.	
23. Vestiture – setae on abdominal venter:	short;	elongate.	
24. Vestiture – setae on abdominal venter:	erect;	adpressed.	
25. Vestiture – setae on abdominal venter:	hair-like;	scale-like.	
26. Vestiture – scale-like setae on abdominal venter:	lanceolate;	clavate.	
27. Metapleural scent gland orifice:	closed;	elevated rim, circular loop.	
28. Male genitalia – distal U-shaped endosomal sclerite:	absent;	present.	
29. Male genitalia – U-shaped endosomal sclerite cleft:	shallow;	deep;	none.
30. Male genitalia – U-shaped endosomal sclerite basal branches:	short;	elongate;	very short.
31. Male genitalia – U-shaped endosomal sclerite distal margin:	straight;	sinuate/convex.	
32. Male genitalia – U-shaped endosomal sclerite cleft shape:	rounded;	square.	
33. Male genitalia – paired basal endosomal sclerites:	absent;	present.	
34. Male genitalia – shape of paired basal endosomal sclerites:	semicircular with raised bumps;	other.	

Table 4. Data matrix of character states and species of *Inoma* Hacker, 1927 and outgroups. (–) inapplicable, (?) unknown.

	Characters																																
Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
outgroups																																		
Lasiacantha sp. 1	1	1	1	0	1	2	1	1	1	1	1	2	0	1	1	1	0	1	0	1	1	1	0	1	1	1	0	1	0	2	0	0	0	–
Lasiacantha sp. 2	1	1	1	0	1	2	1	0	1	1	1	2	0	1	1	1	0	1	0	1	1	1	0	1	1	0	0	0	1	1	0	1	0	–
'Inoma' angusta	1	0	1	1	1	2	1	0	0	–	0	0	0	2	0	0	1	1	0	1	0	–	–	–	–	–	0	0	?	?	?	?	?	–
Tingis drakei	1	0	0	1	0	0	0	0	0	–	0	0	0	2	0	0	0	0	–	–	0	–	–	–	–	–	1	0	2	–	0	–	0	–
Tingis perkensi	1	0	0	1	0	0	0	0	0	–	0	0	0	2	0	0	0	0	–	–	0	–	–	–	–	–	1	0	2	–	0	–	?	–
Ulonemia sp.	1	0	0	1	0	0	0	0	0	–	0	0	0	2	0	0	0	0	–	–	0	–	–	–	–	–	1	0	?	?	?	?	?	–
Inoma																																		
arrernte	0	1	1	0	1	0	0	0	1	1	0	1	1	0	0	0	1	1	1	0	1	0	1	1	1	0	0	1	0	1	0	0	1	0
breviseta	1	1	1	0	1	2	1	1	1	0	0	1	1	0	0	0	1	1	0	1	1	0	1	1	1	1	0	1	?	?	?	?	?	–
fuscata	1	1	1	0	1	2	1	0	1	0	0	1	1	0	0	0	1	1	0	1	1	0	1	1	1	1	0	1	1	1	0	0	1	1
innamincka	0	1	1	0	1	0	0	0	1	1	0	1	1	0	0	0	1	1	1	0	1	0	1	1	1	1	0	1	0	1	0	0	1	0
kalbarri	1	1	1	0	1	1	1	0	1	1	0	1	1	0	0	0	1	1	0	1	1	0	1	0	0	–	0	1	0	0	1	0	1	1
multispinosa	0	1	1	0	1	2	1	1	0	–	0	1	1	0	0	0	1	1	0	1	0	–	–	–	–	–	0	1	1	1	1	1	1	1
silveirae	0	1	1	0	1	1	1	0	1	1	0	1	1	0	0	0	1	1	0	1	1	0	1	0	0	–	0	1	1	1	0	0	0	–
solusa	1	1	1	0	1	2	1	0	1	1	0	1	1	0	0	0	1	1	0	0	1	0	1	0	0	–	0	1	?	?	?	?	?	–
stysi	1	1	1	0	1	2	1	0	1	1	0	1	1	0	0	0	1	1	0	0	1	0	1	0	0	–	0	1	0	1	0	0	0	–

outwardly curved cephalic occipital spines (7-1), recurved setiferous tubercles (19-1), and, paired basal endosomal sclerites are unarmed (34-1). In addition, it is supported by a single homoplastic character: base of setiferous tubercles elongate (20-1).

Node 4. The clade of (*I. fuscata* sp. nov. + (*I. breviseta* sp. nov. + *I. multispinosa*) has a Bremer support of 1, and < 50% bootstrap support. It is defined by two synapomorphies: setiferous tubercles of AIII are tapered (10-1) and the distal U-shaped endosomal sclerite is cleft deeply (29-1).

Node 5. The sister-species relationship of *I. breviseta* sp. nov. + *I. multispinosa* is hypothesised by a Bremer support of 1 and 51% bootstrap support. In terms of character states, it is defined by a single synapomorphy: bifurcate cephalic medial spine (8-1), and two homoplasious attributes of the distal U-shaped endosomal sclerite, namely the sclerite basal branches are elongate (31-1) and the distal margin of the sclerite is not straight (32-1).

Node 6. The clade of ((*I. kalbarri* sp. nov. + *I. silveirae* sp. nov.) + (*I. solusa* sp. nov. + *I. stysi* sp. nov.)) is defined by two abdominal vestiture synapomorphies: erect (24-1) and the scale-like (25-1) setae. This node has adequate Bremer support but low bootstrap support (< 50%).

Node 7. The sister-species relationship of *I. kalbarri* sp. nov. + *I. silveirae* sp. nov. is defined by a single synapomorphy: elongate cephalic occipital spine (6-1), and Bremer support of 1.

Node 8. The sister-species relationship of *I. solusa* sp. nov. + *I. stysi* sp. nov. is defined by a single homoplasious character: elongate base of setiferous tubercles (29-1) and Bremer support of 1. This character state also defines clade 3.

Although each node of the *Inoma* ingroup is supported by at least one synapomorphy, only two clades have > 50% bootstrap support and > 2 Bremer support. This work posits the phylogenetic value of endosomal characters for ingroup relationships of species within a single lace bug genus. We regard this as instructive for future studies where genitalic variation exists, albeit of a subtle nature (see paragraph below). Previous use of male genitalia in systematics of the Tingidae is limited. Lee (1969) has undertaken the most detailed study of the male genitalia thus far with other authors, also documenting differences (Drake & Davis 1960), with Lis (1999) demonstrating phylogenetic signal.

None-the-less phenotypic variation of lace bugs, as is the case in *Inoma*, is greatest and most obvious for external characters, particularly of the armature and texture of the dorsum. The spines and vestiture characters in this *Inoma* analysis constitutes more than 60% of all the characters observed.

Biogeography

An area cladogram of the *Inoma* complex is given in Figure 15. The areas of endemism follow those of Crisp et al. (1995) for vascular plants (redrawn in Figure 15). Paralogy-free subtree analysis (sensu Nelson & Ladiges 1996, Ladiges 1998) was undertaken but resulted in an uninformative minimal tree. As a result, the following discussion is presented as a narrative (sensu Ball 1976), based on the given area cladogram.

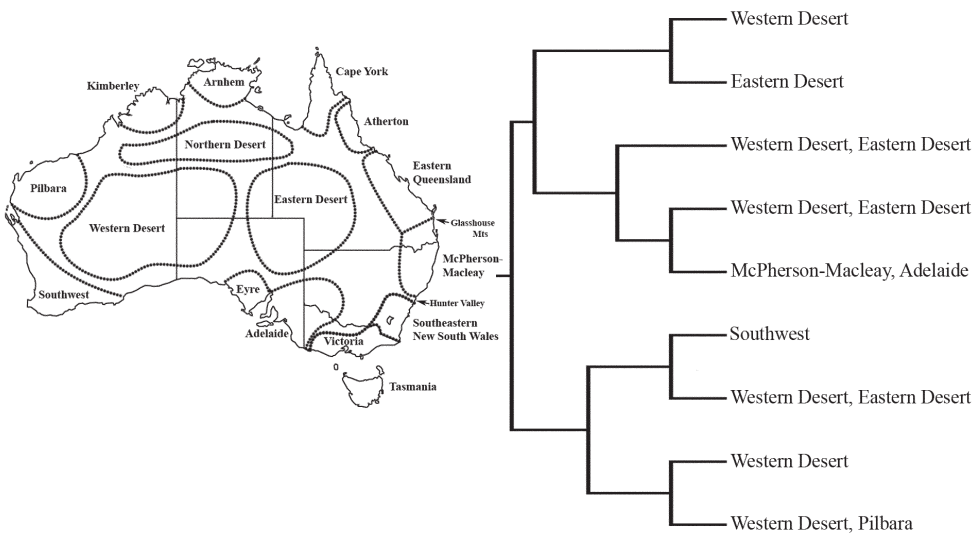

Fig. 15. Area cladogram for *Inoma* species. Map of biogeographic areas redrawn from Crisp et al. (1995).

Inoma is primarily found in the arid zone of Australia and is not found in the tropics. Most species are only known from one or two localities. The majority of species are found in central Australia, in the MacDonnell Ranges east of Alice Springs. Of the nine species of *Inoma*, six are found in this region, on the eastern edge of the Western Desert area of endemism for vascular plants (Crisp et al. 1995). Three of these species, are also found in the Eastern Desert area of endemism, always exhibiting significant distributional disjunction about the Simpson Desert. Two species, ***I. stysi*** sp. nov. and ***I. silveirae*** sp. nov., are found in the western part of the Western Desert area of endemism, with ***I. stysi*** sp. nov. found predominantly in the western part of the Western Desert, and also extending northwest to the Pilbara area of endemism.

Clade 2 (see Figure 14) exhibits a more eastern distribution pattern, with four of the five species found either in the Eastern Desert or in southeastern Australia. Two of the species found in the Eastern Desert are also found in the Western Desert, with ***I. arrernte*** sp. nov. found only in the eastern edge of the Western Desert area of endemism. *Inoma multispinosa* is a highly autapomorphic taxon, and is the only species which is found outside of the arid zone of Australia, although it is widely distributed from southeast Queensland (McPherson–Macleay area of endemism), to the southern gulfs of South Australia (Adelaide area of endemism). In all sister-species pairs of clade 2, the distributional disjunction is significant (> 200 km), with ***I. innamincka*** sp. nov. and ***I. multispinosa***, separated by > 500 km.

Clade 6 (see Figure 14) is near exclusive to the western component of the continent. Although, there are multiple cases of local sympatry between *Inoma* species in this clade, distributions are always allopatric for sister-species pairs, and no secondary sympatry needs to be inferred. The distributions of the two sister-species pairs are highly disjunct, with ***I. kalbarri*** sp. nov. known only from coastal and more inland southwest Western Australia (area of endemism), and separated from ***I. silveirae*** sp. nov. by hundreds of kilometres. *Inoma*

Table 5. Host plant species and families for species of *Inoma* Hacker, 1927. (1) – only singleton recorded from host plant. * – as in Stevens (2001 onwards).

Inoma species	Host plant species	Host plant family*	Host plant order*	Angiosperm clade*
arrernte	*Anemocarpa saxatilis*	Asteraceae	Asterales	asterid II
	Halgania cyanea	Boraginaceae	unplaced	asterid I
	Rutidosis helichrysoides (1)	Asteraceae	Asterales	asterid II
	Solanum ellipticum (1)	Solanaceae	Solanales	asterid I
breviseta	*Eremophila gilesii*	Myoporaceae	Lamiales	asterid I
	Eremophila sp. (1)	Myoporaceae	Lamiales	asterid I
fuscata	*Eremophila gilesii*	Myoporaceae	Lamiales	asterid I
	Eremophila freelingii	Myoporaceae	Lamiales	asterid I
	Aristida jerichoensis	Poaceae	Poales	monocot
innamincka	*Teucrium racemosum*	Lamiaceae	Lamiales	asterid I
kalbarri	*Dicrastylis fulva*	Lamiaceae	Lamiales	asterid I
	Pityrodia teckiana	Lamiaceae	Lamiales	asterid I
multispinosa	*Dillwynia retorta*	Fabaceae	Fabales	rosid I
silveirae	*Newcastelia cephelantha*	Lamiaceae	Lamiales	asterid I
	Dicrastylis lewellinii	Lamiaceae	Lamiales	asterid I
	Dicrastylis gilesii var.*gilesii*	Lamiaceae	Lamiales	asterid I
	Dicrastylis beveridgei	Lamiaceae	Lamiales	asterid I
	Dicrastylis morrisonii	Lamiaceae	Lamiales	asterid I
	Ptilotus obovatus (1)	Amaranthaceae	Caryophyllales	unplaced
	Alyogyne pinoniana (1)	Malvaceae	Malvales	rosid II
solusa	*Eremophila* (?)(1)	Myoporaceae	Lamiales	asterid I
stysi	*Eremophila forrestii*	Myoporaceae	Lamiales	asterid I
	Eremophila macdonnellii	Myoporaceae	Lamiales	asterid I

solusa sp. nov. and *I. stysi* sp. nov. are greatly separated geographically, with the former found only in central Australia, and the latter predominantly in the western section of the Western Desert area of endemism and the Pilbara area of endemism. The single occurrence of *I.stysi* sp. nov. in central Australia is considerably further south from the locality of *I. solusa* sp. nov. *Inoma silveirae* sp. nov. is the most broadly distributed species, found in south central to southwestern Queensland, as far west as central Western Australia, with the majority of records in the MacDonnell Ranges of central Australia. It is locally sympatric with *I. breviseta* sp. nov. and *I. fuscata* sp. nov. in central Australia and *I. stysi* sp. nov. in Western Australia, none of which belong to clade 6.

Host plant association

The following discussion is a narrative-based assessment of host plant relationships of the genus *Inoma*. The diversity of host plant associations is not indicative of cospeciation and as such we have refrained from optimizing host plant associations on the *Inoma* phylogeny. Knowledge of the degree of host plant specialisation for *Inoma* is still in its infancy, with the only plant records taken during recent collections (Cassis et al. 2007; see Table 5). Three of

the nine *Inoma* species are only known from a single host plant, and two of these (*I. innamincka* sp. nov. and *I. solusa* sp. nov.), have been found only once. *Inoma multispinosa* has been collected at multiple locations, but the Canberra collection event is the only one where a host plant was recorded. All other species have been collected at multiple locations and with numerous host plant associations, from two to seven plant species (Table 5).

In terms of the phylogenetic position of the *Inoma* host plants, nearly all are asterid angiosperms, mostly asterid I taxa, with *I. arrernte* sp. nov. also found on two asterid II species (*sensu* Stevens 2001, Angiosperm Phylogeny Group classification). This is of particular interest in understanding host plant relationships of Australian true bugs, where most heteropteran clades are found primarily on rosid angiosperms (Cassis & Gross 1995, Cassis & Vanags 2006). This is the first case known to us, where a genus of Australian true bugs is primarily found on asterid angiosperms.

The major association of *Inoma* species is with the plant genera, *Eremophila* and *Dicrastylis*, both of which belong to the angiosperm order Lamiales. *Eremophila* is endemic to Australia and comprises perennial woody shrubs and small trees. The genus is the most species rich member of the Southern Hemisphere family Myoporaceae, with over 200 described species, most of which are found in the arid zone of Western Australia (> 66% of species endemic to Western Australia), with lesser areas of high diversity in central Australia and western Queensland (Chinnock 2007).

Four species of *Inoma* (*I. brevista* sp. nov., *I. fuscata* sp. nov., *I. solusa* sp. nov. and *I. stysi* sp. nov.) have been found on *Eremophila*, with only the last species, found on another plant genus (*Dicrastylis*). The *Eremophila* associations are found in both the major subclades of *Inoma* (clades 2 and 6, Figure 14), as follows: 1) *I. fuscata* sp. nov. + (*I. breviseta* sp. nov. + *I. multispinosa*), with the former two species both found on *Eremophila gilesi*, and *I. fuscata* sp. nov. also found on *Eremophila freelingii*; and, 2) *I. solusa* sp. nov. + *I. stysi* sp. nov., with the former on an undetermined species of *Eremophila*, and the latter on *Eremophila forrestii* (+ *Dicrastylis fulva*).

In contrast, the plant genus *Dicrastylis* (family Lamiaceae; transferred to Lamiaceae in Stevens (2001), is less diverse, composed of 26 species of low perennial shrubs (Conn 1992). It is found mostly in the arid zone, in all states and territories, except Victoria. Three species of *Inoma* (including *I. stysi* sp. nov.) are found on *Dicrastylis*, including the sister-species *I. kalbarri* sp. nov. + *I. silveirae* sp. nov., with the last found on four *Dicrastylis* species, as well as another labiate genus, *Newcastelia* (and probable sitting records on *Alyogyne pinoniana* and *Ptilotus obovatus*).

Discussion

The diversification of true bugs in Australia is poorly understood from phylogenetic and ecological-evolutionary perspectives. In terms of both their distribution (largely non-overlapping distribution of *Inoma* species; exclusively so for sister-species) and multiple occurrences within single areas of endemism (Cracraft 1992, Crisp et al. 1995), this *Inoma* case study is suggestive of finer-scale speciation patterns. This is not surprising, in that it is well-known that invertebrates often exhibit narrow range endemism, although in Australia this has been mostly attributed more to the open and closed forests of the Great Dividing

Range and southwest Western Australia global biodiversity hotspot. Within *Inoma*, only four species are broadly distributed (across more than one state or territory; *I. breviseta* sp. nov., *I. fuscata* sp. nov., *I. multispinosa* and *I. silveirae* sp. nov.).

The greatest species diversity of *Inoma* exists in central Australia, with five of the nine species found in the MacDonnell Ranges of the Northern Territory, east and west of Alice Springs. Of these five, *I. arrernte* sp. nov. and *I. solusa* sp. nov. are only known from this region, with *I. breviseta* sp. nov. also known from the Flinders Ranges, South Australia.

The distribution patterns and area relationships of *Inoma* are novel in comparison to other true bugs which have been analysed cladistically. To date, we have detected the following repeated distribution patterns: east-west temperate (e.g., Cassis & Silveira (2001) – *Nerthra alaticollis* species-group; Cassis & Moulds (2001) – *Kirkaldyella* Poppius), eastern Australian (e.g., Cassis & Silveira (2002) – *Nerthra elongata* species-group), and wet tropics + Melanesia (e.g., Cassis & Silveira (2006) – *Nerthra kerzhneri* Cassis & Silveira, 2006; Cassis et al. (2003), Cassis & Monteith (2006) – *Vannius* complex).

The host plant associations of *Inoma* show a weak phylogenetic signal, found mostly on lamiaceous (or related) plants. However, these associations need to also be explored from a plant functional attribute perspective, as nearly all of these plants have either woolly or sticky trichomes. This is not unknown in other true bugs, where such plants are hypothesized to have low predator and parasite loads, as well as low herbivore competition (Wheeler 2001). The most noteworthy examples, include the mirid subtribe Dicyphina (Cassis 1986) and the Berytidae (Henry 1997). As with these groups, particularly the Dicyphina, multiple species of *Inoma* are found on the same host plant (and same collection event). We did not find any sister-species of *Inoma* co-occurring, ruling out any putative hypothesis of sympatric speciation.

In relation to the evolution of their host plants, it has been suggested that the Myoporaceae (inclusive of *Eremophila*) represents a recent radiation over the past few million years, from Gondwanan ancestors (Chinnock 2007). Moreover, for *Eremophila*, it has been proposed that its distribution has been dramatically influenced by the formation of Quaternary sand sheets in the past 30,000 years (Crocker & Wood 1947, Bowler 1976, Chinnock 2007). *Inoma*, like *Eremophila* is relatively depauperate in temperate and tropical Australia, and a hypothesis of recent codiversification of these taxa in arid Australia, at least species pairs in central Australia, can be posited. However, as stated previously, the phylogenetic analysis is not presently suggestive of cospeciation patterns, whereas geographic influences are putatively more important than host plant affiliation. Future studies will address these factors, through a broader systematic survey of *Eremophila* species, particularly in the McDonnell Ranges of the Northern Territory, and across the Eastern and Western Desert areas of endemism, particularly those influenced by the Simpson Desert. To date, we have sampled but < 10% of all *Eremophila* species and only a handful of *Dicrastylis* species. Further survey will explore the host breadth of *Inoma* species, including a search for new species belonging to this genus of lace bug, and the surveying of plants with glandular trichomes.

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