

## Taxonomic and phylogenetic revision of the Gelastocephalini (Hemiptera: Cixiidae)

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**Abstract.** Planthoppers of the family Cixiidae Spinola, 1839 are economically important owing to their ability to transmit phytoplasmas causing yellows-type diseases. The tribe Gelastocephalini Emeljanov, one of 16 tribes within the subfamily Cixiinae, has never been revised comprehensively. Twenty new genera (*Aubirestus*, *Balyadimetopia*, *Barbonia*, *Candicarina*, *Corylonga*, *Fletcherolus*, *Gelastocaledonia*, *Gurrundus*, *Guttala*, *Hartliebia*, *Holgus*, *Lariviera*, *Lipsia*, *Melanoclypeus*, *Novotarberus*, *Payastylus*, *Rokebia*, *Schuerrera*, *Wernindia*, *Yarnikada*) and 50 new species (*Aubirestus semicirculatus*, *Balyadimetopia frederi*, *B. krahalla*, *B. marci*, *Barbonia spectabilis*, *Candicarina geroldi*, *C. pulchra*, *Carolus carinatus*, *C. stiriae*, *Corylonga aaroni*, *C. krottendorfi*, *C. leighi*, *C. lobata*, *C. loisae*, *C. mahmudae*, *C. triangula*, *Fletcherolus lanceolatus*, *F. monospinosus*, *Gelastocaledonia monteithi*, *Gelastocephalus velifer*, *Gurrundus fuscomarginatus*, *G. nectostylus*, *Guttala bernhardtae*, *G. mona*, *G. nickeli*, *G. robierae*, *Hartliebia towinna*, *Holgus ancistrus*, *H. liafredis*, *H. spiralis*, *H. unispinosus*, *Lariviera yalhi*, *L. yokunna*, *Lipsia mystrostylus*, *Melanoclypeus cristatus*, *M. uncinatus*, *Novotarberus flagellospinosus*, *N. pseudorhynchus*, *N. remanei*, *Payastylus brichrius*, *P. gekiae*, *P. kerna*, *Rokebia australis*, *Ronaldia emeljanovi*, *Schuerrera clypeocarinata*, *S. ecarinata*, *Wernindia bubalis*, *W. lorda*, *W. rhomboidea*, *Yarnikada ulliae*) are described. This increases the number of known Gelastocephalini from seven to 27 genera and from nine to 60 species. A new combination, *Novotarberus jacobii*, is proposed for *Gelastocephalus jacobii* from New Caledonia and *Cixius merula* was transferred into the genus *Schuerrera*, resulting in a new combination, *Schuerrera merula*. A preliminary cladistic analysis of morphological data including all species of Gelastocephalini supported the monophyly of the tribe and its genera. The short male anal style is recognised as a synapomorphy for the tribe. The subtribe Rhigedanina was shown to be monophyletic whereas Gelastocephalina is paraphyletic. Three alternative hypotheses are presented to explain the current distribution of the tribe, which is restricted to Australia and New Caledonia. The species *Novotarberus jacobii* and *Gelastocaledonia monteithi* seem to be Gondwanan relicts.

**Additional keywords:** Auchenorrhyncha, Australia, biogeography, cladistic analysis, Cixiidae, Fulgoromorpha, Gelastocephalina, Gelastocephalini, New Caledonia, Rhigedanina.

### Introduction

This paper reports on a revision of the Australian plant-hoppers in the family Cixiidae Spinola, 1839. Cixiids are distributed worldwide with their highest diversity in the tropics (Emeljanov 2002). Comprising ~146 genera and more than 2000 described species, Cixiidae is one of the largest families within the Fulgoromorpha (Holzinger *et al.* 2002). Morphological features such as Y-shaped claval veins, the placement of antennae and eyes, the shape of spines on tibia and tarsus, and behavioural characters, like feeding on phloem and jumping, characterise Fulgoromorpha (O'Brien

2002). Worldwide, 20 families and ~10000 species are recognised (Holzinger *et al.* 2003). Cixiidae and Delphacidae are of the greatest economic importance within Fulgoromorpha (O'Brien and Wilson 1985). A review of the family Cixiidae, including a generic checklist of the world and general information on ecology and economic importance, was published by Holzinger *et al.* (2002).

Cixiidae are known to act as vectors of phytoplasmas, causing yellows-type diseases in several wild and cultivated plants (Julia 1982; O'Brien and Wilson 1985; Howard 1987; Wilson and O'Brien 1987; Wilson 1988; Maixner *et al.*

1995; Liefting *et al.* 1997; Liefting *et al.* 1998; Howard *et al.* 2001; Alma 2002). Yellows diseases are also known from Australia. However, the insects that transmit these diseases such as Australian lucerne yellows (AluY) (Pilkington *et al.* 1999, 2002) and Australian grapevine yellows (AGY) (Magarey and Wachtel 1985; Padovan *et al.* 1995) are still unknown. With the number of cixiids known to transmit yellows diseases in other parts of the world, Australian species also need to be considered as potential vectors. This means that there is a genuine need for reliable descriptions and identification aids for the Australian Cixiidae that will be the basis for more detailed investigations of their behaviour and pest status.

At the start of this project only 59 species of Cixiidae were known from Australia. In order to get an estimate of the taxonomic diversity of the group in Australia, and to determine which morphological characters to use for analyses, the project initially focussed on the Gelastocephalini Emeljanov 2000, a tribe only known from Australia and New Caledonia with nine species in seven genera.

#### *Taxonomic history*

Emeljanov (2000) established the tribe Gelastocephalini with two new subtribes Gelastocephalina and Rhigedanina. The definition of the tribe Gelastocephalini is investigated and further discussed in this paper.

Seven genera of Gelastocephalini, containing nine species, were then known from Australia and New Caledonia. Of these species, *Gelastocephalus ornithoides* and *Carolus crispus* were described by Kirkaldy in 1906. Jacobi (1928) established the genus *Tarberus* to accommodate one new species, *T. semicarinatus*. Three years later Muir (1931) added a species from New Caledonia, *Tarberus jacobii*. In 1949, Fennah described *Dysoliarus unicornis*, a species with a very distinctive process on the frons. Fennah (1969) synonymised the type species of *Tarberus*, *T. semicarinatus*, with *Gelastocephalus ornithoides*, thereby making *Tarberus* a junior objective synonym of *Gelastocephalus*. This also meant that *T. jacobii* was moved to the genus *Gelastocephalus* as *Gelastocephalus jacobii* (Muir).

Finally, Emeljanov (2000) described the following Gelastocephalini: *Metaplacha tobiasi*, *Ronaldia fennahi*, *Orphninus mouldsi*, *Rhigedanus fomibundus* and *Rhigedanus maculipennis*.

In this same paper, he grouped his two *Rhigedanus* species along with *O. mouldsi* and *D. unicornis* under the subtribe Rhigedanina, leaving all other Gelastocephalini in the subtribe Gelastocephalina.

The phylogeny of Gelastocephalini, in fact of the whole family Cixiidae, is not well understood. Emeljanov (2002) compiled a preliminary phylogram of the family Cixiidae based on several morphological characters but did not include the subfamily Borystheninae and the tribes Benarellini and Gelastocephalini.

## Material and methods

### *Phylogenetic analysis*

#### *Morphological characters*

Male adults were coded for 83 morphological characters plus three modified characters (see character list, Table 1). Character states were scored as missing values '?' where the state was unavailable for examination, e.g. the specimen was damaged or parts of the specimen were missing. In cases where two or more character states occurred within one species, all states were coded in the matrix (such multistate characters) were treated as uncertain when searching for the most parsimonious trees. The main consequence of this is that the parsimony algorithm used in PAUP (Phylogenetic Analysis Using Parsimony) (Swofford 2002) chooses the variable state that minimises the tree length for a particular tree.

Of the characters, 47 are binary and 39 are multistate (character states ranging from 3–9). Two different datasets were analysed.

Dataset *A* consists of the characters 1–83. In the analyses performed with this dataset the following characters were treated as ordered (numbers identify characters in the list, Table 1): 3, 7, 8, 12, 14, 19, 25, 31–33, 35, 39, 41, 44–45, 47–48, 63, 70, 72–76, 78, 80–83; the remaining 54 characters were treated as unordered.

Dataset *B* is derived from dataset *A* but excludes characters based on continuous data, which means characters 3, 45, 48, 70–83 were deleted and characters 25, 44 and 47 replaced with the modified characters 25\*, 44\* and 47\*. The analyses performed with dataset *B* treated all characters as unordered.

#### *Selection of taxa*

All 60 species currently recognised in the tribe Gelastocephalini have been included in the phylogenetic analysis and used as terminal taxa.

#### *Selection of outgroups*

Since the phylogeny of the family Cixiidae, in particular the position of the tribe Gelastocephalini within Cixiidae, is unknown, sister groups of Gelastocephalini cannot be determined with certainty. Therefore, in order to root phylogenetic trees the following taxa, representing different tribes of Cixiidae, were selected as outgroups for various analyses: *Oliarus* sp. (tribe Pentastirini), '*Cixius*' *sidnicus* Stål, 1859 (note the statement in Emeljanov (2000: 251): 'The genus *Cixius*, in its current concept, is not represented in Australia...') and *Apartus michalki* Wagner, 1948 (tribe Cixiini), *Volcanalia* sp. (tribe Oecleini), *Cajeta singularis* Stål, 1866 (tribe Cajetini) and four undescribed Australian species (outgroup 1–4) that appear to be closely related to Gelastocephalini.

#### *Parsimony analysis*

Cladistic analyses using outgroup comparison (Maddison *et al.* 1984; Nixon and Carpenter, 1993) were conducted on a morphological dataset using PAUP 4.0 WIN 32/DOS Beta Version 8 (with Beta 10 Updates) (Swofford 2002). Owing to the high number of taxa and characters included in the analysis, an exhaustive search could not be performed, therefore heuristic methods searching for most parsimonious trees were applied. The default settings of PAUP were used with the following exceptions. In each analysis, 1000 iterations of random stepwise addition of taxa were performed; optimisation of ancestral states, when more than one optimal assignment existed, was carried out under the ACCTRAN criterion (Swofford and Maddison 1987); chuckscore = 370 nchuck = 100 limitperrep = yes was applied in the 'unscaled' equal weighting analysis of dataset *B*; limitrearr = 1000000 limitperrep = yes was used for the successive approximations weighting analyses of dataset *B*.

**Table 1. List of morphological characters and their states, irrespective of character state polarity***Head*

- (1) *Median ocellus*: (0) absent; (1) present.  
 (2) *Shape of apex of vertex*: (0) broadly rounded; (1) broadly truncate; (2) broadly pointed; (3) narrowly rounded or truncate; (4) narrowly pointed.  
 (3) *Median carina of vertex*: (0) absent; (1) incomplete, up to 1/4 length of vertex; (2) incomplete, >1/4–1/2 length of vertex; (3) incomplete, >1/2–3/4 length of vertex; (4) incomplete, >3/4 length of vertex; (5) complete.  
 (4) *Lateral carinae of vertex*: (0) slightly elevated; (1) strongly elevated.  
 (5) *Number of transverse carinae between vertex and clypeus*: (0) one; (1) two.  
 (6) *Maximum width of frons*: (0) no more than 2× apical width, steadily broadening; (2) more than 2× apical width, broadening over a very short distance, therefore lateral carinae distinctly concave.  
 (7) *Position of maximum width of frons*: (0) distinctly ventrad of centre of frontoclypeal suture; (1) more or less around centre of frontoclypeal suture; (2) distinctly dorsad of centre of frontoclypeal suture.  
 (8) *Median carina of frons*: (0) absent; (1) present, incomplete; (2) present, complete.  
 (9) *Lateral carinae of frons*: (0) slightly elevated; (1) strongly elevated.  
 (10) *Lateral carinae of frons in facial view*: (0) convex, evenly rounded; (1) convex, rectilinear apically; (2) sinuate, s-shaped; (3) sinuate, double s-shaped.  
 (11) *Lateral carinae of frons foliaceous, distinctly extending laterally, concealing base of antennae*: (0) no; (1) yes.  
 (12) *Shape of frontoclypeal suture*: (0) straight; (1) slightly semicircular, bent upwards, median part not reaching lower margin of antennal scape; (2) strongly semicircular, bent upwards, median part reaching at least lower margin of antennal scape.  
 (13) *Median carina of postclypeus*: (0) absent or evanescent; (1) well developed.  
 (14) *Lateral carinae of postclypeus*: (0) absent; (1) evanescent; (2) well developed.  
 (15) *Median carina of anteclypeus*: (0) absent or evanescent; (1) well developed.  
 (16) *Median carina distinctly more elevated on anteclypeus than on postclypeus*: (0) no; (1) yes.  
 (17) *Lateral carinae on postclypeus strongly enlarged, foliaceous*: (0) no; (1) yes.

*Thorax*

- (18) *Median carina of pronotum*: (0) absent; (1) present.  
 (19) *Angle of hind margin of pronotum*: (0) obtuse (>>90°); (1) more or less rectangular; (2) acute (<<90°).  
 (20) *Pronotal carinae elevated medially to form ear-shaped lobes*: (0) no; (1) yes.  
 (21) *Vertex lowered in relation to the hind margin of pronotum*: (0) no; (1) yes.  
 (22) *Sublateral carinae on mesonotum*: (0) absent; (1) present.

*Forewing*

- (23) *Resting position*: (0) shallowly tectiform; (1) steeply tectiform (apices of wings touching over a long distance, lateral parts of mesonotum plunging down).  
 (24) *Concavity at costal border*: (0) absent; (1) present.  
 (25) *Number of tubercles on costa*: (0) none; (1) 1–10; (2) 11–20; (3) more than 20.  
 (26) *Tubercles between veins on apex of wing*: (0) absent; (1) present.  
 (27) *Two or three dark bullate spots on apex of wing*: (0) absent; (1) present.  
 (28) *Sc, R and M distad of basal cell*: (0) Sc+R fused, forming a common stem Sc+R, M emerging separately from basal cell; (1) Sc+R+M fused, forming a common stem Sc+R+M.  
 (29) *Forking of Sc+R*: (0) basad of fork CuA1+CuA2; (1) same level or distad of fork CuA1+CuA2.  
 (30) *Position of r-m*: (0) basad of fork MA–MP; (1) same level or distad of fork MA–MP.  
 (31) *Position of icu at CuA*: (0) basad of apex of clavus; (1) at same level as apex of clavus; (2) distad of apex of clavus.  
 (32) *Position of icu at CuP*: (0) basad of apex of clavus; (1) at same level as apex of clavus; (2) distad of apex of clavus.  
 (33) *R apically forked*: (0) no; (1) bifid; (2) trifid; (3) more than three branches.  
 (34) *Additional subapical cell between branches of R*: (0) absent; (1) present.  
 (35) *MA apically forked*: (0) no; (1) bifid; (2) trifid; (3) more than three branches.  
 (36) *Additional subapical cell between branches of MA*: (0) absent; (1) present.  
 (37) *Position of veins delimiting subapical cells C4 and C5 distally*: (0) more or less at same level; (1) vein delimiting C4 distinctly distad of vein delimiting C5.  
 (38) *Length of subapical cell C5*: (0) more or less same length as C4; (1) distinctly longer than C4.  
 (39) *Number of apical cells*: (0) 8; (1) 9; (2) 10; (3) 11; (4) 12 or more.

*Hind leg*

- (40) *Large lateral spines on hind tibia*: (0) absent; (1) present.  
 (41) *Number of apical teeth on hind tibia*: (0) 5; (1) 6; (2) 7; (3) 8 or more.  
 (42) *Inner teeth on apex of hind tibia basally fused, further extending than outer teeth*: (0) no; (1) yes.  
 (43) *Gap (diastema) in row of apical teeth on hind tibia*: (0) absent; (1) present (Fig. 1F).  
 (44) *Number of apical teeth on 1st hind tarsomere*: (0) 6; (1) 7; (2) 8; (3) 9; (4) 10; (5) 11; (6) 12; (7) 13 or more.  
 (45) *Number of apical teeth on 2nd hind tarsomere*: (0) <7; (1) 7–8; (2) 9–10; (3) 11–15; (4) 16 or more.  
 (46) *Size of apical teeth on 2nd hind tarsomere*: (0) all teeth more or less the same; (1) outer teeth larger than inner teeth.  
 (47) *Number of platellae on 1st hind tarsomere*: (0) 0; (1) 1–4; (2) >4.

(continued next page)

**Table 1.** (continued)

- (48) *Number of platellae on 2nd hind tarsomere*: (0) <5; (1) 5; (2) 6; (3) 7; (4) 8; (5) 9; (6) >9.  
 (49) *Number of teeth on 2nd hind tarsomere minus 2 equals number of platellae*: (0) no; (1) yes.  
 (50) *Shape of 2nd hind tarsomere*: (0) cylindrical; (1) triangular.
- Male abdomen*
- (51) *Number of sclerotised plates forming sternite 6*: (0) one; (1) two.  
 (52) *Number of sclerotised plates forming sternite 7*: (0) one; (1) two.  
 (53) *Number of sclerotised plates forming sternite 8*: (0) one; (1) two.  
 (54) *Shape of pygofer*: (0) as in Fig. 103A; (1) as in Fig. 103B; (2) as in Fig. 103C; (3) as in Fig. 103D; (4) as in Fig. 103E; (5) as in Fig. 103F.  
 (55) *Shape of ventromedian process*: (0) moderately developed, triangular (apical angle more or less rectangular) as in Fig. 104A (1) slightly developed, triangular (apical angle obtuse) as in Fig. 104B; (2) moderately developed, truncate or emarginate apically as in Fig. 104C, D; (3) strongly developed, triangular (apical angle acute) as in Fig. 104E.  
 (56) *Shape of genital styles in ventral view*: (0) not spoon-shaped (Figs 82–83E, 84F); (2) broadly spoon-shaped (Figs 66E, 76F, 77G, 78H, 79F, 86E, 96–97F, 98E).  
 (57) *Genital styles in ventral view shaped as in Figs 45–46E*: (0) no; (1) yes.  
 (58) *Genital styles in lateral view triangularly shaped as in Figs 55D, 77F, 78G, 83D, 96–97E, 98D*: (0) no; (1) yes.  
 (59) *Genital styles in lateral view shaped like a bird head (Figs 90–92E)*: (0) no; (1) yes.  
 (60) *Shaft of male genital styles bearing small tooth as in Fig. 2D*: (0) no; (1) yes.  
 (61) *Shape of anal tube in dorsal view*: (0) as in Fig. 105A; (1) as in Fig. 105B, C; (2) as in Fig. 105D, E; (3) as in Fig. 105F; (4) as in Fig. 105G; (5) as in Fig. 105H; (6) as in Fig. 105I.  
 (62) *Shape of anal tube in lateral view*: (0) as in Fig. 106A; (1) as in Fig. 106B; (2) as in Fig. 106C; (3) as in Fig. 106D, E; (4) as in Fig. 106F; (5) as in Fig. 106G; (6) as in Fig. 106H; (7) as in Fig. 106I.  
 (63) *Abdominal segment XI in lateral view*: (0) distinctly shorter than anal style; (1) more or less as long as anal style; (2) distinctly longer than anal style (Fig. 2E).  
 (64) *Phallosome bearing a very long spine arising ventrolaterally near apex and a shorter curved spine above midlength as in Figs 96–97B, 98A*: (0) absent; (1) present.  
 (65) *Spines on the aedeagus arranged as in Figs 57–61B, 62C, 63B*: (0) no; (1) yes.  
 (66) *Spines on the aedeagus arranged as in Figs 76B, 77C, 78A*: (0) no; (1) yes.  
 (67) *Pair of very small spines on ventral side of phallosome as in Fig. 54A*: (0) absent; (1) present.  
 (68) *Phallosome bearing a large triangular ventral ridge with another small triangular ridge on top of it (Figs 64–65A)*: (0) absent; (1) present.  
 (69) *Phallosome bearing a ventral ridge forming a long process apically (Figs 94–95A)*: (0) absent; (1) present.
- Measurements*
- (70) *Body length*: (0) ≤4.50 mm; (1) 4.51–7.49 mm; (2) ≥7.50 mm.  
 (71) *Body width / body length*: (0) <0.23; (1) ≥0.23.  
 (72) *Width of vertex / length of vertex*: (0) <1; (1) 1.00–1.99; (2) 2.00–2.99; (3) = 3.  
 (73) *Distance from anterior margin of eye to transverse carina between vertex and clypeus / diameter of eye*: (0) <0.5; (1) 0.5–1; (2) >1.  
 (74) *Width / length of frons*: (0) <0.5; (1) 0.5–0.89; (2) 0.9–1.29; (3) ≥1.3.  
 (75) *Length of postclypeus / length of frons*: (0) <0.6; (1) 0.6–0.9; (2) >0.9.  
 (76) *Length of pronotum / body length*: (0) ≤0.02; (1) 0.021–0.04; (2) >0.04.  
 (77) *Length of mesonotum / body length*: (0) ≤0.2; (1) >0.2.  
 (78) *Body width / length of mesonotum*: (0) <1; (1) 1–1.2; (2) >1.2.  
 (79) *Length of forewing / body length*: (0) <0.8; (1) ≥0.8.  
 (80) *Width of forewing / length of forewing*: (0) <0.28; (1) 0.28–0.33; (2) >0.33.  
 (81) *Distance from base of wing to pterostigma / length of forewing*: (0) <0.55; (1) 0.55–0.65; (2) >0.65.  
 (82) *Number of tubercles on costa / distance base of forewing to pterostigma*: (0) <5; (1) 5–10; (2) >10.  
 (83) *Length of hind tibia / body length*: (0) <0.23; (1) 0.23–0.28; (2) >0.28.
- List of modified characters for dataset B:*
- (25)\*. *Tubercles on costa*: (0) absent; (2) present.  
 (44)\*. *Number of apical teeth on 2nd hind tarsomere*: (0) 6; (1) 7; (2) 8; (3) 9; (4) 10; (5) 11; (6) 12; (7) 13; (8) 14.  
 (47)\*. *Number of platellae on 1st hind tarsomere*: (0) 0; (1) 1; (2) 2; (3) 3; (4) 4; (5) 5; (6) 6; (7) 7; (8) 9.

Several weighting methods were tested. Some analyses were performed using ‘unscaled’ equal weighting, this means no *a priori* weighting was applied (see Accessory Material on the *Invertebrate Systematics* website for NEXUS files of the unscaled weighting matrices of Dataset A and Dataset B). Other analyses included ‘scaled’ weighting, where characters are weighted in relation to their number of character states. As PAUP cannot handle fractional weights and the use of the default baseweight (baseweight = 1000) would have caused problems in this analysis due to roundoff error, a baseweight of 420 was chosen for dataset A, this being the lowest common multiple (LCM) of the numbers 1, 2, 3, 4, 5, 6 and 7, that represent the number of charac-

ter states present in the dataset minus one. Using the command ‘weights scale/baseweight = 420’, PAUP 4.0 assigns a weight of 420 to all binary characters and the weights shown in Table 2 to all multistate characters (see Accessory Material on the *Invertebrate Systematics* website for NEXUS file of the scaled weighting matrix of Dataset A). Dataset B contains characters with up to nine character states, therefore a baseweight of 840 was applied (see Accessory Material on the *Invertebrate Systematics* website for NEXUS file of the scaled weighting matrix of Dataset B).

Since dataset A includes ordered as well as unordered characters, a modified version of the ‘scaled’ weighting regime was also examined,

that downweights ordered multistate characters according to their number of character states (see Table 2), whereas binary characters and unordered multistate characters are given the baseweight of 420 (see Accessory Material on the *Invertebrate Systematics* website for NEXUS file of the modified scaled weighting matrix of Dataset A).

In order to find the topologies supported by the most consistent characters, successive approximations character weighting (Farris 1969, 1988; Carpenter 1988) was used for analyses of both datasets. The maximum value of the rescaled consistency index was used as a measure of fit. Based on the fit of the characters to the trees gained in the heuristic analysis, each character was weighted *a posteriori* and another heuristic search performed. This process of reweighting and searching was repeated until the weights no longer changed (Farris 1988) or identical sets of trees were obtained in consecutive searches.

### Taxonomic analysis

#### Terminology

The morphological terms applied here are illustrated in Figs 1, 2.

Anufriev and Emeljanov (1988) proposed a new terminology for the divisions of the fulgoroid head and some of these terms were further explained by Emeljanov (2002). This new terminology included introduction of the terms 'metope' (for frons) and 'coryphe' (for vertex). This was based on Weber (1935) who showed that the genuine frons is a small triangular area around the median ocellus. Emeljanov (2002) also explains that the transverse carina dividing the metope into eumetope and acrometope was named 'intermetopal keel' and the carina separating metope and coryphe was called 'anterior keel' of coryphe. In some tribes of Cixiidae, including the Gelastocephalini, where only one transverse carina is present between the coryphe and clypeus, the homology of this carina with either one or the other of these keels remains ambiguous. Consequently, it is often difficult to determine what constitutes the limit between coryphe and metope. Therefore, because the morphology of the head in Gelastocephalini (and other tribes of Cixiidae with only a single transverse carina) remains unresolved, the original terminology of vertex and frons is adopted here. It is acknowledged that the terms 'vertex' and 'frons', as used in this study, may not necessarily be homologous with structures similarly termed in other insect groups.

Furthermore, in this study the term 'clypeus' refers to a combination of the post- and anteclypeus, and the term 'face' includes both frons and clypeus. A gap in the row of apical spines on the hind tibia is considered large if it is at least as wide as the base of the third tooth (counted from the external side).

The following is a list of the main measurements taken in this study:

Body length: tip of head to tip of wing

Body width: distance between tegulae

Width of vertex: width at the level of the tip of basal emargination

Length of vertex: transverse carina to tip of basal emargination

Distance from anterior margin of eye to transverse carina between vertex and frons: shortest distance

Width of frons: at the level of the frontoclypeal suture

Length of frons: transverse carina to frontoclypeal suture

Width of forewings: at the level of apex of clavus

#### Generic concept

Generic limits were based on the generic concept described in Larivière (1999: 17), 'A genus should be a monophyletic group composed of one or more species separated from other genera by a decided gap'. In this study gaps between genera were in part defined by factors such as the number of evolutionary steps (character state changes) and degree of homoplasy in characters. In addition to characters included in the phylogenetic analysis performed in PAUP, other characters, e.g. diagnostic genitalic characters that cannot currently be used in phylogeny because structural homology is uncertain, were also used to group species together.

#### Species concept

The biological species concept defines species as groups of interbreeding natural populations that are reproductively isolated from other such groups. The biological properties of individuals that prevent the interbreeding of populations are in many cases not obvious, but morphological difference can give an indication of the underlying degree of reproductive isolation (Remane 1968; Mayr 1970, 1996; Wessel and Hoch 1999). In Gelastocephalini, as in other groups of Fulgoromorpha, the structure of the male genitalia is one of the main features distinguishing species (Fletcher 1985). This is based on the hypothesis that differences in the morphology of the male genitalia act as a barrier to interbreeding and hence to gene flow between different species (Remane 1968; Larivière and Hoch 1998; Larivière 1999; Wessel and Hoch 1999).

#### Preparation of male genitalia

Males were dissected by softening the entire specimen for 1–2 days in a humid chamber: a plastic box containing a paper towel soaked with vinegar to prevent mould. Mounted specimens were pinned on a piece of Styrofoam and put in the humid chamber. After softening, the specimens were demounted and the pygofer carefully removed using forceps and pins. The specimens were then remounted and the pygofer transferred to a beaker containing hot soapy water for few minutes to be softened further before examination. For the short-term, genitalia were stored in cavity slides (square piece of plexiglass, with a hole drilled into it, glued onto a microscopic slide) containing glycerol. For long-term storage, the genitalia were transferred into micro-vials containing glycerol.

#### Descriptions

Taxa are arranged alphabetically except for the type species that are listed first within each genus. Taxonomic descriptions were based primarily on male specimens. In the illustrations of the male genitalia, small-case letters were used to identify spines (or pairs of spines) on the phallosome. The position and arrangement of these spines vary between species, but in cixiid classification there is currently no basis to establish the homology of these structures. Consequently, letters identifying spines based on their structural position may or may not represent spines that are homologous between taxa.

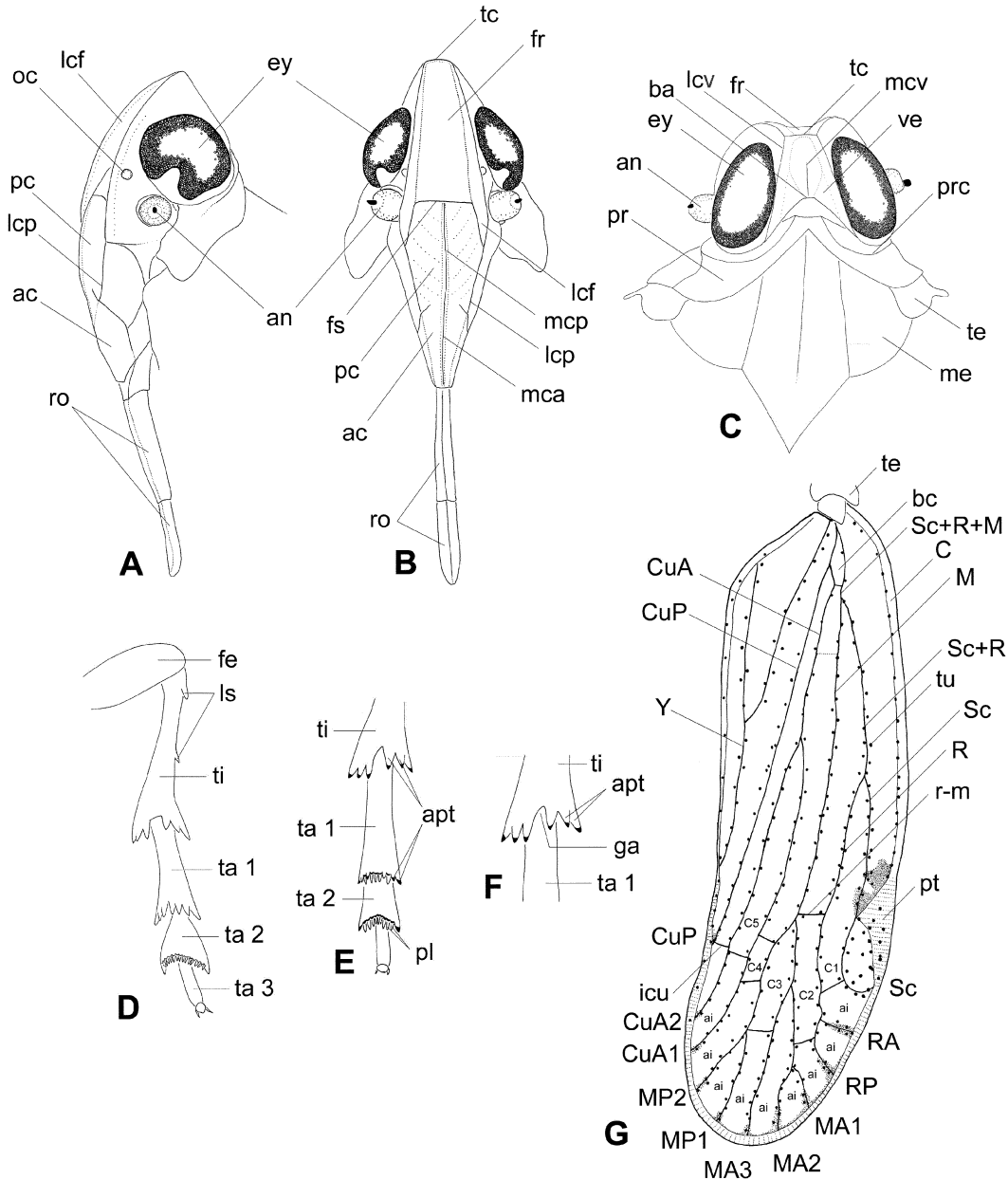
#### Associated plants, distribution

Very few associated plant records exist for the Gelastocephalini. These are listed in Table 3.

The geographic distribution section accompanying the descriptions of genera lists the regions from which taxa have been recorded. In some cases, females were used to provide additional distributional records for genera even when specific identification of these specimens was not possible. Since vast parts of Australia have not been comprehensively

**Table 2. List of weights assigned to multistate characters under the scaled weighting regime**

Number of characters states	Weight assigned
2	420
3	210
4	140
5	105
6	84
7	70
8	60



**Fig. 1.** *Novotarberus jacobii*: A, head left lateral; B, head facial; C, head and thorax dorsal. *Rhigedanus maculipennis*: D, hind leg. *Holgus liafredis*: E, hind tibia and tarsomeres; F, hind tibia and 1st tarsomere. *Novotarberus jacobii*: G, forewing. Abbreviations: ac, anteclypeus; an, antennae; ai, apical cell; apt, apical teeth; ba, basal emargination; bc, basal cell; C, Costa; C1–C5, subapical cells 1–5; CuA, Cubitus anterior; CuA1, Cubitus anterior 1; CuA2, Cubitus anterior 2; CuP, Cubitus posterior (= clavus); ey, eye; fe, femur; fr, frons; fs, frontoclypeal suture; ga, gap in row of apical teeth (= diastema *sensu* Emeljanov); icu, intercubitus; lcf, lateral carina of frons; lcp, lateral carina of postclypeus; ls, lateral spines of hind tibia; M, Media; MA1, Media anterior 1; MA2, Media anterior 2; MA3, Media anterior 3; mca, median carina of anteclypeus; me, mesonotum; mcp, median carina of postclypeus; mcv, median carina of vertex; MP1, Media posterior 1; MP2, Media posterior 2; oc, ocellus; pc, postclypeus; pl, platellae; pr, pronotum; prc, pronotal carina; R, Radius; pt, pterostigma; r–m, crossvein between Radius and Media; RA, Radius anterior; RP, Radius posterior; ro, rostrum; Sc, Subcosta; Sc+R, ScR-stalk; Sc+R+M, ScRM-stalk; ta 1, 1st tarsomere; ta 2, 2nd tarsomere; ta 3, 3rd tarsomere; tc, transverse carina (between vertex and frons); te, tegula; ti, tibia; tu, tubercle; ve, vertex; Y, Y-vein (Anal-vein).

surveyed, actual distributions may be much wider than indicated by the material available for study.

#### Illustrations

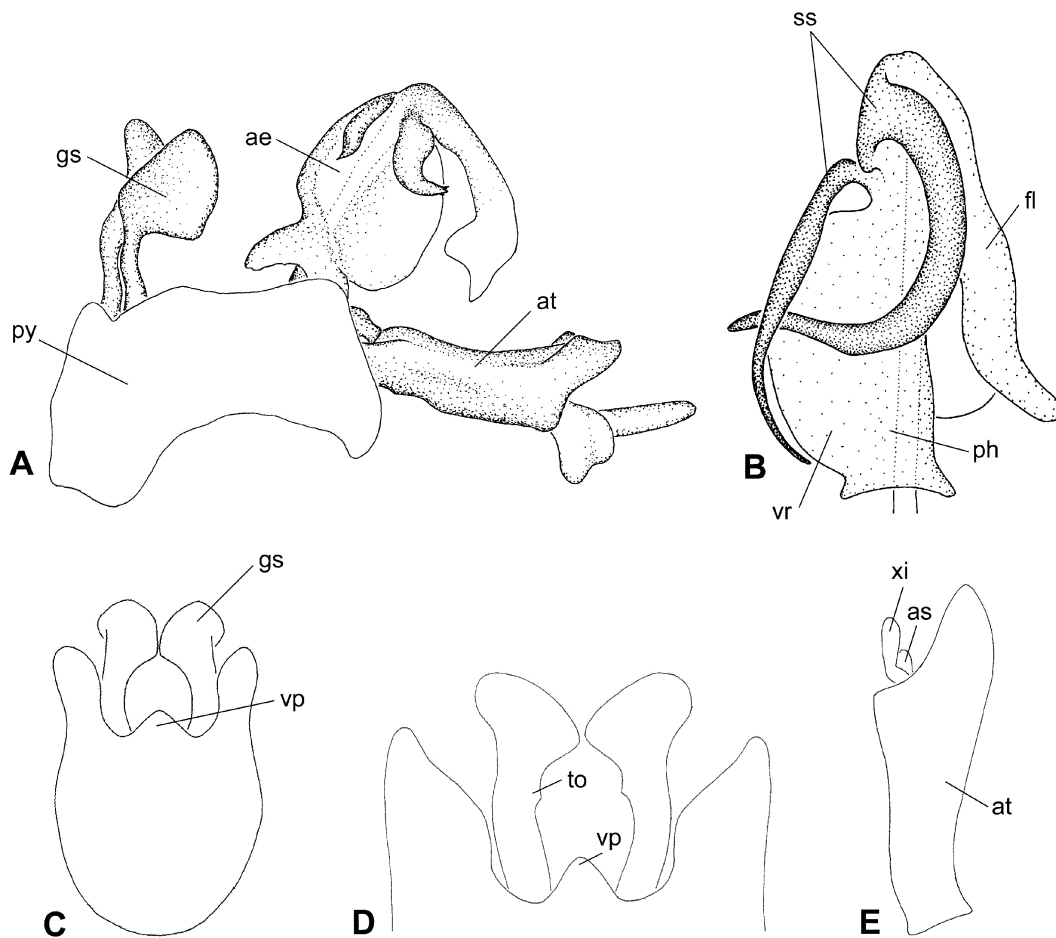
Scale bars given in the habitus photographs are 1 mm. No scale bars are provided for photographs of the head and illustrations of the male genitalia, since the shape of these structures is more important than their size. In general, the length of the aedeagus ranges between 0.3 and 0.8 mm, the length of the anal tube between 0.3 and 0.7 mm and the width of pygofer in lateral view between 0.2 and 0.6 mm.

#### Australian State abbreviations

NSW	New South Wales
NT	Northern Territory
Qld	Queensland
SA	South Australia
Tas.	Tasmania
Vic.	Victoria
WA	Western Australia

#### Institutional abbreviations

AM	Australian Museum, Sydney
ANIC	Australian National Insect Collection, CSIRO, Canberra
ASCU	Agricultural Scientific Collections Unit, NSW Department of Primary Industries, Orange
BMNH	The Natural History Museum, London
BPBM	Bernice Pauahi Bishop Museum, Honolulu
LOB	Lois O'Brien private collection, United States of America
MAMU	Macleay Museum, University of Sydney
NRS	Naturhistoriska Riksmuseet, Stockholm
QDPI	Queensland Department of Primary Industries, Brisbane
QM	Queensland Museum, Brisbane
SAM	South Australian Museum, Adelaide
UQIC	University of Queensland Insect Collection, Brisbane
WAM	Western Australian Museum, Perth
WADA	Department of Agriculture Western Australia: Perth



**Fig. 2.** *A* *Cixius similis*, male genitalia right lateral left lateral. *B* *Melanoclypeus cristatus*, aedeagus right lateral. *C*, *Schuerrera clypeocarinata*, pygofer and genital styles ventral. *D*, *Corylonga aaroni*, genital styles ventral; *E*, *C. krottendorfi*, anal tube left lateral. Abbreviations: ae, aedeagus; as, anal style; at, anal tube; fl, flagellum (moveable apical part of the aedeagus); gs, genital style; ph, phallosome (periandrium; covering basal part of the aedeagus); py, pygofer; ss, sclerotised spine; to, tooth on inner side of basal arm; vp, ventromedian process; vr, ventral ridge; xi, abdominal segment XI.

## Results

### Phylogenetic analysis

The results of character coding are shown in the data matrix (Table 4).

For purposes of comparison, the trees presented in Figs 3–9 were based on analyses using the same set of outgroups: outgroup 1, *Volcanalia* sp.; outgroup 2, *Cajeta singularis* and ‘*Cixius*’ *sidnicus*. However, several other analyses of both datasets using different sets of outgroups and excluding some of the characters that were assumed to be more homoplasious than others have also been performed, producing similar cladograms.

Trees of the following analyses are shown in Figs 3–9.

### Dataset A

A heuristic search with all characters equally weighted (weight = 1) retrieved 8287 most parsimonious trees (tree 1: length = 598 steps; *CI* = 0.2425, *HI* = 0.7575; *RI* = 0.6148; *RC* = 0.1491; *CI* excluding uninformative characters = 0.2412), a majority rule consensus tree of which is presented in Fig. 3.

Analysis of the matrix under the scaled weighting regime (that downweights all multistate characters) produced 35 most parsimonious cladograms (tree 1: length = 138822 steps, baseweight = 420; *CI* = 0.2398; *HI* = 0.7602; *RI* = 0.6156; *RC* = 0.1476; *CI* excluding uninformative characters = 0.2375). A strict consensus tree is presented in Fig. 4.

The modified scaled weighting regime resulted in three most parsimonious trees (tree 1: length = 166340 steps, baseweight = 420; *CI* = 0.2531, *HI* = 0.7469; *RI* = 0.6140 *RC* = 0.1554; *CI* excluding uninformative characters = 0.2512). These trees differed in the relationships of species within the genus *Corylonga* relative to each other. Figs 5 and Fig. 6 represent a phylogram of one of three most parsimonious trees.

### Dataset B

A heuristic search with all characters equally weighted (weight = 1) produced 3553 most parsimonious trees (tree 1:

length = 369 steps; *CI* = 0.3035, *HI* = 0.6965; *RI* = 0.6406; *RC* = 0.1944; *CI* excluding uninformative characters = 0.2997), a majority rule consensus tree of which is presented in Fig. 7.

Analysis of the matrix under the scaled weighting regime retrieved 117 most parsimonious cladograms (tree 1: length = 179151 steps, baseweight = 840; *CI* = 0.2964; *HI* = 0.7036; *RI* = 0.6624; *RC* = 0.1964; *CI* excluding uninformative characters = 0.2898). The trees varied in the arrangement of species within the genus *Corylonga*. A few trees did not support the monophyly of the genus *Candicarina*. A phylogram of one of 117 most parsimonious trees is presented in Figs 8, 9.

No modified scaled weighting regime was applied, since all characters in dataset *B* are unordered.

Some groupings remained consistent in all trees obtained from all analyses, whereas other groupings, varied in different analyses. Species of the following genera, *Corylonga* Löcker & Fletcher, gen. nov., *Fletcherolus* Löcker & Larivière, gen. nov., *Lariviera* Löcker & Fletcher, gen. nov., *Melanoclypeus* Löcker & Fletcher, gen. nov., *Payastylus* Löcker & Fletcher, gen. nov., *Rhigedanus* Emeljanov, *Ronaldia* Emeljanov, and *Schuerrera* Löcker & Fletcher, gen. nov. formed clades in all trees obtained, whereas for all other genera, monophyly was contradicted by at least one tree.

The relationships of genera relative to each other varied considerably between different analyses, however, the genera *Candicarina* Löcker & Larivière, gen. nov., *Gelastocephalus* Kirkaldy and *Melanoclypeus* grouped together in many analyses often also including the genus *Wernindia* Löcker & Fletcher, gen. nov. Another consistent grouping (only contradicted by the equal weighting analysis of dataset *B*) comprised the genera, *Orphninus*, *Dysoliarius* and *Rhigedanus*, described by Emeljanov (2000) in the subtribe Rhigedanina, which supported the monophyly of the subtribe. The subtribe Gelastocephalina, however, was shown to be paraphyletic in all analyses.

Rather unexpected was the placement of the outgroups *Cajeta singularis* and ‘*Cixius*’ *sidnicus* within the ingroup in some of the trees obtained.

**Table 3. Associated plant records**

Numbers in brackets give the number of specimens found on this host plant.

Taxon	Host plant
<i>Balyadimetopia krahalla</i>	<i>Eucalyptus marginata</i> (Myrtaceae; 1)
<i>Candicarina pulchra</i>	<i>Eucalyptus marginata</i> (Myrtaceae; 4), <i>Acacia falcata</i> (Mimosaceae; 1)
<i>Candicarina</i> sp.	<i>Eucalyptus marginata</i> (Myrtaceae; 3), <i>Acacia falcata</i> (Mimosaceae; 1)
<i>Carolus carinatus</i>	<i>Leptospermum laevigatum</i> (Myrtaceae; 1)
<i>Gelastocephalus ornithoides</i>	<i>Melaleuca nodosa</i> (Myrtaceae; 1)
<i>Gelastocephalus</i> sp.	<i>Caldcluvia paniculosa</i> (Cunoniaceae; 1), ‘mistletoe’ (Loranthaceae; 1)
<i>Hartliebchia towinna</i>	<i>Melaleuca quinquenervia</i> (Myrtaceae; 1)
<i>Lariviera yalthei</i>	<i>Allocasuarina pusilla</i> (Casuarinaceae; 1)
<i>Melanoclypeus cristatus</i>	<i>Eucalyptus largiflorens</i> (Myrtaceae; 1)
<i>Wernindia lorda</i>	<i>Rhizophora stylosa</i> (Rhizophoraceae; 1)



Table 4. Data matrix

Species	Characters																																														
	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	35	36	37	38	39	40	41	42	43				
Outgroups	1	0	3	0	1	1	2	0	2	0	2	1	2	1	0	0	1	0	0	0	0	1	0	0	0	2	0	0	0	0	1	0	2	2	1	0	2	1	0	2	1	1	0	1	1	0	
<i>Oliarus</i> sp.	1	2	1	1	1	?	?	2	1	0	1	?	1	2	1	0	0	1	0	0	0	0	0	0	3	1	0	0	0	0	1	0	2	2	1	0	2	1	0	2	1	0	1	1	1	1	0
<i>Apartus michalki</i>	0	0,1,2	3	0	1	0	2	2	1	0	1	1	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	1,2	0	1,2	1	1	1	2	0	1	1	1	0	
<i>Cixius sidicus</i>	0	1	1	0	1	0	2	2	1	0	1	2	1	0	0,1	1	0	0	0,1	1	0	1	0	0	1	0	0	0	0	0	0	1	2	1,2,3	0,1	2,3	1	1	1	2	0	3	0	0			
<i>Cajata singularis</i>	0	2	0	1	0	2	2	1	0	2	1	0	2	1	0	0	?	0	0	0	0	0	0	1	2	0	0	0	0	0	1	2	0	2	0	2	0	1	1	0	0	1	1	1	1		
<i>Volcanalia</i> sp.	0	2	3	1	1	1	2	2	0	0	1	1	2	1	0	0	1	1	0	0	0	0	1	2	0	0	1	2	0	0	1	2	2	2	0	1	1	1	0	0	1	1	0	0	1		
Outgroup 1	0	2	2	0	0	1	2	2	0	0	1	1	2	1	0	0	1	0	0,1	1	0	0	1	2	0	0	1	2	0	0	1	1,2	2	1	0	2	0	1	1	1	0	0	1	1	0		
Outgroup 2	0	2	2	0	0	1	2	2	0	0	1	1	2	1	0	0	0,1	1	0	0	0	1	2	0	0	1	2	0	0	1	0	1,2	2	1	0	2	0	1	1	1	0	0	1	1	0		
Outgroup 3	0	2	3	1	1	1	2	2	0	0,2	1	1	2	1	0	0	1	1	0	0	0	1	2	0	0	1	2	0	0	1	0	2	2	1	0	1	0	1	0	1	0	0	1	0	0		
Outgroup 4	0	2	5	1	1	1	2	2	0	1	1	2	1	1	0	0	1	1	0	0	0	1	2	0	0	1	2	0	0	1	0	2	2	1,3	0	0,1	0	1	1	0	0	0	1	0			
Rhagedanina																																															
<i>Dysoliarius unicornis</i>	0	1	4	0	0	0	0,1	?	0	3	1	2	1	2	1	0	0	1	0	1	0	0	1	0	0	1	0	0	0	1	1	0	2	2	0,1	2	1	1	1	2,3	1	1	1	1			
<i>Orphinus mouldsi</i>	0	1	2	1	0	2	0,1	0	1	2	1	2	1	2	1	0	0	0,1	1	0	0	1	0	0	1	0,1	2,3	0	0	1	0	1	2	1,2	1	0,1	2	0	1	1	1	1	1	1			
<i>Rhagedanus fomibaudus</i>	0	1	1,2	1	0	0,2	1	0	1	3	1	2	1	2	1	0	0,1	0	0	1	1	0	0	1	0	0	1	0,1	0	0	1	2	2	1	0	2,3	0,1	1	1	2,3	1	1	1	1			
<i>R. maculipennis</i>	0	1	2	1	0	2	1	0	1	3	1	1,2	1	2	1	0	0	0	1	1	0	0	1	1	0	0	1	1,2	2	1	0,1	1,2,3	1	1	1	1,2,3	1	1	1	1	1	1	1	1			
Gelastocephalina																																															
<i>Aubirestus semicirculatus</i>	0	0	3	1	0	1	1	2	0	1	1	2	1	2	?	0	0	0	1	0	0	0	0	0	2	0	0	0	1	1	0	0	?	1	2	1	2	1	1	1	?	0	1	1			
<i>Balyadimetopia frederi</i>	0	0	4	0	0	1	0	2	0	0	1	2	1	2	1	0	1	1,2	0	0	1	0	0	1	0	3	0	0	1	0	1,2	2	2	1	2	1	2	1	0,1	1	2	0	1	1			
<i>B. irahalla</i>	0	2	3	0	0	1	0	2	0	0	1	2	1	2	1	0	0,1	0	0	0	0	0	0	0	2	0	0	0	1	0	1	2	2	1	2	1	2	1	1	1	2	0	1	1			
<i>B. marci</i>	0	1	4	0	0	1	0	2	0	0	1	1	2	1	0	1	1	0	0	0	0	0	0	1	0	2	0	0	1	1	2	1,2	1	2	1	1	2	1	1	1	2	0	1	1			
<i>Barbontia spectabilis</i>	0	2	2	1	0	1	0	2	0	1	1	2	1	0	0	0,1	0	0	0	0	0	0	0	0	2,3	0	0	1	0	1	2	2,3	0	1	1	1	1	1	1	1	1	1	0	1	1		
<i>Candicarina geroldi</i>	0	3	1	1	0	2	0	1	1	2	1	1	1	2	1	0	0	0	0	0	0	0	0	0	2,3	0	0	1	0	1	0,1	2	1,2	0	2	1	?	1	2	0	1	1	1	1			
<i>C. pulchra</i>	0	3	1,2	1	0	1	0	1	1	1,2	1	1	1	2	1	0	0	0,1	0	0	0	0	0	0	2	0	0	1	0	1,2	1,2	1	0	2	1	0,1	1,2	0	1	1	1,2	0	1	1			
<i>Carolus carinatus</i>	0	0	3	1	0	1	1	1	0	3	1	1	2	1	0	0	1	0	0	1	0	0	0	1	2	0	0	1	0	1	2	1,2	2	1	2	1	2	1	1	2,3	0	1	1	1			
<i>C. crispus</i>	0	0	3	1	0	1	1	1	0	3	1	1	2	1	0	0	1	0	0	1	0	0	0	1	2	0	0	1	0	1	2	1	2	1	1	2	1	1	1	2	0	1	1				
<i>C. stirae</i>	0	0	3	1	0	1	1	1	0	3	1	1	2	0	0	0	1	0	0	1	0	0	0	1	2	0	0	1	0	1	1,2	1	3	1	2	1	?	?	3	0	1	1	1				
<i>Corylonga aaroni</i>	0	3	2	1	0	2	1	1	1	3	0	1	2	1	0	0	1	0	0	0	0	0	0	2	0	0	0	0	1	2	2	0	2	0,1	0	1	2	0	1	1	2	0	1	1			
<i>C. krotendorfi</i>	0	3	2	1	0	2	1	1	1	3	0	1	2	1	0	0	1	0	0	0	0	0	0	2	0	0	0	0	0	1	1	2	0	2	1	0	1	2	0	1	1	2	0	1			
<i>C. leighi</i>	0	3	1	1	0	2	1	1	1	3	0	1	2	1	0	0	1	0	0	0	0	0	0	2	0	0	0	0	0	0,1	1	1	2	1	2	1	2	1	0	1	2	0	1	1			
<i>C. lobata</i>	0	3	2	1	0	2	1	1	1	3	0,1	1	2	1	0	0	1,2	0	0	0	0	0	0	2	0	0	0	0	0,1	1	1	2	2	2	1	2	1	0	1	2,3	0	1	1	1			
<i>C. loisae</i>	0	3	2	1	0	2	1	1	1	3	0	1	2	1	0	0	1,2	0	0	0	0	0	0	2	0	0	0	0	0,1	1	1	2	2	2	1	2	1	0	1	2	0	1	1				
<i>C. malmudae</i>	0	3	2	1	0	2	1	1	1	3	0	1	2	1	0	?	1	0	0	0	0	0	0	2	0	0	0	0	0,1	1	1	1	2	1	2	1	0	1	2	0	1	1	1				
<i>C. triangula</i>	0	3	2	1	0	2	1	1	1	3	0,1	1	2	1	0	0	2	0	0	0	0	0	0	2	0	0	0	0	0,1	1	1	1	2,3	0	2	1	0	1	?	?	0	1	1				
<i>Fletcherolus lanceolatus</i>	0	2	2	1	0	1	2	0	1	2	0	1	2	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	1	1	2	1	1	2	1	1	1	2	0	1	1				
<i>F. monospinosus</i>	0	2	2	1	0	1	2	0	3	0	1	2	1	0	0	0	0,1	0	0	0	0	0	0	2	0	0	0	0	0	0	1	1	2	1	2	1	0	1	2	0	1	1	1				
<i>Gelastocaledonia monteithi</i>	0	1	2,3	1	0	1	1	1	0	1,2	1	1	2	1	0	0	1	0,1	0	0	0	0	0	2	0	0	0	0	0	0,1	0,1	2	2	1,2	0	1,2	0	1	1,2,3	0	1	1	1				
<i>Gelastocephalus ornithoides</i>	0	3	1	0	1	0	1	0	1	1,2	0	1	1	0,1	0	0	1	{23}	0	0	0	0	0	1	{23}	0	0	0	0	0	0,1	1,2	1,2	0	2	1	1	2	0	1	1	1	1				
<i>G. velfer</i>	0	3	2	1	0	1	?	0	1	1	0	?	1	1	0	0	1	3	0	0	0	0	1	3	0	0	0	0	0	1	2	1	2	1	0	2	1	1	1	1	1	0	1	1			
<i>Gurundus fuscumarginatus</i>	0	0	2	1	0	1	1	1	1	1	0	1	2	1	0	0	1	0,1	2	0	0	0	0	2	0	0	0	0	0	1	1	2	1	2	1	1	1	1	1	2	0	1	1				
<i>G. necostylus</i>	0	0	2	1	0	1	1	0	1	1	0	1	2	1	0	0	?	1	0	0	0	0	0	2	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	1	1				
<i>Guttala bernhardiae</i>	0	1	1	1	0	1	0	0	1	2	1	2	0	2	0	0	0	1	0	0	0	0	0	2	0	0	0	0	0	0	0	2	2	0	1	1	1	1	1	1	0	1	1				
<i>G. mona</i>	0	1	1	1	0	1	0	0	1	2	1	2	0	2																																	

Table 4. (continued)

Species	Characters																																														
	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	35	36	37	38	39	40	41	42	43				
<i>Melanoclypeus cristatus</i>	0	3	1	1	0	1	0	0	1	2	0	1,2	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1	1	1	1	1	1	0	2	1	1	1	1	0	1	1	1	
<i>M. uncinatus</i>	0	3	1	1	0	1,2	0	1	2	0	0,1	1,2	1	2	1	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0,1	1	1	1	1	1	0	2	0,1	1	1	1	1,2	0	1	1	1
<i>Metapilacha tobiasi</i>	0	2	2	1	0	1	0	2	0	2	1	2	1	2	1	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	2	1,2	1	0	2	0,1	0	0	0	1	0	0	1	1	
<i>Novotarbentus flagellospinatus</i>	0	1	1	0	1,2	0	0	1	2	0	2	1	2	1	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	1	0	3	0	1	0	2	2	1	0	1	0	1	0	1	1	1	
<i>N. jacobii</i>	0	1	3	1	0	1	0	0	2	0	2	1	2	1	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	1	0	1	0	2	2	1	0	2	1	0	1	0	1	0	1	1	
<i>N. pseudorpinatus</i>	0	3	1	1	0	1	0	0	1	2,3	0	?	1	2	1	0	0	0	0	0	0	0	0	0	0	0,1	0	0	0	0,1	0	1	2	1	1	0	2	0	1	1	0	1	0	1	1	1	
<i>N. remanei</i>	0	1	1	0	1	0	1	2	0	2	0	2	1	2	1	0	0	0	0	0	0	0	0	0	0	3	0	0	1	0	0,1	1	0	2	2	2	0	2	1	1	1	2	0	1	1	1	
<i>Payastylus brichrius</i>	0	1	2	1	0	2	1	2	0	2	1	1	0	2	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	2	2	0	2	1	1	1	1	1	?	1	1	1	1	
<i>P. gekkiae</i>	0	4	2	1	0	1	1	2	0	1,2	1	1	1	0	2	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	1	2	2	0	2	1	1	1	1	1	1	1	0	1	1
<i>P. kernae</i>	0	0	3	1	0	1	1	2	0	1	1	1	0	2	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	2	2	0	2	1	0	1	0	1	0	1	1	1
<i>Rokebia australis</i>	0	1	3	1	0	1	?	1	0	1	1	?	1	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	1	0	1	1	1	1
<i>Ronaldia emeljanovi</i>	0	2	2	0	0	1	?	1	0	0	1	2	1	2	1	0	1	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	2	2	0	2	1	1	1	1	2,3	0	2	1	1	
<i>R. fennahi</i>	0	2	3	0	0	0,1	2	0	0,1	1	2	1	2	1	1	0	1	0	1	0	0	0	0	0	0	2	0	0	0	0	0	1	1	2	1,2	2	0	2	0,1	1	1	2	0	1,2	0	1	1
<i>Schuerera chypeocarinata</i>	0	1	3	0	0	1	1	2	0	2	1	2	0	2	0	0	0	0	0	0	0	0	0	0	2,3	0	0	0	0	0	0	2	2	2,3	1	3	1	1	1	3,5	0	1	1	1	1		
<i>S. ecarinata</i>	0	1	3	1	0	1	0	2	0	0,2	1	2	0	2	0	0	0	0	0	0	0	0	0	0	1,2	0	0	0	0	0	1	1	2	2	2	2	1	1	1	1	2	0	1	1	1	1	
<i>S. merula</i>	0	1	2	0,1	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	1	2	1,2	2	1	1,2	0,1	1	1	1	0	1	1	1	1	
<i>Wernandia bubalis</i>	0	1	2	0,1	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	1	0,1	1	0	2,3	1	1	1	1	1	1	0	1	1		
<i>W. lorida</i>	0	1	1	1	0	1	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0,1	2	0	0	0	0	0	0,1	2	2	0	0	2	1	0	2	1	0	1	1	1	1	
<i>W. rhomboidea</i>	0	1	1	1	0	2	1	1	0	2	0	1	0	2	0	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	0	1	1	1	1	1	1	0	2	1	1	1	1	1	1	1	
<i>Yarnikada ulliae</i>	0	2	3	1	0	1	2	0	1	1	1	1	1	1	1	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	1	2	2	1	0	2	1	1	1	1	1	1,2	0	1	1	

Species	Characters																																																		
	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	25*	44*	47*								
<i>Oliarus sp.</i>	1	1	0	0	0	0	1	1	0	0	4	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0				
<i>Apartus michalki</i>	2	1	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?				
<i>Cixius sidicus</i>	5	3	1	2	6	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0				
<i>Cajeta singularis</i>	6	3	1	0	6	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
<i>Volcanalia sp.</i>	0	0	0	0	0	0	?	?	?	?	5	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
Outgroup 1	0	0	0	0	0	0	1	1	0	1	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
Outgroup 2	0	0	0	0	0	0	1	0	0	0	3	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
Outgroup 3	0	0	0	0	0	0	1	1	0	1	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Outgroup 4	0	0	0	0	0	0	1	1	0	1	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Rhigedania	5,6,7	4	1	0	6	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Dysolitanus unicoloris</i>	2	3	1	0	5,6	1	1	?	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Orphinus mouldsi</i>	1	4	1	0	6	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Rhigedanus fomibundus</i>	0,1	3,4	1	0	6	1	1	0	1	?	0,1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>R. maculipennis</i>	1	2	1	0	4	1	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Gelastoccephalina</i>	3	2	1	1	3	1	1	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Ambirestus semicirculatus</i>	2,3,4	2	1	1,2	3	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Bahvadimetopia frederi</i>	5	2	1	2	3	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>B. krakalla</i>	2	2	1	0	3	1	1	1	1	1</																																									

Table 4. (continued)

Species	Characters																																																
	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	25*	44*	47*						
<i>C. leighi</i>	5,6	2	1	2	4	1	1	1	?	?	1	0	0	0	0	0	0	1	1	0	2	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	1	0	0	1	5,6	6,7				
<i>C. lobata</i>	4	2	1	2	4	1	1	1	1	1	0	0	0	0	0	0	0	1	1	0	2	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	1	0	1	0	1	4	5			
<i>C. loisae</i>	4,6	2	1	2	3,4	1	1	?	?	?	0	0	0	0	0	0	0	1	1	0	2	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	1	4,6	5,7			
<i>C. mahmudae</i>	4	2	1	2	4	1	1	1	1	1	0	0	0	0	0	0	0	1	1	0	2	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	4	5					
<i>C. triangula</i>	4,5,6	2	1	2	4	1	1	1	1	1	1	0	0	0	0	0	0	1	1	0	2	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	4,5,6	5,6				
<i>Fletcherolus lanceolatus</i>	1	2	1	0	3	1	1	1	1	1	0	0	0	0	0	0	0	1	1	0	3	2	0	0	0	0	1	0	1	1	0	1	1	1	1	1	1	1	1	1	0	1	0	1	1	0			
<i>F. monospinosus</i>	1	2	1	0	3	1	1	1	1	1	0	0	0	0	0	0	0	1	1	0	3	2	0	0	0	0	1	0	1	1	0	1	1	1	1	1	1	1	1	1	0	1	0	1	1	0			
<i>Gelastocaladonia monteithi</i>	3,4	2,3	1	1	3,5	1	1	0	0	1	1	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	3,4	2,3			
<i>Gelastocephalus ornithoides</i>	1	1	1	1	1	1	1	0,1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?			
<i>G. welfjeri</i>	1	1	1	0	2	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?			
<i>Gururundus fuscumarginatus</i>	1	1	1	0	2	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?			
<i>G. nectosyrilus</i>	1	1	1	0	2	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?			
<i>Guttata bernhardtae</i>	5	2	1	2	4	1	1	?	?	?	?	1	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0		
<i>G. mona</i>	5	2	1	2	4	1	1	?	?	?	?	1	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	5	
<i>G. nickeli</i>	7	3	1	2	4	1	1	?	?	?	?	1	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	5	
<i>G. robierae</i>	5	2	1	2	4	1	1	?	?	?	?	1	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	5
<i>Hartriebia towinna</i>	1	1	1	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	
<i>Holgus ancistrus</i>	5	2	1	2	3,4	1	1	1	1	1	0	0	2	0	1	0	0	0	0	1	1	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	5
<i>H. spiralis</i>	5	2	1	2	4	1	1	?	?	?	?	1	0	0	2	0	1	0	0	1	1	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	5	5	
<i>H. unispinosus</i>	1	1	1	0	2	1	1	1	1	1	0	0	2	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	
<i>Lariviera yalhti</i>	2,3	1	1	1	1,2	1	1	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	
<i>L. yokunna</i>	3	1	1	1	2	1	1	1	1	1	0	0	0	0	0	0	0	0	0	1	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	
<i>Lipisia mystrotylus</i>	4	2	1	1	4	1	1	1	1	1	1	0	1	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	3	4
<i>Melanoclypeus cristatus</i>	1	1	1	0	2	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>M. uncinatus</i>	1	1	1	0	2	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Metaplacha tobiasi</i>	2,3	2	1	1	3	1	1	?	?	?	?	1	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	
<i>Novotarbus flagellospinosus</i>	3,4	2	1	1	3	1	1	0	0	1	1	0	0	0	0	0	0	0	0	2	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2,3
<i>N. jacobii</i>	3	2	1	1	3	1	1	?	?	?	?	0	0	0	0	0	0	0	0	0	2	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>N. pseudorhynchus</i>	2	2	1	1	3	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>N. remanei</i>	4	2	1	1	3,4	1	1	?	?	?	?	1	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Payastylus brichrius</i>	0,1	2	1	0	3	1	1	?	?	?	?	1	0	0	0	0	0	0	0	1	3	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>P. gekatae</i>	1,2	1	0	2,3	1	1	1	?	?	?	?	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>P. kernaee</i>	0	1	1	0	2	1	1	?	?	?	?	1	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Rokebia australis</i>	1	1	1	0	1,2	1	1	0	0	0	0	2	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Ronaldia emeljanovi</i>	1	1,2	1	0	1,2,3	1	1	?	?	?	?	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>R. fennahi</i>	4	2	1	2	3	1	1	?	?	?	?	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Schuerrera clypeocarinata</i>	4,5	2	1	2	3	1	1	?	?	?	?	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>S. ecarinata</i>	4	2	1	1	3	1	1	1	1	1	0	0	2	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>S. merula</i>	3	2	1	2	3	1	1	1	1	1	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Wernandia bubalis</i>	3	2	1	0	3																																												

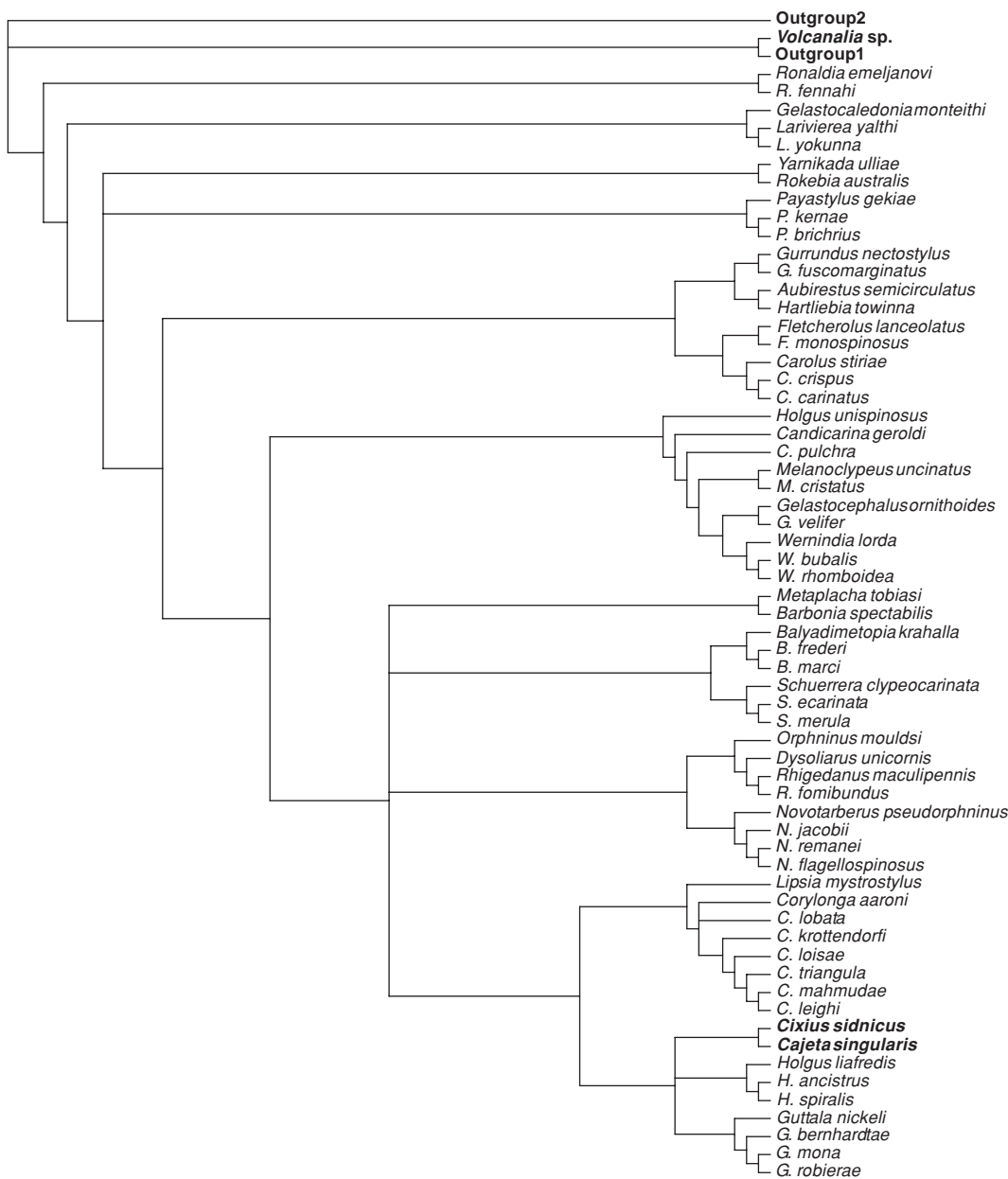
A more detailed discussion of these results is presented at the end of this paper.

**Taxonomic analysis**

New taxa in the following section have been jointly authored by B. Löcker and one co-author. For a list of genera and species of Gelastocephalini see Table 5.

**Key to genera of Gelastocephalini**

1. Pronotal carinae strongly elevated, forming more or less distinct ear-shaped lobes; hind tibia with large lateral spines; 2nd hind tarsomere with more than nine apical teeth . . . . . 2
2. Pronotal carinae only slightly elevated, not forming ear-shaped lobes; hind tibia usually without large lateral spines; if with large lateral spines, then 2nd hind tarsomere with at most nine apical teeth . . . . . 4
2. Frons with prominent apical process (Fig. 13A–C) . . . . . *Dysoliarius* Fennah
- Frons without such process. . . . . 3
- 3(2). Lateral carinae of frons distinctly widening at level of antennae (Fig. 14C, E); vertex, in lateral view, distinctly lowered in



**Fig. 3.** Majority rule consensus tree of all most parsimonious trees of dataset A obtained under the equal weighting regime (outgroups in bold).

- relation to hind margin of pronotum, not forming a common plane; pronotal carinae forming distinct ear-shaped lobes (Fig. 10); male phallosome not fimbriate below midlength (Fig. 46A) . . . . . *Rhigedanus* Emeljanov
- Lateral carinae of frons only slightly widening at level of antennae (Fig. 13E); vertex, in lateral view, not lowered in relation to hind margin of pronotum, forming a common plane; pronotal carinae forming poorly defined ear-shaped lobes; male phallosome fimbriate below midlength (Fig. 44A) . . . . . *Orphninus* Emeljanov
4. Forewings with 2–3 dark, bullate spots (Fig. 28F), sometimes reduced to dark streaks (Fig. 28F) . . . . . *Guttata*, gen. nov.
- Forewings without bullate spots or dark streaks . . . . . 5
- 5(4). Face in lateral view in two planes meeting at postclypeus (Fig. 42A) . . . . . *Wernindia*, gen. nov. (part)
- Face in lateral view more or less evenly convex (Fig. 25F) . . . . . 6
- 6(5). Lateral carinae of frons white to pale yellow . . . . . 7
- Lateral carinae of frons darker . . . . . 12
- 7(6). Face dark brown to black . . . . . 8
- Face paler . . . . . 12
- 8(7). Median carina of face concolorous with face . . . . . 9
- Median carina of face not concolorous with face . . . . . 12
- 9(8). First hind tarsomere with seven apical teeth, without platellae; vertex very narrow (Fig. 17D); male genital styles as in Figs 52E, F; 53F–G . . . . . *Candicarina*, gen. nov.
- First hind tarsomere with more than seven apical teeth and 1–5 platellae; vertex wider (Figs 31D, 32B, 41D); male genital styles different . . . . . 10
- 10(9). Median carina of frons present, incomplete (~1/2–3/4 as long as frons); 2nd hind tarsomere with fewer than nine apical teeth and seven platellae; subapical cells C4 and C5 of equal length; shape of male genital styles as in Figs 80–81D, E, with inner side of basal arm bearing small tooth . . . . . *Lariviera*, gen. nov.
- Median carina of frons absent; 2nd hind tarsomere with nine apical teeth and seven platellae; subapical cell C4 distinctly shorter than C5; shape of male genital styles different, inner side of basal arm lacking tooth . . . . . 11
- 11(10). Median carina of postclypeus evanescent; hind tibia with row of apical teeth interrupted by a narrow gap; 1st hind tarsomere with five platellae . . . . . *Wernindia*, gen. nov. (part)
- Median carina of postclypeus well developed; hind tibia with row of apical teeth interrupted by a wide gap; 1st hind tarsomere with fewer than five platellae . . . . . (part)
- . . . . . *Novotarberus*, gen. nov. (part)
- 12(6–8). Face yellow and very wide (frons less than 1.4× longer than wide) as in Figs 15E; 16C, E; 38E, 39C . . . . . 13
- Face not as above . . . . . 14
- 13(12). Median carina distinctly more elevated on anteclypeus than on postclypeus; lateral carinae of postclypeus well developed although not strongly enlarged or foliaceous; 1st hind tarsomere without platellae; male genital styles as in Figs 94; 95D, E . . . . . *Ronaldia* Emeljanov
- Median carina not distinctly more elevated on anteclypeus than on postclypeus; lateral carinae of postclypeus strongly enlarged, foliaceous; 1st hind tarsomere with at least three platellae; male genital styles as in Figs 48E, F; 49–50D, E . . . . . *Balyadimetopia*, gen. nov.
- 14(12). Face yellow or orange except for brown to black apical portion of anteclypeus; frons lacking median carina (Figs 25C, E; 33C, E) . . . . . 15
- Face, including anteclypeus, usually differently coloured, if yellow then frons with incomplete median carina . . . . . 16
- 15(14). Tip of head in lateral view acutely angled (Fig. 11A) . . . . . *Gelastocephalus* Kirkaldy
- Tip of head in lateral view obtusely angled (Fig. 11B) . . . . . *Melanoclypeus*, gen. nov.
- 16(14). First hind tarsomere lacking platellae . . . . . 17
- First hind tarsomere bearing at least one platella . . . . . 27
- 17(16). Body length of males >6.0 mm, females >7.2 mm; phallosome of male with a pair of very small spines ventrally near base (Figs 54A, B; 55–56A) . . . . . *Carolus* Kirkaldy
- Body length of males <5.5 mm, females <7.2 mm; phallosome of male lacking such spines ventrally near base . . . . . 18
- 18(17). Second hind tarsomere with seven apical teeth and five platellae . . . . . 19
- Second hind tarsomere with at least eight teeth and six platellae . . . . . 20
- 19(18). Tip of head in lateral view acutely angled (Fig. 11A); hind tibia with row of apical teeth interrupted by a narrow gap; forewing with concavity present on costal border (Fig. 29A), costa with more than 15 tubercles; male genital styles as in Fig. 75D, E . . . . . *Hartliebina*, gen. nov.
- Tip of head in lateral view obtusely angled (Fig. 11B); hind tibia with row of apical teeth interrupted by a wide gap; forewing without concavity on costal border, costa with fewer than 10 tubercles; male genital styles as in Fig. 93E, F . . . . . *Rokebia*, gen. nov.
- 20(18). Median carina of frons complete (extending from frontoclypeal suture to transverse carina) . . . . . 21
- Median carina of frons incomplete or absent . . . . . 26
- 21(20). Hind tibia with row of apical teeth interrupted by a narrow gap; shape of head as in Figs 23D, E; 24B, C . . . . . *Fletcherolus*, gen. nov.
- Hind tibia with row of apical teeth interrupted by a wide gap; shape of head different . . . . . 22
- 22(21). Lateral carinae of frons straight in facial view, thick, enlarging towards clypeus, pale yellow in colour (Fig. 17C); male genital styles as in Fig. 51E, F; phallosome with a large ventral ridge bearing a sclerotised spine (Fig. 51A, B) . . . . . *Barbonia*, gen. nov.
- Lateral carinae of frons convex or sinuate in facial view, thinner, not enlarging towards clypeus, differently coloured; male genital styles different; phallosome without a spine-bearing ridge . . . . . 23
- 23(22). Median carina of postclypeus well developed . . . . . 24
- Median carina of postclypeus evanescent or absent . . . . . *Payastylus*, gen. nov.
- 24(23). Tip of head in lateral view acutely angled (Fig. 11A) . . . . . 25
- Tip of head in lateral view obtusely angled (Fig. 11B) . . . . . *Yarnikada*, gen. nov.
- 25(24). Vertex about as wide as an eye in dorsal view (Fig. 31B); 2nd hind tarsomere with eight apical teeth and six platellae; male genital styles spoon-shaped as in Fig. 79E, F, with inner side of basal arm bearing a small tooth . . . . . *Holgus*, gen. nov. (part)
- Vertex much wider than an eye in dorsal view (Fig. 15B); 2nd hind tarsomere with 10 apical teeth and eight platellae; male genital styles as in Fig. 47E, F, not spoon-shaped, inner side of basal arm smooth, without tooth . . . . . *Aubivestus*, gen. nov.
- 26(20). Tip of head in lateral view acutely angled (Fig. 11A); 1st hind tarsomere with seven apical teeth; 2nd hind tarsomere with eight apical teeth and six platellae . . . . . *Gurrundus*, gen. nov.
- Tip of head in lateral view obtusely angled (Fig. 11B); 1st hind tarsomere with eight or nine apical teeth; 2nd hind tarsomere with nine apical teeth and seven platellae . . . . . *Wernindia*, gen. nov. (part)

- 27(16). Median carina on frons complete (reaching from the frontoclypeal suture to the transverse carina) ..... 28  
 Median carina on frons incomplete or absent ..... 29
- 28(27). Body length of males <3 mm, females <3.5 mm; 1st hind tarsomere with 8–9 apical teeth and 1–2 platellae .....  
 ..... *Metaplacha* Emeljanov  
 Body length of males >3.5 mm, females >4.5 mm; 1st hind tarsomere with 10–12 apical teeth and 4–6 platellae .....  
 ..... *Schuerrera*, gen. nov.
- 29(27). Median carina on postclypeus absent or evanescent; male genital styles as in Fig. 100D, E .....  
 ..... *Wernindia*, gen. nov. (part)  
 Median carina on postclypeus well developed; male genital styles different ..... 30
- 30(29). Vertex about as long as transverse carina (Fig. 24D) .....  
 ..... *Gelastocaledonia*, gen. nov.  
 Vertex at least twice as long as transverse carina ..... 31
- 31(30). Frons without median carina; inner side of basal arm of male genital styles lacking a small tooth ..... 32  
 Frons with incomplete median carina; inner side of basal arm of male genital styles bearing a small tooth (Fig. 2D) ..... 33
- 32(31). Body length <5 mm; face mid to dark brown with paler carinae .....  
 ..... *Novotarberus*, gen. nov. (part)  
 Body length >6 mm; face, including carinae, yellow .....  
 ..... *Lipsia*, gen. nov.
- 33(31). Vertex more than 1.7× longer than wide (Figs 20–22B, D; 23B), produced before eyes by more than 1/2 of an eye length; frons more than 2.1× longer than wide; shape of male genital styles as in Figs 57–63G .....  
 ..... *Corylonga*, gen. nov.  
 Vertex less than 1.3× longer than wide (Figs 29D; 30B, D), produced before eyes by less than 1/2 of an eye length; frons less than 1.5× longer than wide; male genital styles broadly spoon-shaped as in Figs 76F, 77G, 78H .....  
 ..... *Holgus*, gen. nov. (part)

#### Subtribe **RHIGEDANINA** Emeljanov

The following three genera were grouped in the subtribe Rhigedanina by Emeljanov (2000).

Information on monophyly and synapomorphies of this subtribe can be found in the discussion section of this paper, see ‘Monophyly and paraphyly of the subtribes’.

#### Genus **Dysoliarus** Fennah

*Dysoliarus* Fennah, 1949: 590.

Type species *Dysoliarus unicornis* Fennah, 1949, by original designation.

#### Description

##### Morphology

**Head.** Vertex slightly lowered in relation to the hind margin of the pronotum, not forming a common plane; as long as wide, produced before eyes by 1/2–3/4 of an eye length; apex broadly truncate; caudal border almost straight; lateral carinae slightly elevated (in some ♀ strongly elevated); median carina almost complete. Frons bearing prominent apical process; frons 1.1–1.5× longer than wide (excluding apical process), position of maximum width dis-

tinctly ventrad or around centre of frontoclypeal suture; lateral carinae double s-shaped, slightly elevated, lateral margins foliaceous, concealing base of antennae. Frontoclypeal suture semicircular, median part reaching at least lower margin of antennal scape; postclypeus with well developed lateral carinae and median carina; anteclypeus with well developed median carina.

**Thorax.** Pronotum with undulating carinae, the latter strongly elevated medially, forming distinct ear-shaped lobes; hind margin rather obtusely angled. Mesonotum with three distinct or evanescent longitudinal carinae. Forewing 3.0–3.5× longer than wide; costa without (rarely with 1–2) tubercles; concavity at costal border present; Sc+R+M forming long common stem; fork of Sc+R distad of fork of CuA1+CuA2; r-m1 basad of fork MA–MP; position of icu at CuP distad of apex of clavus; 10–11 apical cells. Hind leg: tibia with two large lateral spines of unequal length; six apical teeth in row interrupted by a wide gap; 1st tarsomere with 11–14 apical teeth and no platellae; 2nd tarsomere with 25–40 apical teeth and 23–38 platellae.

#### Distribution

NSW, Qld, SA, WA.

#### Remarks

The prominent apical process of the frons is diagnostic for this genus. Ear-shaped pronotal lobes are shared with *Rhigedanus* and *Orphninus* (although poorly defined in *Orphninus*). All other genera of Gelastocephalini lack ear-shaped lobes on the pronotum.

#### **Dysoliarus unicornis** Fennah

(Figs 13A–C, 43)

*Dysoliarus unicornis* Fennah, 1949: 591, fig. 4A–F.

#### Material examined

**Holotype.** ♂ (examined), Australia: WA: Dedari, 40 miles west of Coolgardie, 11.–21.i.1936 (R. E. Turner), B.M.196–28, ‘Carolus unicornis Fenn. Type’ (BMNH).

**Other material examined.** **Australia: WA:** 1♀, 82.2 km W of Agnew towards Sandstone, 650 m, 28°00.634’S 119°56.727’E, *Santalum lanceolatum*, Santalaceae, 26.x.1996, (Schuh & Cassis) (AM). **Qld:** 1♂, SE Qld, Isla Gorge, Lookout turnoff, 25°12’S 149°48’E, 380 m, open for[est], intercept, 22.ix–15.xii.1997 (D. Cook) (QM). **SA:** 1♀, Murray R. (H. S. Cope) (SAM). **NSW:** 1♀, 10 km E of Nyngan, at light, 26.x.1978 (K. F. Lambkin & D. R. Smith) (QM); 1♀, 28 km N of Dubbo, 3.xi.1982 (J. Doyen) (ANIC).

#### Description

##### Colour

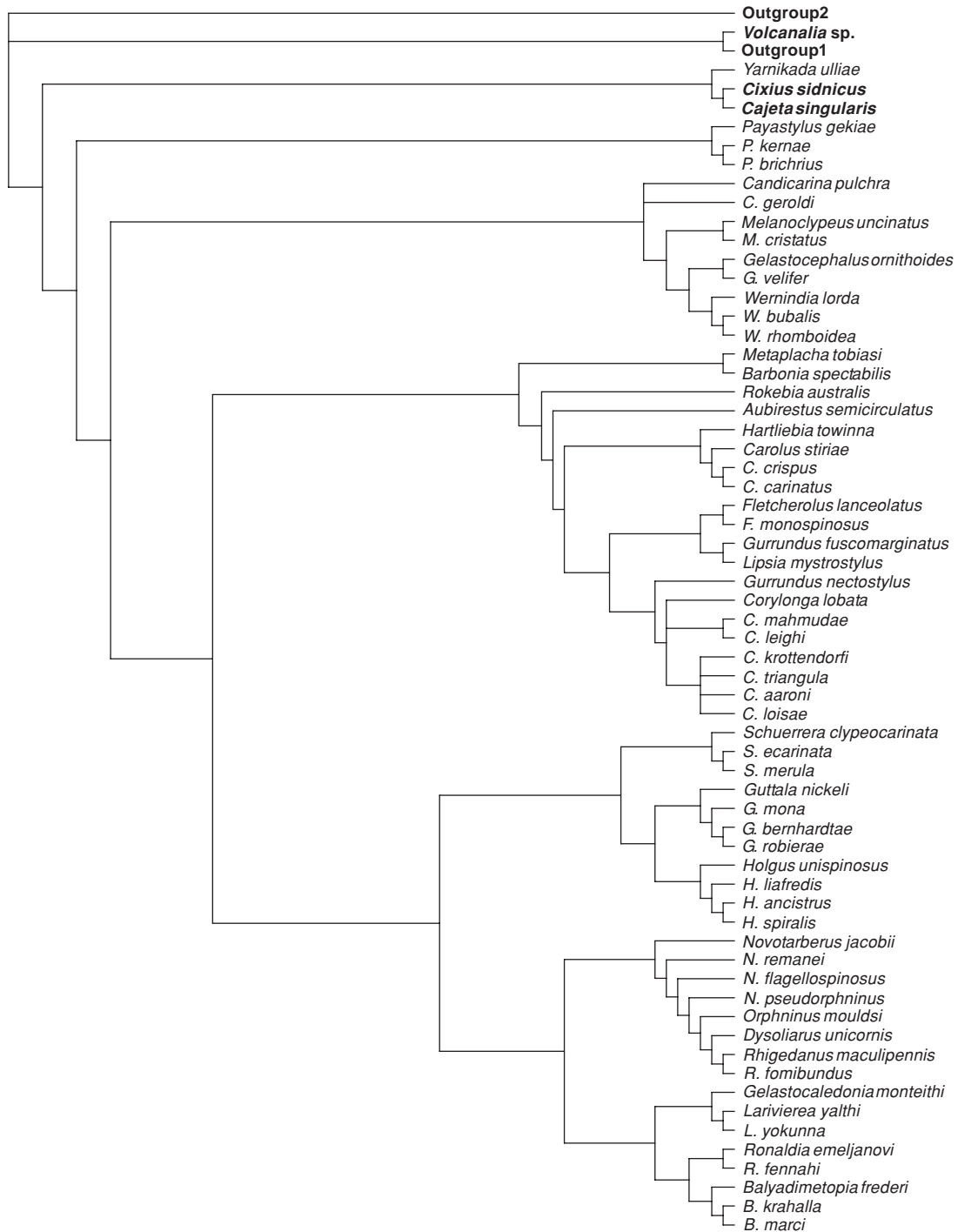
Vertex straw coloured, except for central part dark brown and transverse carina red brown; face dark brown, carinae straw coloured, apical process of frons mid brown with apical part dark brown; pronotum straw coloured, with

brown marks, ear-shaped lobes red brown; mesonotum dark brown, central part and carinae paler; legs yellow to brown; forewing hyaline colourless, veins light brown, tubercles mid brown; abdominal sternites dark brown, intersegmental membranes yellow.

### Morphology

Body length (excluding apical process of frons): ♂ 5.4–7.7 mm; ♀ 7.3–10.5 mm.

*Male genitalia.* Anal tube as in Fig. 43C, D; ventro-median process of pygofer and genital styles as in Fig. 43E,



**Fig. 4.** Strict consensus tree of all most parsimonious trees of dataset *A* obtained under the scaled weighting regime (outgroups in bold).

*F. Aedeagus* (Fig. 43A, B): phallosome with a long, slightly curved spine (*a*) arising ventrally near apex and a long, strongly curved spine (*b*) arising ventrolaterally above midlength; flagellum unarmed.

#### Remarks

In his description of the genus *Dysoliarius*, Fennah (1949: 591) stated, ‘.. Sc+R and M not forming a common stalk ..’. However, in the material examined here, including the holotype, a very long Sc+R+M common stem is present.

#### Genus *Orphninus* Emeljanov

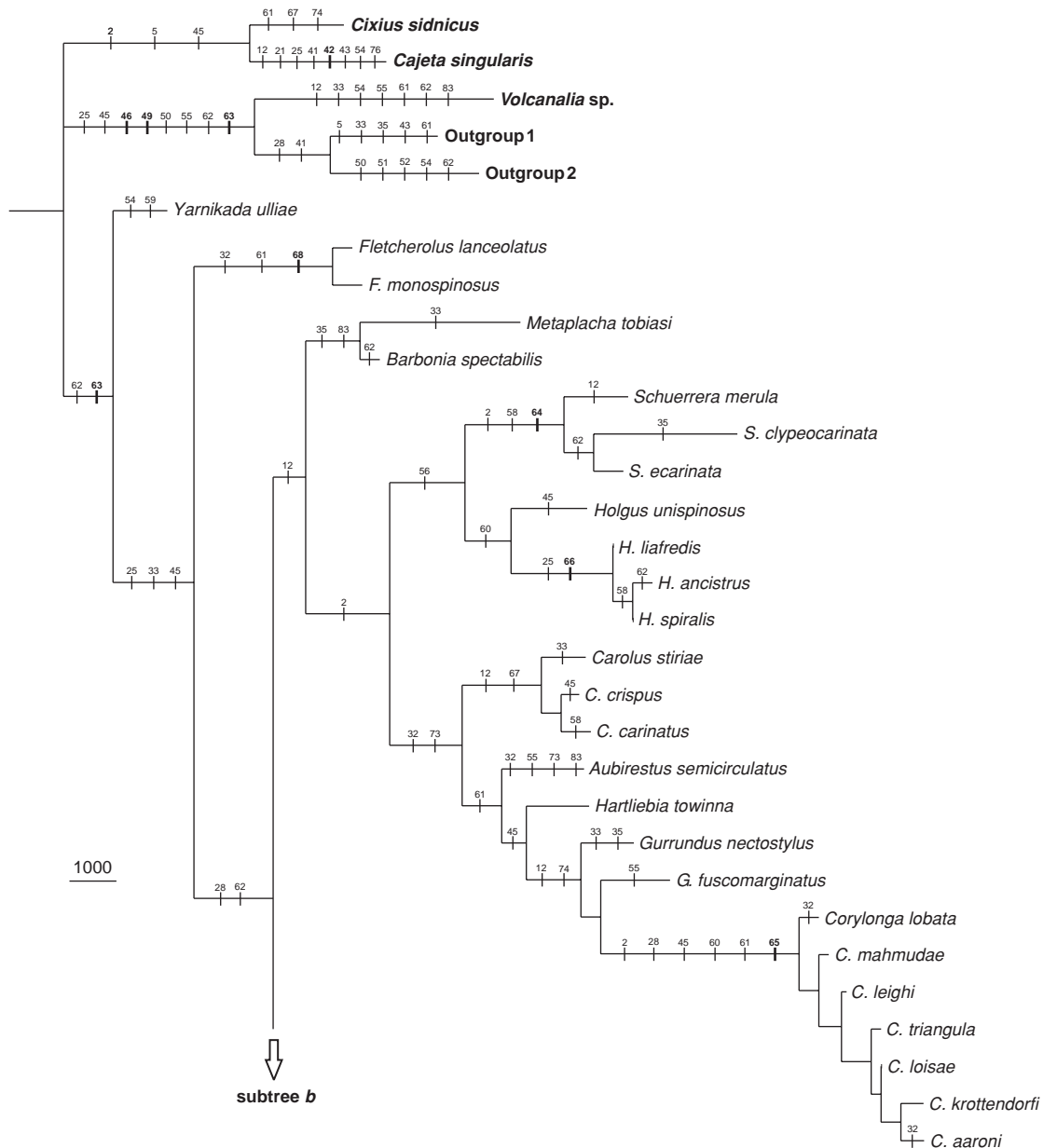
*Orphninus* Emeljanov, 2000: 263.

Type species *Orphninus mouldsi* Emeljanov, 2000, by original designation.

#### Description

##### Morphology

*Head.* Vertex not lowered in relation to hind margin of pronotum, forming a common plane; 2.0–2.2× longer than wide, produced before eyes by 1/4–1/3 of an eye length; apex

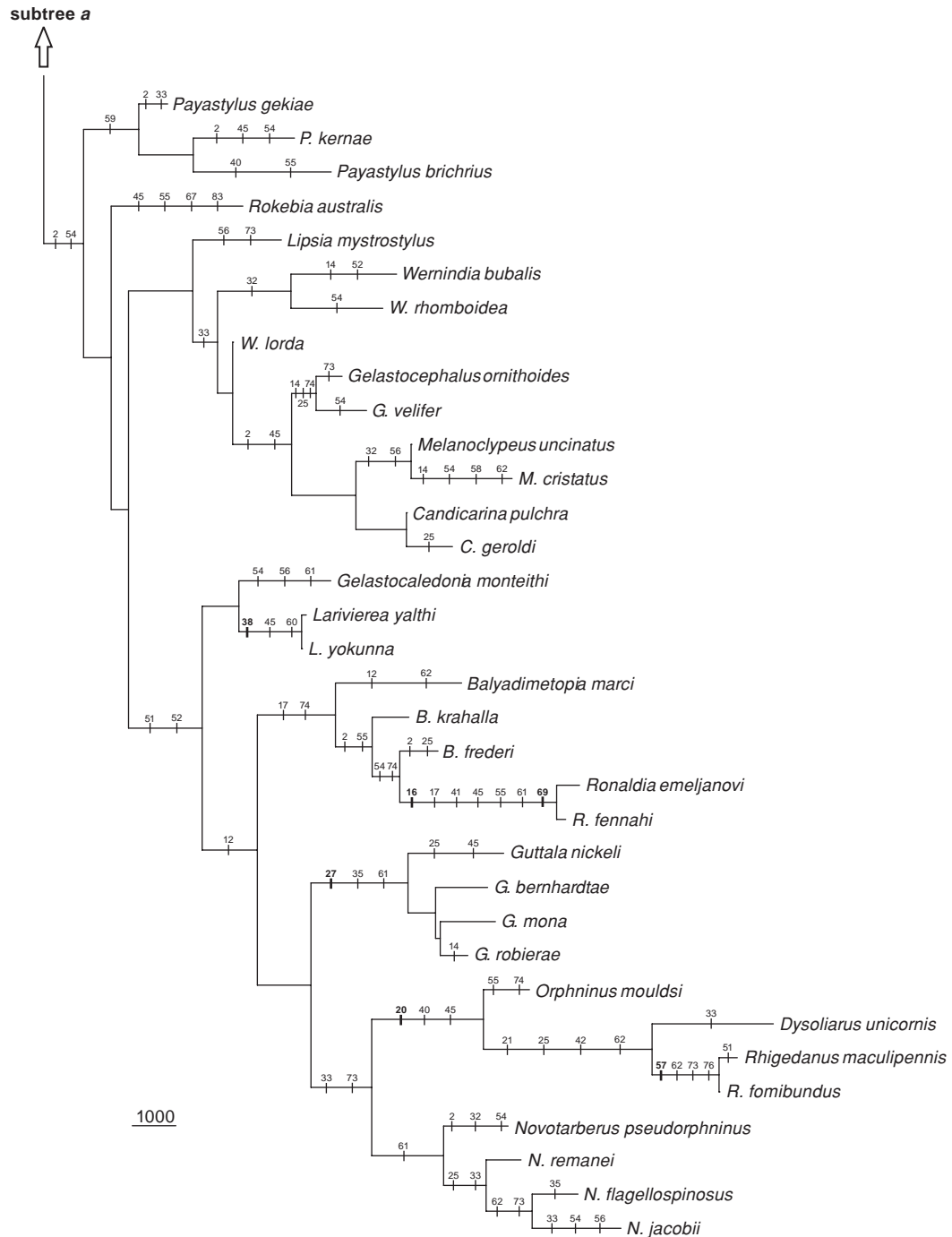


**Fig. 5.** Subtree *a* of the phylogram of one of three most parsimonious trees of dataset *A* obtained under the modified scaled weighting regime. Character numbers of all aut- and synapomorphies with consistency index (CI)  $\geq 0.25$  are indicated (outgroups and aut- and synapomorphies with CI = 1 in bold).



broadly truncate; caudal border v-shaped; lateral carinae strongly elevated; median carina incomplete, 1/4–1/2 as long as vertex. Frons at least 2.3× longer than wide, position of maximum width distinctly ventrad or around centre of frontoclypeal suture; lateral carinae slightly s-shaped, slightly widening at level of antennae (Fig. 13E); strongly

elevated, lateral margins foliaceous, concealing base of antennae; median carina absent. Frontoclypeal suture semi-circular, median part reaching at least lower margin of antennal scape; postclypeus with well developed lateral carinae and median carina; anteclypeus with well developed median carina.



**Fig. 6.** Subtree *b* of the phylogram of one of three most parsimonious trees of dataset *A* obtained under the modified scaled weighting regime. Character numbers of all aut- and synapomorphies with consistency index (*CI*) ≥ 0.25 are indicated (outgroups and aut- and synapomorphies with *CI* = 1 in bold).

*Thorax.* Pronotum with undulating carinae, the latter strongly elevated medially forming poorly defined ear-shaped lobes; hind margin right or obtusely angled. Forewing 3.0–3.5× longer than wide; costa with 15–24 tubercles; concavity at costal border present or absent; Sc+R+M forming long common stem; fork of Sc+R distinctly basad of fork of CuA1+CuA2; r-m1 distad of fork MA–MP; position of icu at CuP distad of or at same level as apex of clavus; nine apical cells. Hind leg: tibia with three large lateral spines (basal spine shorter than others); six apical teeth in row interrupted by a wide gap; 1st tarsomere with (7–)8 apical teeth and no platellae; 2nd tarsomere with

11–12 (15 in one specimen) apical teeth and 9–10 (13, one specimen) platellae.

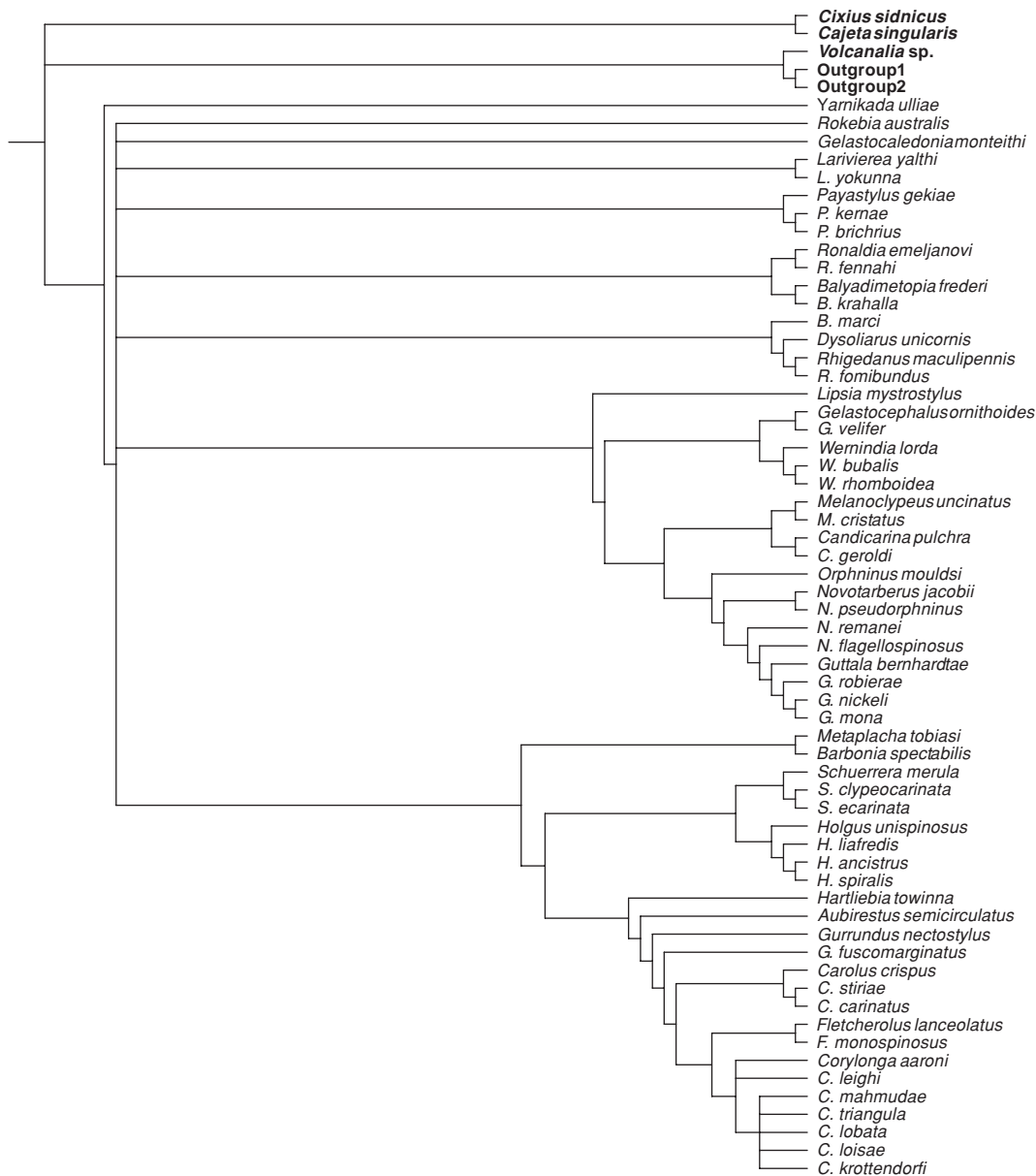
*Male genitalia.* Phallosome fimbriate below midlength (Fig. 44A).

*Distribution*

ACT, NSW, Qld.

*Remarks*

The ear-shaped lobes are poorly defined compared to those found in *Rhigedanus* and *Dysoliarius*. The combination of characters of the 2nd hind tarsomere with 15 apical teeth and



**Fig. 7.** Majority rule consensus tree of all most parsimonious trees of dataset *B* obtained under the equal weighting regime (outgroups in bold).

13 platellae was observed in one specimen only and may be an aberration. However, this kind of variation has been observed in other genera included by Emeljanov (2000) in the subtribe Rhigedanina.

***Orphnius mouldsi*** Emeljanov

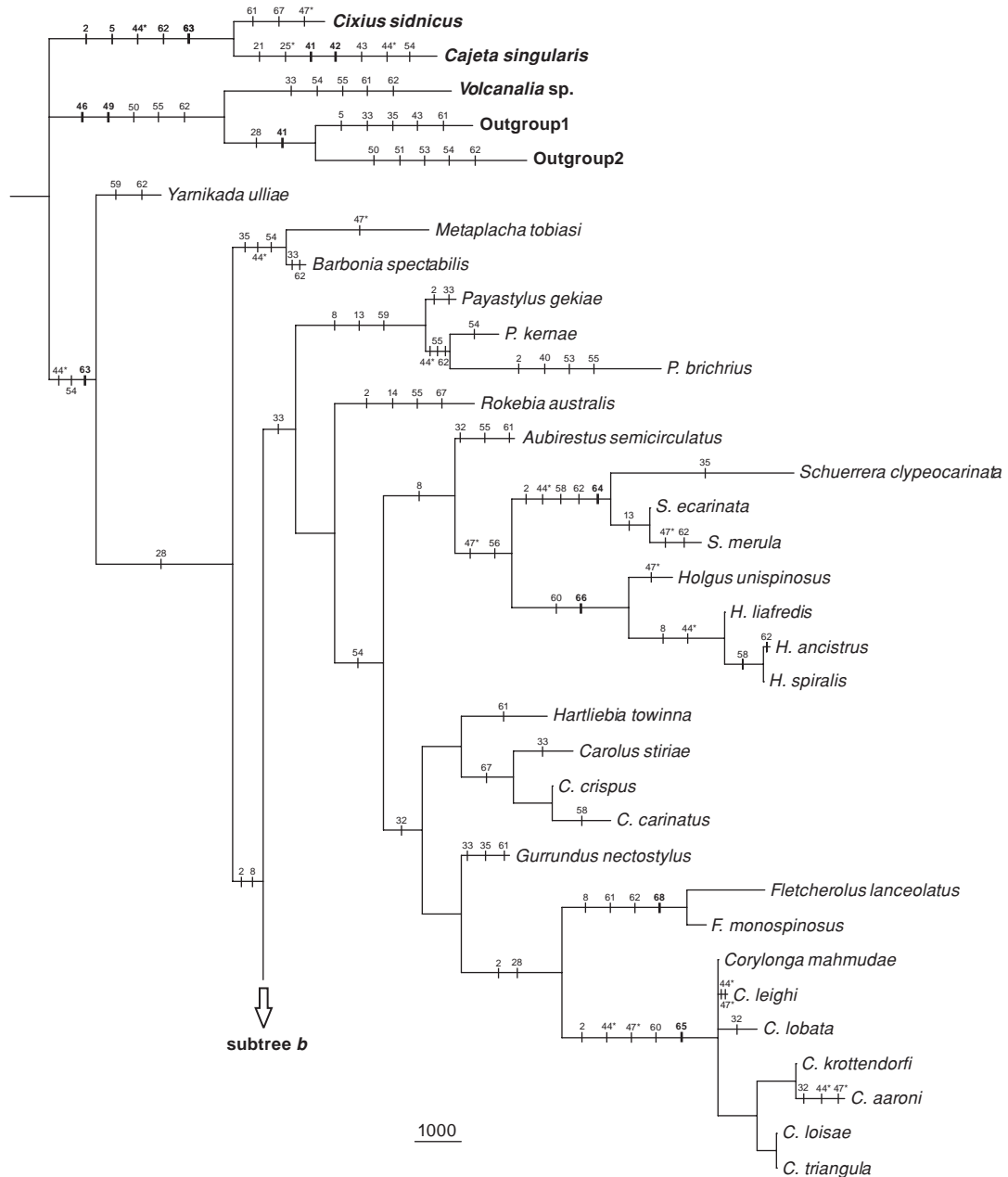
(Figs 13D–F, 44)

*Orphnius mouldsi* Emeljanov, 2000: 264, figs 37–48.

*Material examined*

*Holotype*. ♂ (examined), Australia: Qld: 10 km of St Lawrence turnoff, Waverley Rg, 21.xii.1987 (M. S. & B. J. Moulds) (ASCU ASCTHE028294).

*Paratypes*. **Australia**: **NSW**: 11 ♀ (examined), same data as holotype (ASCU); 1 ♂, 4 ♀ (3 ♀ examined), junction of Barradine Rd and



**Fig. 8.** Subtree *a* of the phylogram of one of 117 most parsimonious trees of dataset *B* obtained under the modified scaled weighting regime. Character numbers of all aut- and synapomorphies with consistency index (CI)  $\geq 0.25$  are indicated (outgroups and aut- and synapomorphies with CI = 1 in bold).

Newell Hwy, 11.xii.1987 (M.S. & B.J. Moulds) (ASCU). **ACT**: 1 ♀, Canberra, Black Mt, 12.xi.1963 (J. F. B. Common & M. S. Upton) (ANIC).

*Other material examined.* **Australia**: **Qld**: 1 ♂, St Anthonpe, 9.x.1924 (QM); 9 ♀, Gurgeena Plateau, site 2, 25°27'S 151°23'E, 360 m, open forest, mv light, 14.x.2001 (Monteith & Cook) (QM); 1 ♀, Fletcher, iii.1948 (E. S.[utton]), (BMNH); 1 ♀, Fletcher, 18.x.1931 (E. Sutton), (BMNH).

### Description

#### Colour

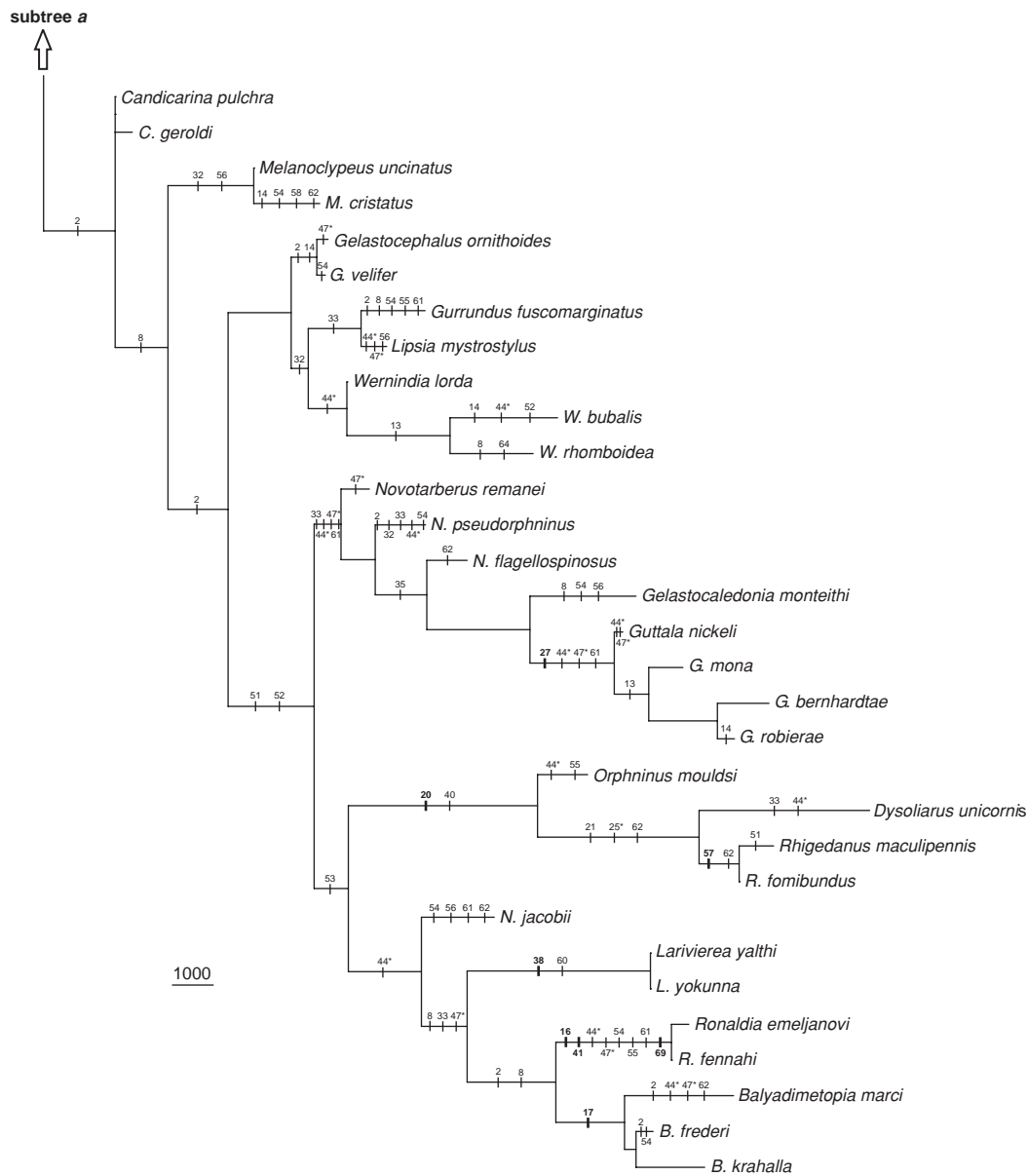
Vertex dark brown to black, lateral carinae yellow, median carina mid brown; frons dark brown to black, lateral carinae

yellow; clypeus and genae dark brown; lateral parts of head yellow to orange; pronotum yellow; mesonotum dark brown to black; legs yellow, apical teeth on hind tibia and 1st tarsomere brown; forewing hyaline white with yellow and brown areas, veins and tubercles concolorous with cells; abdominal sternites dark brown to black, intersegmental membranes yellow.

### Morphology

*Body length.* ♂ 6.2–6.3 mm; ♀ 6.3–7.5 mm.

*Male genitalia.* Anal tube as in Fig. 44B, C; ventro-median process of pygofer and genital styles as in Fig. 44D, E. Aedeagus (Fig. 44A): phallosome fimbriate below midlength



**Fig. 9.** Subtree *b* of the phylogram of one of 117 most parsimonious trees of dataset *B* obtained under the modified scaled weighting regime. Character numbers of all aut- and synapomorphies with consistency index (CI)  $\geq 0.25$  are indicated (outgroups and aut- and synapomorphies with CI = 1 in bold).

and with a long, moderately curved spine arising laterally near apex; flagellum unarmed.

Genus *Rhigedanus* Emeljanov

*Rhigedanus* Emeljanov, 2000: 264.

Type species *Rhigedanus fomibundus* Emeljanov, 2000, by original designation.

Description

Morphology

Body length. ♂ 6.1–7.8 mm, ♀ 7.8–10.4 mm.

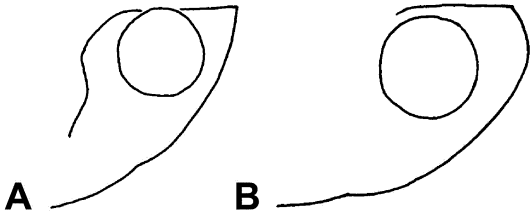
*Head.* Vertex distinctly lowered in relation to hind margin of pronotum, not forming a common plane; 1.1–1.5× longer than wide; apex broadly truncate; caudal border shallowly u- or v-shaped; median carina less than 1/2 as long as vertex. Frons with its maximum width around centre of frontoclypeal suture; lateral carinae strongly elevated, subparallel for most of their length, then strongly widening at level of antennae (Fig. 14C, E), strongly elevated, lateral margin foliaceous, concealing base of antennae; median carina absent. Postclypeus with well developed lateral carinae and median carina.

**Table 5. Alphabetical checklist of Gelastocephalini taxa**  
Subtribes, genera and type species in bold

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Subtribe ‘ <b>Gelastocephalina</b> ’ Emeljanov, 2000	<i>spiralis</i> Löcker & Larivière, sp. nov.
Genus <b><i>Aubirestus</i></b> Löcker & Larivière, gen. nov.	<i>unispinosus</i> Löcker & Larivière, sp. nov.
<i>semicirculatus</i> Löcker & Larivière, sp. nov.	Genus <b><i>Lariviera</i></b> Löcker & Fletcher, gen. nov.
Genus <b><i>Balyadimetopia</i></b> Löcker & Larivière, gen. nov.	<i>yalthi</i> Löcker & Fletcher, sp. nov.
<i>frederi</i> Löcker & Larivière, sp. nov.	<i>yokunna</i> Löcker & Fletcher, sp. nov.
<i>krahalla</i> Löcker & Larivière, sp. nov.	Genus <b><i>Lipsia</i></b> Löcker & Fletcher, gen. nov.
<i>marci</i> Löcker & Larivière, sp. nov.	<i>mystrostylus</i> Löcker & Fletcher, sp. nov.
Genus <b><i>Barbonia</i></b> Löcker & Larivière, gen. nov.	Genus <b><i>Melanoclypeus</i></b> Löcker & Fletcher, gen. nov.
<i>spectabilis</i> Löcker & Larivière, sp. nov.	<i>cristatus</i> Löcker & Fletcher, sp. nov.
Genus <b><i>Candicarina</i></b> Löcker & Larivière, gen. nov.	<i>uncinatus</i> Löcker & Fletcher, sp. nov.
<i>geroldi</i> Löcker & Larivière, sp. nov.	Genus <b><i>Metaplacha</i></b> Emeljanov, 2000
<i>pulchra</i> Löcker & Larivière, sp. nov.	<i>tobiasi</i> Emeljanov, 2000
Genus <b><i>Carolus</i></b> Kirkaldy, 1906	Genus <b><i>Novotarberus</i></b> Löcker & Fletcher, gen. nov.
<i>carinatus</i> Löcker & Larivière, sp. nov.	<i>flagellospinosus</i> Löcker & Fletcher, sp. nov.
<i>crispus</i> Kirkaldy, 1906	<i>jacobii</i> Muir 1931 comb. nov.
<i>stiriae</i> Löcker & Larivière, sp. nov.	<i>pseudorphninus</i> Löcker & Fletcher, sp. nov.
Genus <b><i>Corylonga</i></b> Löcker & Fletcher, gen. nov.	<i>remanei</i> Löcker & Fletcher, sp. nov.
<i>aaroni</i> Löcker & Fletcher, sp. nov.	Genus <b><i>Payastylus</i></b> Löcker & Fletcher, gen. n
<i>krottendorfi</i> Löcker & Fletcher, sp. nov.	<i>brichrius</i> Löcker & Fletcher, sp. nov.
<i>leighi</i> Löcker & Fletcher, sp. nov.	<i>gekiae</i> Löcker & Fletcher, sp. nov.
<i>lobata</i> Löcker & Fletcher, sp. nov.	<i>kernae</i> Löcker & Fletcher, sp. nov.
<i>loisae</i> Löcker & Fletcher, sp. nov.	Genus <b><i>Rokebia</i></b> Löcker & Fletcher, gen. nov.
<i>mahmudae</i> Löcker & Fletcher, sp. nov.	<i>australis</i> Löcker & Fletcher, sp. nov.
<i>triangula</i> Löcker & Fletcher, sp. nov.	Genus <b><i>Ronaldia</i></b> Emeljanov, 2000
Genus <b><i>Fletcherolus</i></b> Löcker & Larivière, gen. nov.	<i>emeljanovi</i> Löcker & Fletcher, sp. nov.
<i>lanceolatus</i> Löcker & Larivière, sp. nov.	<i>fennahi</i> Emeljanov, 2000
<i>monospinosus</i> Löcker & Larivière, sp. nov.	Genus <b><i>Schuerrera</i></b> Löcker & Fletcher, gen. nov.
Genus <b><i>Gelastocaledonia</i></b> Löcker & Larivière, gen. nov.	<i>clypeocarinata</i> Löcker & Fletcher, sp. nov.
<i>monteithi</i> Löcker & Larivière, sp. nov.	<i>ecarinata</i> Löcker & Fletcher, sp. nov.
Genus <b><i>Gelastocephalus</i></b> Kirkaldy, 1906	<i>merula</i> (Distant), comb. nov.
<i>ornithoides</i> Kirkaldy, 1906	Genus <b><i>Wernindia</i></b> Löcker & Fletcher, gen. nov.
<i>velifer</i> Löcker & Larivière, sp. nov.	<i>bubalis</i> Löcker & Fletcher, sp. nov.
Genus <b><i>Gurrundus</i></b> Löcker & Larivière, gen. nov.	<i>lorda</i> Löcker & Fletcher, sp. nov.
<i>fuscomarginatus</i> Löcker & Larivière, sp. nov.	<i>rhomboidea</i> Löcker & Fletcher, sp. nov.
<i>nectostylus</i> Löcker & Larivière, sp. nov.	Genus <b><i>Yarnikada</i></b> Löcker & Fletcher, gen. nov.
Genus <b><i>Guttala</i></b> Löcker & Larivière, gen. nov.	<i>ulliae</i> Löcker & Fletcher, sp. nov.
<i>bernhardtae</i> Löcker & Larivière, sp. nov.	Subtribe <b><i>Rhigedanina</i></b> Emeljanov, 2000
<i>mona</i> Löcker & Larivière, sp. nov.	Genus <b><i>Dysoliarus</i></b> Fennah, 1949
<i>nickeli</i> Löcker & Larivière, sp. nov.	<i>unicornis</i> Fennah, 1949
<i>robierae</i> Löcker & Larivière, sp. nov.	Genus <b><i>Orphninus</i></b> Emeljanov, 2000
Genus <b><i>Hartliebia</i></b> Löcker & Larivière, gen. nov.	<i>mouldsi</i> Emeljanov, 2000
<i>towinna</i> Löcker & Larivière, sp. nov.	Genus <b><i>Rhigedanus</i></b> Emeljanov, 2000
Genus <b><i>Holgus</i></b> Löcker & Larivière, gen. nov.	<i>fomibundus</i> Emeljanov, 2000
<i>ancistrus</i> Löcker & Larivière, sp. nov.	<i>maculipennis</i> Emeljanov, 2000
<i>liafredis</i> Löcker & Larivière, sp. nov.	

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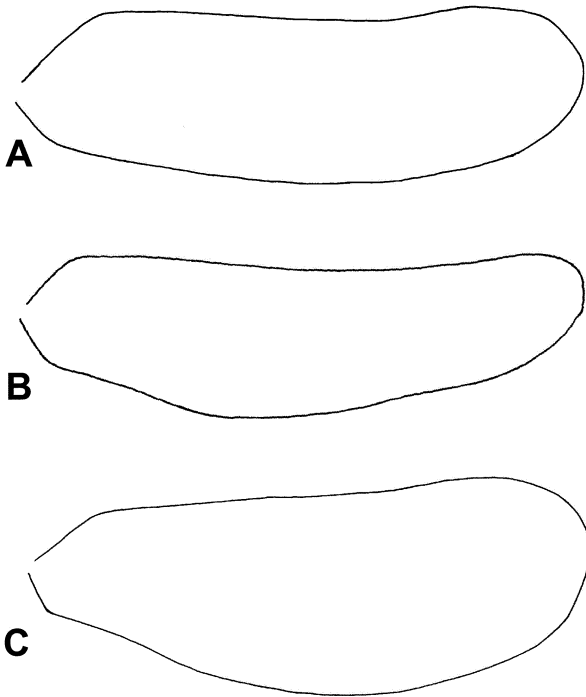
**Fig. 10.** Shape of tip of head, lateral view. *A*, *Lipsia mystrostylus*; *B*, *Melanocypeus cristatus*.

**Thorax.** Pronotum long in relation to body length, declivous, carinae strongly elevated medially forming distinct ear-shaped lobes; carinae and lateral parts of hind border of pronotum strongly elevated; hind margin obtusely angled. Mesonotum with three distinct or evanescent longitudinal carinae. Forewing 2.5–3.5× longer than wide; concavity at costal border present; Sc+R+M forming long common stem; r-m1 distad of or at same level as fork MA–MP; position of icu at CuP distad of apex of clavus. Hind tibia with six apical teeth in row interrupted by a wide gap; 1st tarsomere without platellae.

**Male genitalia.** Anal tube as in Figs 45C, 46C; ventro-median process of pygofer and genital styles as in Figs 45D, E; 46D, E. Aedeagus (Figs 45A, 46A): phallosome with a straight spine arising left laterally near apex.

#### *Distribution*

ACT, NSW, SA, WA.



**Fig. 11.** Shape of forewing. *A*, *Novotarberus jacobii*; *B*, *N. flagellospinus*; *C*, *N. remanei*.

#### *Remarks*

Emeljanov (2000) described a pattern of infusate spots on the wings of males and females of *Rhigedanus maculipennis*. In the material examined here, this colour pattern was also detected in a male and a female specimen of *Rhigedanus fomibundus*. Therefore, it cannot be used for differentiating the two species in *Rhigedanus*. Females could only be identified to genus level. The measurements of females given above are derived from eight specimens from NSW, SA and WA. In the description of *Rhigedanus* Emeljanov (2000) stated that the median carina of the vertex is absent. This differs from our observations that showed a distinct, although incomplete median carina less than 1/2 as long as the vertex.

In the phylogenetic analysis all weighting regimes support the monophyly of the genus *Rhigedanus*. The shape of the anal tube (Figs 45C, 46C) and genital styles (Figs 45D, E; 46D, E) are synapomorphies for this genus. Other characteristics of *Rhigedanus* are a long pronotum in relation to the body length (this feature is also shared with *Cajeta singularis*) and the strongly elevated carinae and lateral borders of the pronotum. The feature, vertex distinctly lowered in relation to the hind margin of the pronotum (not forming a common plane) and the presence of distinct ear-shaped lobes on the pronotum are shared with the genus *Dysoliarus*, these conditions are not observed in any other Gelastocephalini.



**Fig. 12.** Ear-shaped lobes, *Rhigedanus fomibundus*.

**Key to species of *Rhigedanus***

- 1. Spine on phallotheca half as long as flagellum (Fig. 45A) . . . . .  
     . . . . . *R. fomibundus* Emeljanov
- Spine on phallotheca as long as flagellum (Fig. 46A) . . . . .  
     . . . . . *R. maculipennis* Emeljanov

***Rhigedanus fomibundus* Emeljanov**

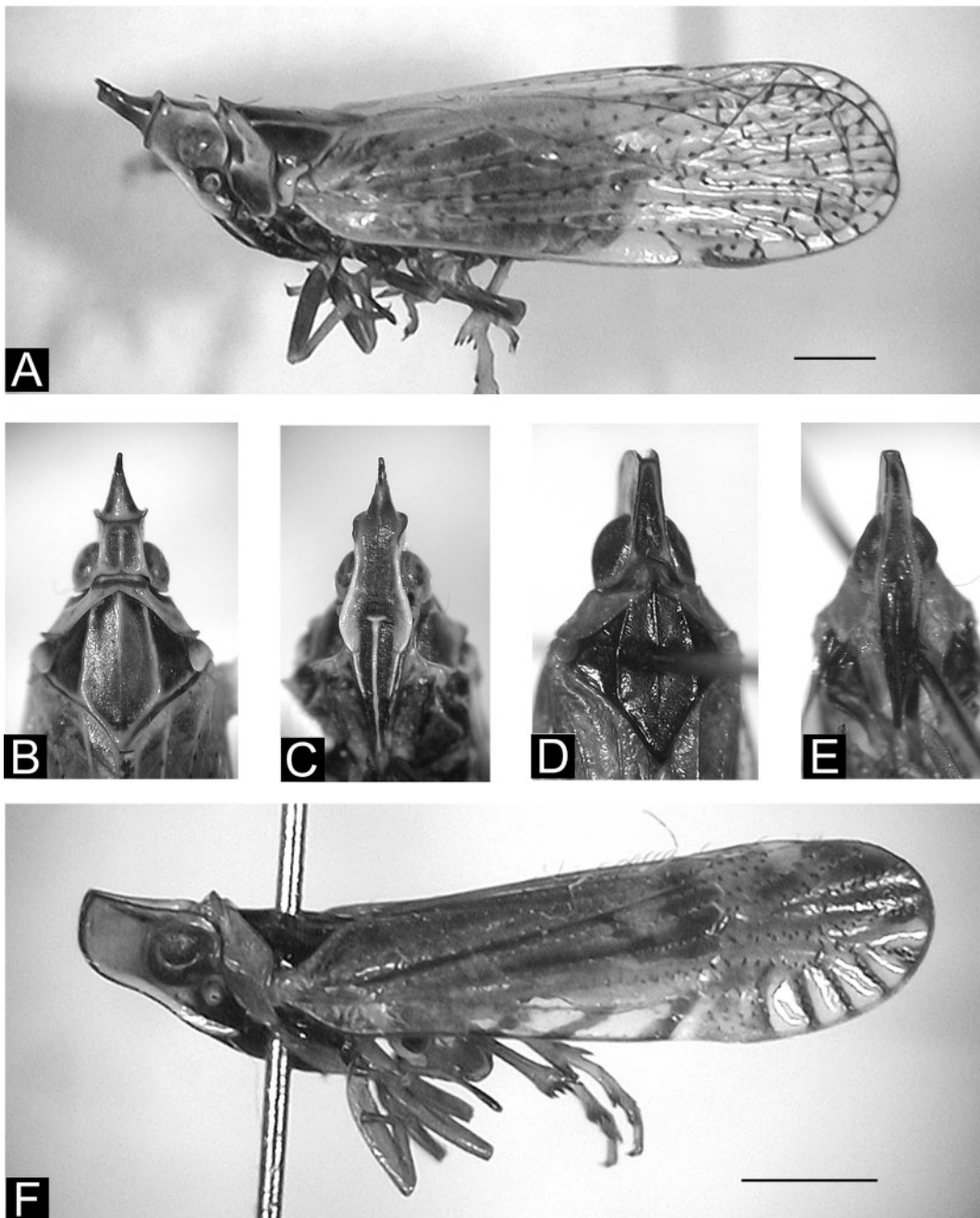
(Figs 14A–C, 45)

*Rhigedanus fomibundus* Emeljanov, 2000: 269, figs 49–59, 62–63.

*Material examined*

*Holotype.* ♂, Australia: NSW: ‘Calumet’, 25 m. NE of Binnaway, xi.1921 (A. Musgrave) (AM).

*Paratypes.* **Australia: NSW:** 1♀, same data as holotype; 1♂ (examined), Merriwa, 11.xi.1904 (W. W. F[rogatt]) (ASCU) (genitalia mutilated); 1♀ (examined) (Emeljanov (2000), lists this specimen as a



**Fig. 13.** *Dysoliarus unicornis*: A, habitus; B, C, head. *Orphninus mouldsi*: D, E, head; F, habitus.

male), Condobolin, 10.xi.1972 (D. A. Doolan) (ASCU); 1 ♀ (examined), Grenfell, 1918 (W. W. F[rogatt]) (ASCU); 2 ♀, 25 km E of Enngonia, 30.x.1973 (R. C. Lewis) (ANIC); 2 ♀, Bourke, 24.x.1949 (S. J. Paramonov) (ANIC); 1 ♀, Mt Boppy, 27.x.1957 (E. F. Riek) (ANIC); 3 ♀, 65 km NW of Nyngan, 21.x.1949 (E. F. Riek) (ANIC); 1 ♀, Nandewar Rge nr Narrabi, 6–7.xi.1932 (K. C. McKeown) (AM).

*Other material examined.* **Australia:** **NSW:** 1 ♂, Eubalong West, 17.xi.1992 (J. Bugeja) (ANIC). **ACT:** 1 ♂, Black Mt, light trap, 13.xii.1960 (I. F. B. Common) (ANIC). **WA:** 1 ♂, 13 km South of Tambellup, 1.xii.1996 (R. P. McMillan) (WAM Reg no. 34383), 1 ♂, Lake Grace (A. Douglas) (WAM 34347).

## Description

### Colour

Vertex yellow, central part mid brown, anterior part dark brown with mid brown transverse carina; frons light brown with brown area near frontoclypeal suture, lateral carinae light brown; clypeus mid to dark brown, median carina paler; pronotum yellow in caudal part, dark brown in basal part; mesonotum dark brown, carinae paler; legs light to mid brown; forewing hyaline white to yellowish with scattered brown marks, apex sometimes darker, veins and tubercles light to dark brown; abdominal sternites dark brown to black, intersegmental membranes yellow.

### Morphology

*Body length.* ♂ 6.1–7.5 mm.

*Head.* Vertex produced before eyes by 3/4–1× eye length; lateral carinae strongly elevated. Frons 1.5–1.9× longer than wide. Frontoclypeal suture semicircular, median part reaching at least lower margin of antennal scape; anteclypeus with well developed or evanescent median carina.

*Thorax.* Costa with 0–6 tubercles; fork of Sc+R basad or distad of fork of CuA1+CuA2; 10–11 apical cells. Hind leg: tibia with 1–2 large lateral spines (unequal in length); 1st tarsomere with 7(–8) apical teeth and no platellae; 2nd tarsomere with 18–30 apical teeth and 16–28 platellae.

*Male genitalia.* Anal tube as in Fig. 45B, C; ventro-median process of pygofer and genital styles as in Fig. 45D, E. Aedeagus (Fig. 45A): phallosome with a short (about half the length of flagellum), straight spine arising left laterally above midlength; flagellum unarmed.

### Remarks

Emeljanov's designation of female paratypes is problematic since females of the genus could not be identified to species with confidence.

## *Rhigedanus maculipennis* Emeljanov

(Figs 14D–F, 46)

*Rhigedanus maculipennis* Emeljanov, 2000: 269, figs 60–61.

### Material examined

*Holotype.* ♂ (examined), Australia: WA: 70 km E Balladonia, 3.x.1977 (F. H. Uther Baker) (ASCU ASCTHE026752), (specimen in bad condition: covered with mould, wing damaged).

*Paratypes.* **Australia:** **WA:** 2 ♀, 100 W Eucla, 25.x.1958 (E. F. Rieck) (ANIC); 1 ♀, 1 mi. NE of Mundrabilla Hs., 16.x.1968 (Britton, Upton, Balderson) (ANIC); 1 ♀, John Forrest NP, Darling Ranges, 21.i.1971, mv lamp (G. A. Holloway & H. Hughes) (AM); 1 ♀, 18 mi. E. Pingelly, 1.i.1971, mv lamp (G. A. Holloway & H. Hughes) (AM).

*Other material examined.* **Australia:** **WA:** 1 ♂, 70–75 km ENE of Norseman, collected at night in light trap, 10–16.xi.1978 (T. F. Houston, *et al.*) (WAM Reg. no. 34352). **SA:** 1 ♂, vehicle net nr Binnie Lookout tank, 20 km WNW Coonalpyn, 20.xi.1991 (J. A. Forrest) (SAM).

## Description

### Colour

Vertex mid to dark brown, lateral carinae basally light brown apically dark brown, transverse carina yellow; frons dark brown with black area near the frontoclypeal suture, lateral carinae mid brown; clypeus dark brown, median carina paler; pronotum mid to dark brown; mesonotum dark brown to black; legs light to dark brown; forewing hyaline white to yellowish with brown marks, veins and tubercles dark brown; abdominal sternites mid to dark brown to black, intersegmental membranes yellow.

### Morphology

*Body length.* ♂ 6.9–7.8 mm.

*Head.* Vertex produced before eyes by more than 1× eye length; lateral carinae moderately to strongly elevated. Frons 1.9–2.3× longer than wide. Frontoclypeal suture semicircular, median part not or just reaching lower margin of antennal scape; anteclypeus with well developed median carina.

*Thorax.* Costa without tubercles; fork of Sc+R distad of fork of CuA1+CuA2; 9–11 apical cells. Hind leg: tibia with two large lateral spines (unequal in length); 1st tarsomere with 6–7 apical teeth; 2nd tarsomere with 14–19 apical teeth and 12–17 platellae.

*Male genitalia.* Anal tube as in Fig. 46B, C; ventro-median process of pygofer and genital styles as in Fig. 46D, E. Aedeagus (Fig. 46A): phallosome with a long (about same length as flagellum), almost straight spine arising left laterally near apex; flagellum unarmed.

### Remarks

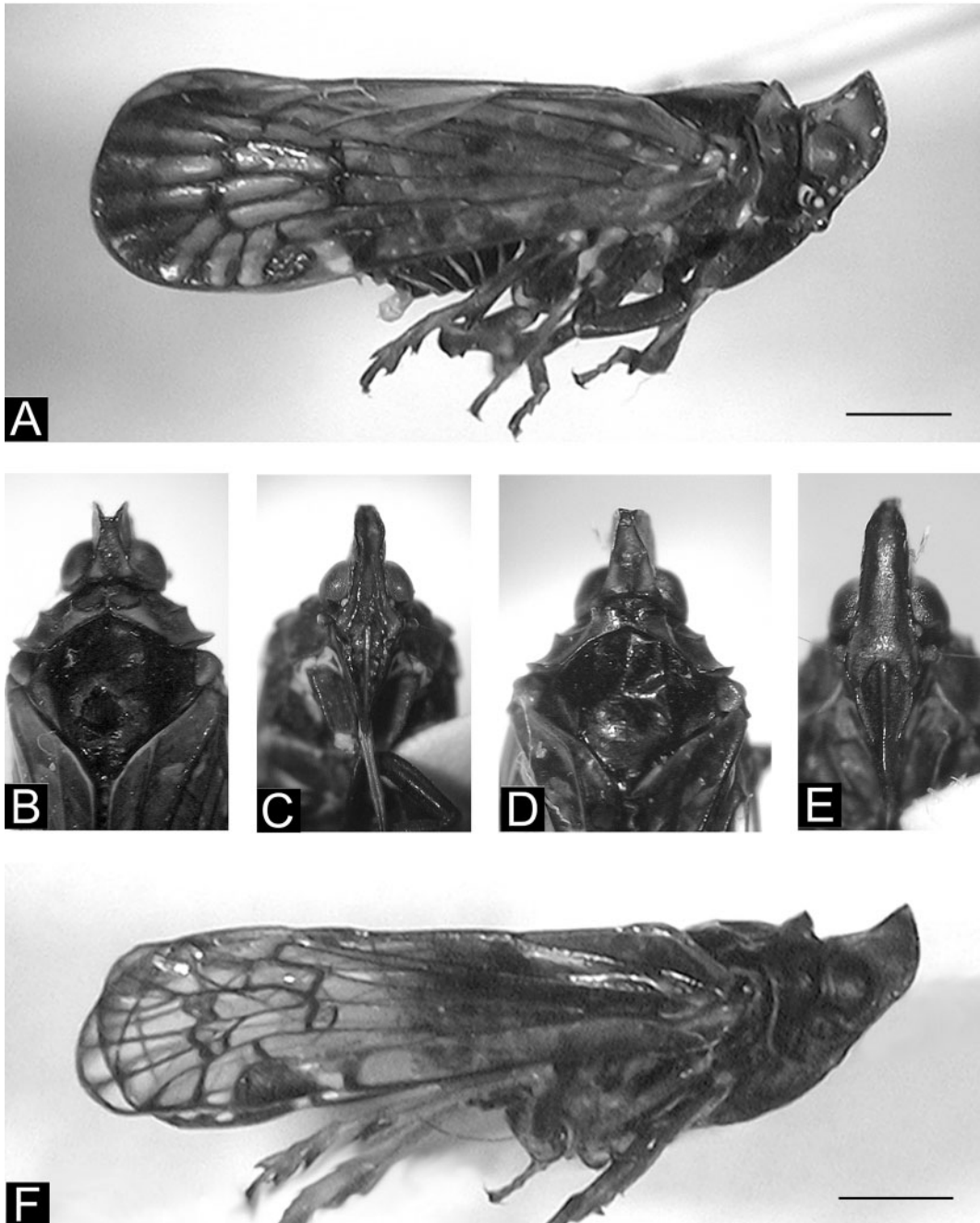
Emeljanov's designation of female paratypes is problematic since females of the genus cannot be identified to species with confidence.



*Subtribe 'Gelastocephalina' Emeljanov*

The genera *Carolus* Kirkaldy, *Gelastocephalus* Kirkaldy, *Metaplacha* Emeljanov and *Ronaldia* Emeljanov were grouped in the subtribe Gelastocephalina by Emeljanov (2000). The current subtribal concept of Gelastocephalina, established by Emeljanov (2000) is retained for convenience,

despite being paraphyletic, pending a more comprehensive reassessment of the higher classification of the Cixiidae. New genera described herein are placed within this subtribe, since they do not show the synapomorphies of Rhigedanina, see 'Monophyly and paraphyly of the subtribes' in the discussion section of this paper.



**Fig. 14.** *Rhigedanus fomibundus*: A, habitus; B, C, head. *Rhigedanus maculipennis*: D, E, head; F, habitus.

Genus *Aubirestus* Löcker & Larivière, gen. nov.Type species *Aubirestus semicirculatus* Löcker & Larivière, sp. nov.*Description**Morphology*

*Head.* Vertex 0.8× as long as wide, produced before eyes by 1/4–1/2 of an eye length; apex broadly rounded; caudal border widely u-shaped; lateral carinae strongly elevated; median carina 1/2–3/4 as long as vertex. Frons 1.1–1.5× as long as wide, position of maximum width around centre of frontoclypeal suture; lateral carinae convex (although rectilinear apically), slightly elevated, lateral margins foliaceous, concealing base of antennae; median carina complete. Frontoclypeal suture semicircular, median part just reaching lower margin of antennal scape; postclypeus with well developed lateral carinae and median carina; anteclypeus with weakly developed median carina.

*Thorax.* Pronotum with sinuate to arched carinae; hind margin rectangular. Forewing 3.5–4.0× longer than wide; costa with 15–18 tubercles; concavity at costal border absent; Sc+R+M forming common stem; fork of Sc+R at same level as fork of CuA1+CuA2; r-m1 distad of fork of MA–MP; position of icu at CuP basad of apex of clavus. Hind leg: tibia with 2–3 small lateral spines (without large lateral spines); six apical teeth in a row interrupted by a wide gap; 1st tarsomere with seven apical teeth and no platellae; 2nd tarsomere with 10 apical teeth and eight platellae.

*Distribution*

SA.

*Etymology*

The generic name is derived from Australian Biological Resources Survey (ABRS) that provided funding for this study. Gender: masculine.

*Aubirestus semicirculatus* Löcker & Larivière, sp. nov.

(Figs 15A–C, 47)

*Material examined*

*Holotype.* ♂, Australia: SA: Greenly I., 5–18.xiii.1947, (S.A. Mus. Exp.) (SAM I21678).

*Paratypes.* **Australia:** SA: 2♀, no other data (MAMU).

*Description**Colour*

Vertex dark brown with white mark on each side along lateral carinae; face mid to dark brown, carinae paler; pronotum yellow brown; mesonotum dark brown, central part paler, carinae light brown; legs straw coloured to mid brown; forewing hyaline grey with mid brown areas, veins concolourous with cells, tubercles mid to dark brown; abdominal

sternites mid to dark brown, intersegmental membranes light brown.

*Morphology*

*Body length.* ♂ 5.1 mm; ♀ 6.3–7.2 mm.

*Male genitalia.* Anal tube as in Fig. 47C, D; ventromedian process of pygofer and genital styles as in Fig. 47E, F. Aedeagus (Fig. 47A, B): phallosome with a very long, strongly curved, sclerotised spine (a), arising left lateral near apex, a membranous spine (b) right lateral about midlength and a small sclerotised tooth ventrally below midlength; flagellum unarmed.

*Remarks*

The following combination of characters is diagnostic for this species: complete, well developed median carina on frons and postclypeus (weakly developed on anteclypeus) and shape of genital styles as in Fig. 47E, F.

*Etymology*

Named after semicircular bent spine on phallosome.

Genus *Balyadimetopia* Löcker & Larivière, gen. nov.Type species *Balyadimetopia frederi* Löcker & Larivière, sp. nov.*Description**Colour*

Vertex brown to black, lateral carinae yellow to brown; face yellow; mesonotum black; abdominal sternites dark brown to black, intersegmental membranes yellow.

*Morphology*

*Body length.* ♂ 3.9–5.5 mm, ♀ 4.7–6.9 mm.

*Head.* Tip of head acutely angled in lateral view (Fig. 11A). Vertex and frons extremely broad (less developed in *B. frederi*). Lateral carinae of vertex slightly to moderately elevated. Lateral carinae of frons convex (evenly rounded), slightly elevated, lateral margins foliaceous, concealing base of antennae; median carina complete. Postclypeus with well developed median carina, lateral carinae strongly enlarged, foliaceous; anteclypeus with well developed median carina, not distinctly more elevated than that of postclypeus.

*Thorax.* Pronotum with sinuate carinae. Concavity at costal border of forewing absent; Sc+R+M forming common stem; r-m1 distad of fork MA–MP; position of icu at CuP distad of apex of clavus; 10 apical cells. Hind tibia with six apical teeth in a row interrupted by a wide gap; 2nd tarsomere with nine apical teeth and seven platellae.

*Male genitalia.* Phallosome with a long spine arising left lateral on the phallosome (Figs 48B, 49–50A).

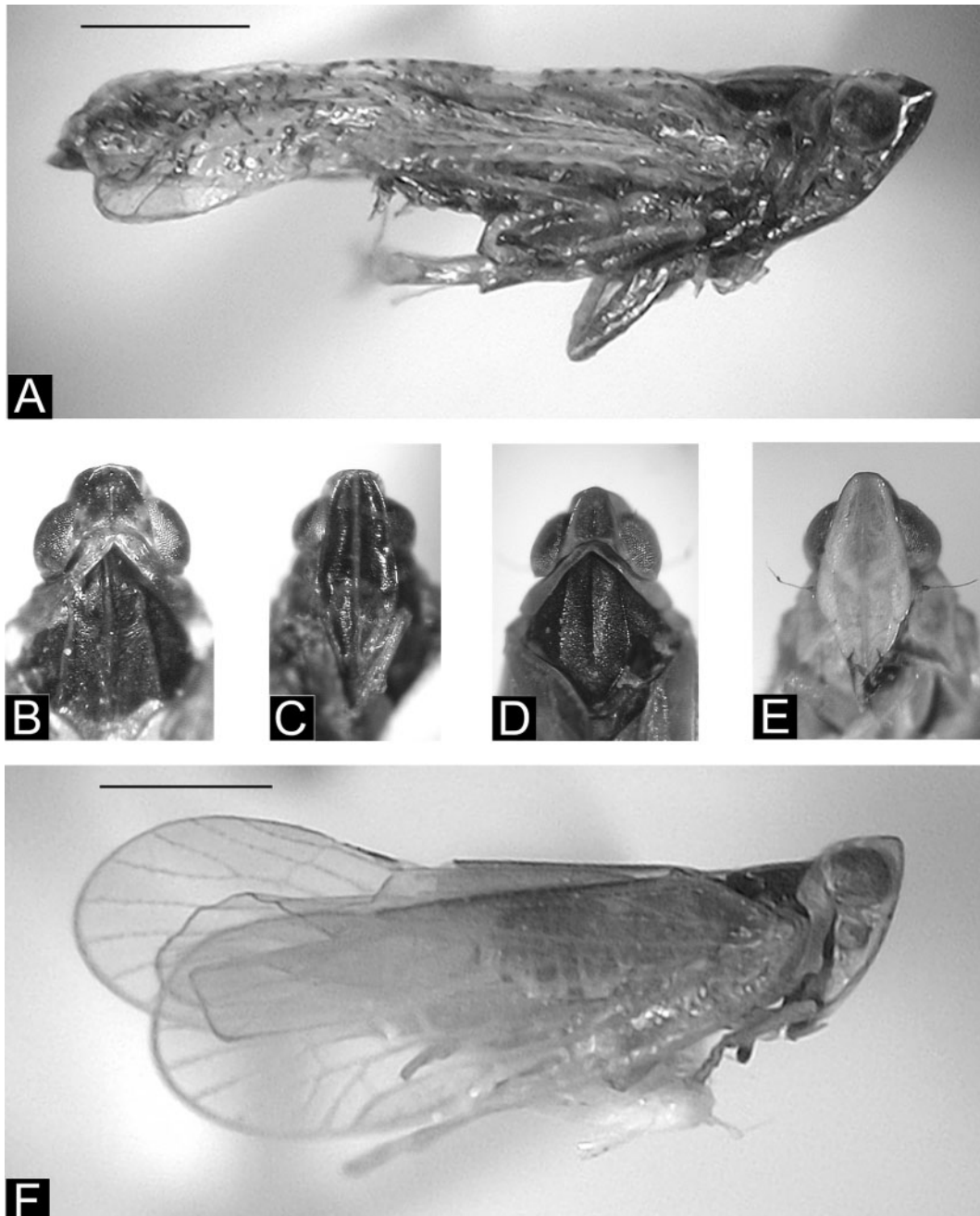
*Distribution*

NSW, WA.

*Remarks*

The three species of *Balyadimetopia* form a clade recovered by most analyses. Due to characters such as the shape of the anal tube in lateral view, the obtuse angle of the hind margin of the pronotum and the forking of Sc+R, *B. marci* is grouped with *Dysoliarius* and *Rhigedanus* in the equal weighting analysis of dataset *B*. However, these characters showed a high degree of homoplasy. Some analyses (e.g. the modified scaled weighting approach of dataset *A*, see Figs 5,

6) suggest the inclusion of the species of *Balyadimetopia* into the genus *Ronaldia*, but several characters such as the presence of three or more platellae on the 1st tarsomere, as opposed to a lack of platellae in *Ronaldia*, contradict this, and the strongly enlarged, foliaceous lateral carinae on the postclypeus represent a clear synapomorphy for this genus. Other characteristics are foliaceous margins of the frons, the acutely angled tip of head in lateral view (Fig. 11*A*), a long spine arising left lateral on the phallosome (Figs 48*B*,



**Fig. 15.** *Aubirestus semicirculatus*: A, habitus; B, C, head. *Balyadimetopia frederi*: D, E, head; F, habitus.

49–50A), and the extremely broad vertex and frons (less developed in *B. frederi*). *Balyadimetopia krahalla* and *B. frederi* share the same type of genital styles (Figs 48E, F; 49D, E).

#### Etymology

The genus is based on ‘balyadi’, which means ‘smooth’ or ‘flat’ in Gooniyandi, an Aboriginal language in Western Australia (Thieberger and McGregor 1994) and refers to the flat and wide frons (= metope *sensu* Emeljanov). Gender: feminine.

#### Key to species of *Balyadimetopia*

1. Forewing hyaline yellow with contrasting dark brown tubercles; aedeagus as in Fig. 49A. . . . . *B. krahalla*, sp. nov.  
Forewing hyaline yellow or mid brown, tubercles concolorous with cells; aedeagus different (Figs 48A, B; 50A). . . . . 2
2. Pronotum black with yellow carinae; vertex less than 0.5× as long as wide, frons less than 1.1× longer than wide; genital styles as in Fig. 50D, E; aedeagus with a large ventral ridge forming a hook-like process below midlength (Fig. 50A) . . . . . *B. marci*, sp. nov.  
Pronotum entirely yellow; vertex more than 0.7× as long as wide; frons more than 1.2× longer than wide; genital styles as in Fig. 48E, F; aedeagus without a ventral ridge bearing a hook-like process . . . . . *B. frederi*, sp. nov.

#### *Balyadimetopia frederi* Löcker & Larivière, sp. nov.

(Figs 15D–F, 48)

#### Material examined

*Holotype*. ♂, Australia: WA: Pemberton, 30.xi.1936 (K. R. Norris) (ANIC).

*Paratypes*. **Australia: WA:** 1♂, 2♀, Yarragil 4P Catchment via Dwellingup, 11–18.xii.1980, Malaise trap (A. Postle) (QDPI); 1♂, Yanchep, 32 mls N of Perth, 13–23.xi.1935 (R. E. Turner) (BMNH). **NSW:** 1♀, Condobolin, 17.x.1900, (ASCU).

*Other material examined*. **Australia: WA:** 1♂, Yarragil Ck and Murray Rd; Dwellingup, jarrah forest, pans, 31.x.1991, (D. Bickel) (AM).

#### Description

##### Colour

Pronotum yellow; legs straw coloured; forewing hyaline yellow, veins and tubercles concolorous with cells.

##### Morphology

*Body length*. ♂ 3.9–5.5 mm; ♀ 4.7–6.1 mm.

*Head*. Vertex 0.8–1.0× as long as wide, produced before eyes by 1/4–1/2 of an eye length; apex broadly rounded; caudal border u-shaped; median carina incomplete, more than 3/4 as long as vertex. Frons 1.2–1.3× longer than wide; position of maximum width distinctly ventrad of centre of frontoclypeal suture. Frontoclypeal suture semi-circular, median part at least reaching lower margin of antennal scape.

*Thorax*. Hind margin of pronotum right or acutely angled. Forewing less than 3× longer than wide; costa with 23–29 tubercles; fork of Sc+R basad of fork of CuA1+CuA2. Hind leg: tibia with 1–3 small lateral spines (without large lateral spines); 1st tarsomere with 8–11 apical teeth and 3–6 platellae; 2nd tarsomere with 7–9 apical teeth and 5–7 platellae.

*Male genitalia*. Anal tube as in Fig. 48C, D; ventro-medial process of pygofer and genital styles as in Fig. 48E, F. Aedeagus (Fig. 48A, B): phallosome with a long, basally straight (sometimes slightly curved) spine arising left laterally above midlength; flagellum unarmed.

#### Remarks

Most specimens have the 1st tarsomere with nine apical teeth and four platellae and the 2nd tarsomere with nine apical teeth and seven platellae.

The specimen listed under ‘Other material examined’ is excluded from the type series because it differs in the shape of the aedeagal spine, *a*, that is enlarged as opposed to thickened at the base in the type series.

#### Etymology

Derived from the name of the first author’s friend Manfred Löcker.

#### *Balyadimetopia krahalla* Löcker & Larivière, sp. nov.

(Figs 16A–C, 49)

#### Material examined

*Holotype*. ♂, Australia: WA: Karragullen, x.1987, from Jarrah *E. marginata*, Pyrethrin knockdown (J. D. Majer) (ASCU ASCTHE007971).

*Paratypes*. **Australia: WA:** 1♂, 3 km N of Lake Cronin, 32°23’S 119°46’E, 19–26.ix.1978, on foliage of *Eucalyptus* sapling (T. F. Houston *et al.*) (WAM); 2♀, Yanchep, x.1966 (J. W. & F. Evans) (ASCU); 1♀, Jandakot, 17.x.1965 (F. H. Uther Baker) (ASCU); 1♀, Augusta, x.1966, (J. W. & F. Evans) (ASCU); 1♀, Swan R. (L. J. Newman) (WADA 15685).

#### Description

##### Colour

Apical portion of anteclypeus black, lateral sides of head partly black; pronotum yellow, central area black, carinae yellow; legs yellow to dark brown; forewing hyaline yellow, veins yellow, tubercles dark brown.

##### Morphology

*Body length*. ♂ 5.3–5.4 mm; ♀ 6.2–6.9 mm.

*Head*. Vertex 0.6× as long as wide, produced before eyes by 1/4–1/2 of an eye length; apex broadly pointed; caudal border u-shaped; median carina incomplete, ~3/4 as long as vertex. Frons less than 1.1× longer than wide; position of maximum width distinctly ventrad of centre of

frontoclypeal suture. The latter semicircular, median part reaching at least lower margin of antennal scape.

*Thorax.* Hind margin of pronotum right or obtusely angled. Forewing 3.0–3.5× longer than wide; costa with ~13 tubercles; fork of Sc+R basad of fork of CuA1+CuA2. Hind leg: tibia with 1–2 small lateral spines (without large lateral spines); 1st tarsomere with 8–10 apical teeth and 3–5 platellae; 2nd tarsomere with nine apical teeth and seven platellae.

*Male genitalia.* Anal tube as in Fig. 49B, C; ventro-median process of pygofer and genital styles as in Fig. 49D, E. Aedeagus (Fig. 49A): phallosome with a long spine, moderately curved basally, arising left laterally above midlength; flagellum unarmed.

#### *Etymology*

Derived from the names of the first author's friends Beate Kraker and Manfred Hall.

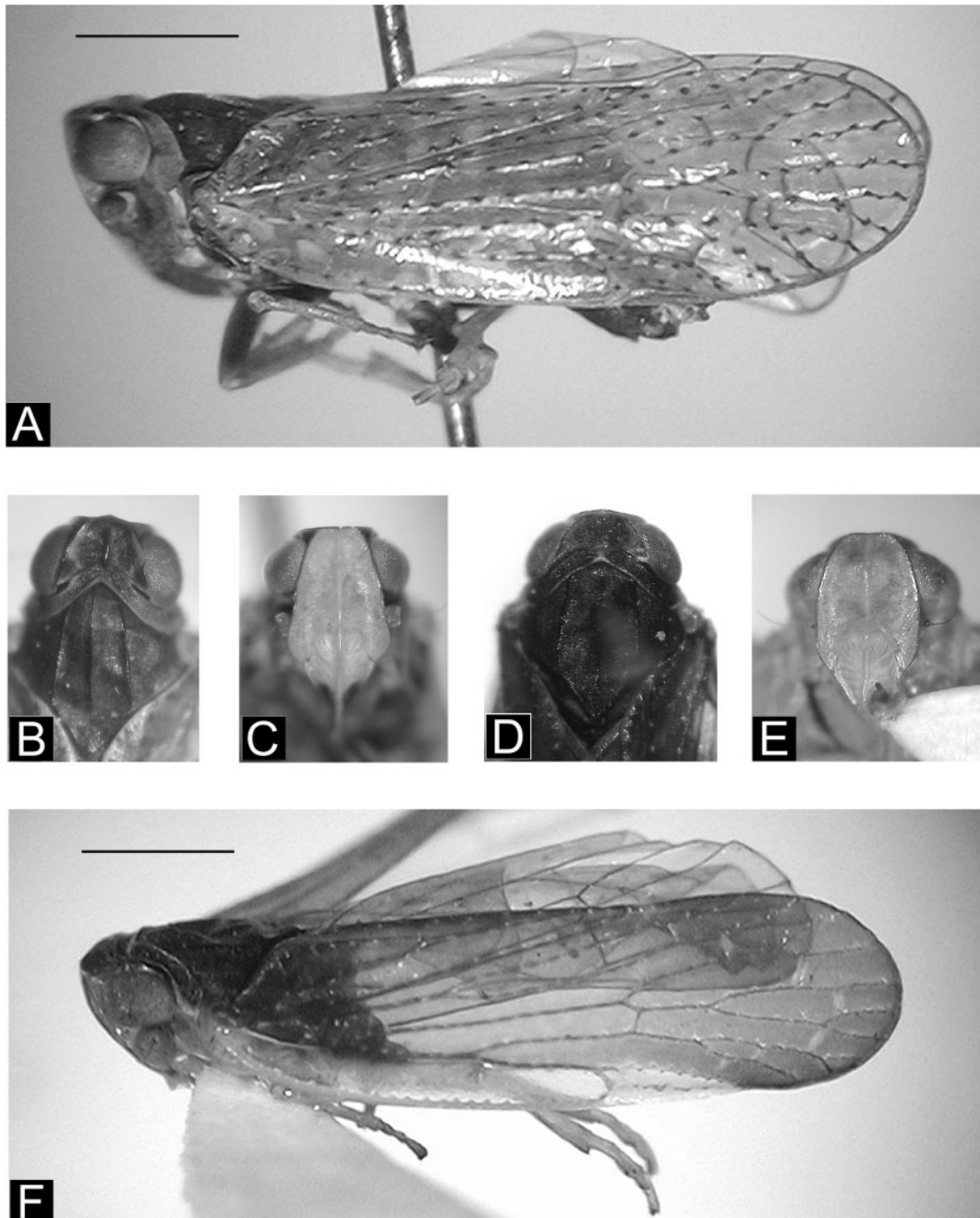


Fig. 16. *Balyadimetopia krahalla*: A, habitus; B, C, head. *Balyadimetopia marci*: D, E, head; F, habitus.

***Balyadimetopia marci*** Löcker & Larivière, sp. nov.

(Figs 16D–F, 50)

*Material examined*

*Holotype.* ♂, Australia: WA: Yarragil 4P Catchment via Dwellingup, 20–27.xi.1980, Malaise trap (A. Postle) (QM T123599, originally from QDPI).

*Description**Colour*

Pronotum black, carinae and hind border yellow; legs yellow; forewing hyaline mid brown except for white costal cell and whitish yellow pterostigma and adjacent cell, veins and tubercles concolorous with cells.

*Morphology*

*Body length.* ♂ 5.3 mm.

*Head.* Vertex 0.4× as long as wide, produced before eyes by less than 1/4 of an eye length; apex broadly truncate; caudal border widely v-shaped; median carina incomplete, more than 3/4 as long as vertex. Frons less than 1.1× longer than wide; position of maximum width around centre of frontoclypeal suture. Frontoclypeal suture semicircular, median part reaching just below lower margin of antennal scape.

*Thorax.* Hind margin of pronotum obtusely angled. Forewing 3.5–4.0× longer than wide; costa with 19–22 tubercles; fork of Sc+R distad of or at same level as fork of CuA1+CuA2. Hind leg: tibia without lateral spines; 1st tarsomere with 11 apical teeth and seven platellae; 2nd tarsomere with nine apical teeth and seven platellae.

*Male genitalia.* Anal tube as in Fig. 50B, C; ventro-median process of pygofer and genital styles as in Fig. 50D, E. Aedeagus (Fig. 50A): phallosome with a long, moderately curved spine left laterally and a large ventral ridge forming hook-like process below midlength; flagellum unarmed.

*Etymology*

Named in honour of the first author's friend Markus Proksch.

Genus ***Barbonia*** Löcker & Larivière, gen. nov.

Type species *Barbonia spectabilis* Löcker & Larivière, sp. nov.

*Description**Morphology*

*Head.* Vertex 0.9–1.0× as long as wide, produced before eyes by 1/4–1/2 of an eye length; apex broadly pointed; caudal border u-shaped; lateral carinae strongly elevated; median carina incomplete, 1/4–1/2 as long as vertex. Frons 1.1–1.5× longer than wide, position of maximum width distinctly ventrad of centre of frontoclypeal suture; lateral carinae rectilinear (basally convex),

thick, enlarging towards clypeus (Fig. 17C), moderately elevated, lateral margins foliaceous, concealing base of antennae; median carina complete. Frontoclypeal suture semicircular, median part reaching at least lower margin of antennal scape; postclypeus with well developed lateral carinae and median carina; anteclypeus with well developed median carina.

*Thorax.* Pronotum with arched (sometimes slightly undulating) carinae; hind margin right or obtusely angled. Forewing 3.0–3.5× longer than wide; costa with 13–21 tubercles; concavity at costal border absent; Sc+R+M forming common stem; fork of Sc+R basad of fork of CuA1+CuA2; r–m1 distad of or at same level as fork MA–MP; position of icu at CuP distad of (rarely at same level as) apex of clavus, nine (rarely 10) apical cells. Hind leg: tibia with 0–3 small lateral spines (without large lateral spines); six apical teeth in a row interrupted by a wide gap; 1st tarsomere with eight apical teeth and no platellae; 2nd tarsomere with nine apical teeth and seven platellae.

*Distribution*

Qld.

*Remarks*

The two monotypic genera, *Metaplacha* and *Barbonia*, group together in every tree retrieved, but considerable differences in the external morphology and male genitalia, reflected by minimal branch lengths of 420 and 3395 in the modified scaled weighting regime of dataset A, inhibit placing *Barbonia spectabilis* in the genus *Metaplacha*.

*Etymology*

Derived from the name of the first author's friend Barbara Kreiner. Gender: feminine.

***Barbonia spectabilis*** Löcker & Larivière, sp. nov.

(Figs 17A–C, 51)

*Material examined*

*Holotype.* ♂, Australia: Qld: Tibrogargon Ck, via Glasshouse, SE Qld, 22.viii.1965 (B. Cantrell) (QM T123593, originally from UQIC).

*Paratypes.* **Australia:** **Qld:** 1♂, Brisbane, 15.iv.1953 (F. A. Perkins) (UQIC Reg. ♂55178); 1♂, Cunningham's Gap, 3.xi.1955 (F. A. Perkins) (UQIC).

*Description**Colour*

Vertex yellow, central part mid brown, brown mark on each side close to caudal border, median carina yellow, lateral carinae yellow to brown; face dark brown with pale yellow carinae; pronotum yellow with brown parts anterior of carinae; mesonotum dark brown, carinae and hind border orange; legs yellow to brown; forewing hyaline white with light brown and mid brown areas, sometimes dark stripes

along apical veins; veins light brown, tubercles dark brown; abdominal sternites dark brown, occasionally mid brown, intersegmental membranes orange, occasionally pale yellowish.

*Morphology*

*Body length.* ♂ 4.5–5.2 mm.

*Male genitalia.* Anal tube as in Fig. 51C, D; ventromedian process of pygofer and genital styles as in Fig. 51E, F. Aedeagus (Fig. 51A, B): phallosome ventrally with a large

sheet-like ridge bearing short, slightly curved spine; flagellum with apical spine.

*Remarks*

The shape of the genital styles (Fig. 51E, F) and the large sheet-like ridge bearing a short, slightly curved spine are diagnostic for this species.

The paratype from Cunningham's Gap is very pale and appears to have been mounted ex ethanol.

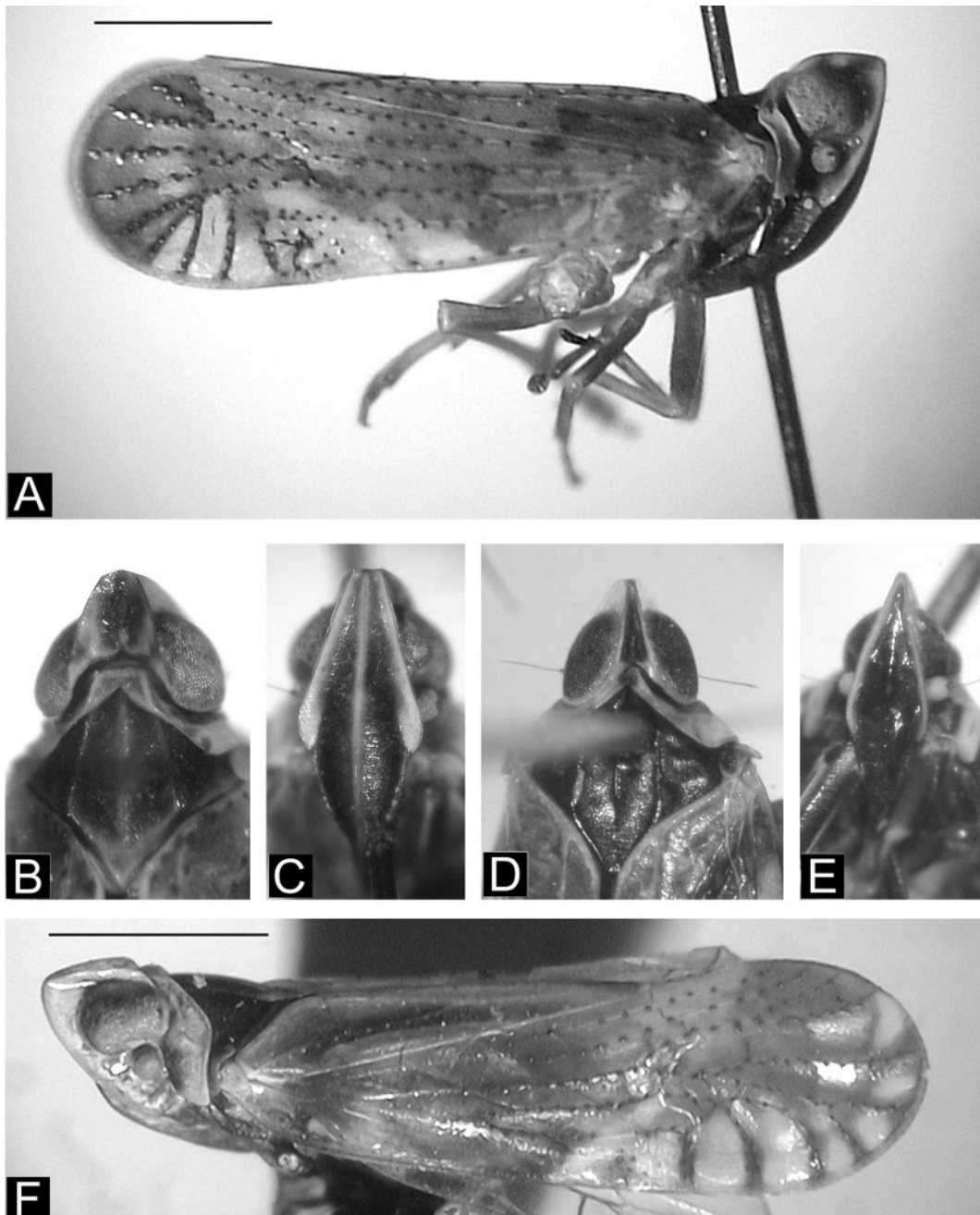


Fig. 17. *Barbonia spectabilis*: A, habitus; B, C, head. *Candicarina pulchra*: D, E, head; F, habitus.

*Etymology*

‘Spectabilis’ is the Latin term for ‘remarkable’.

Genus *Candicarina* Löcker & Larivière, gen. nov.

Type species *Candicarina pulchra* Löcker & Larivière, sp. nov.

*Description**Colour*

Head dark brown to black except for white to yellow lateral carinae on vertex and frons; pronotum yellow, sometimes with few dark brown to black marks; mesonotum dark brown to black; legs yellow to brown; forewing hyaline white with distinct colour pattern consisting of large light brown areas and brown stripes along apical veins, veins concolorous with cells, tubercles mid brown; abdominal sternites dark brown, intersegmental membranes orange.

*Morphology*

*Body length.* ♂ 3.6–4.9 mm, ♀ 3.7–5.4 mm.

*Head.* Vertex 1.4–1.9× longer than wide, produced before eyes by 1/4–1/2 of an eye length; apex narrowly rounded; caudal border u- or v-shaped; lateral carinae strongly elevated. Frons 1.9–2.3× longer than wide, position of maximum width distinctly ventrad of centre of frontoclypeal suture; lateral carinae strongly elevated, lateral margins foliaceous, concealing base of antennae. Frontoclypeal suture semicircular, median part not reaching lower margin of antennal scape; postclypeus with well developed lateral carinae and median carina; anteclypeus with well developed median carina.

*Thorax.* Pronotum with sinuate carinae. Concavity at costal border of forewing absent; Sc+R+M forming common stem; fork of Sc+R basad of fork of CuA1+CuA2; r-m1 distad of fork MA–MP. Hind tibia with six apical teeth in row interrupted by a wide gap; 1st tarsomere with seven apical teeth and no platellae.

*Male genitalia.* Anal tube as in Figs 52C, D; 53D, E; shape of genital styles as in Figs 52E, F; 53F, G; aedeagus with one large spine on phallosome and one to three spines on flagellum (Figs 52A, B; 53A–C).

*Distribution*

NSW, NT, Qld, SA, Vic, WA.

*Remarks*

In the equal weighting regime of dataset A (Fig. 3) the monophyly of *Candicarina* was contradicted. Most of the other analyses, however, retrieved a clade consisting of both species of *Candicarina*. The external and internal morphology, in particular the very narrow vertex (1.4–1.9× longer than wide), the distinct pattern of white and brown patches on the forewings, the shape of the head in lateral view

(Figs 17F, 18A), the chaetotaxy of the 1st tarsomere (seven apical teeth, no platellae), the shape of the genital styles (Figs 52E, F; 53F, G) and the spine on the phallosome, leave no doubt that these two species form one genus.

*Etymology*

‘Candidus’ means ‘shining’ or ‘bright’ in Latin. Named after the bright and shiny lateral carinae on the head. Gender: feminine.

**Key to species of *Candicarina***

- Second hind tarsomere with eight apical teeth and six platellae; phallosome with a long spine arising left lateral; only one sclerotised spine on the flagellum (Fig. 52A) . . . . . *C. pulchra*, sp. nov.  
Second hind tarsomere with seven apical teeth and five platellae; phallosome with a long spine arising ventrally; flagellum with three sclerotised spines (Fig. 53A, B) . . . . . *C. geroldi*, sp. nov.

***Candicarina pulchra* Löcker & Larivière, sp. nov.**

(Figs 17D–F, 52)

*Material examined*

*Holotype.* ♂, Australia: WA: Jarrahdale, SE of Perth, 10.xii.2000, *Eucalyptus marginata* in jarrah forest, 1996 regen. mine site (M. Fletcher & M. Moir) (WAM No. 38310).

*Paratypes.* **Australia: WA:** 3♂, 3♀, same data as holotype (ASCU). **Qld:** 14♂, 11♀, Emerald, 1–6.ix.1981, Malaise trap (D. A. H. Murray) (QDPI); 2♂, 3♀, Emerald, 6–18.ix.1981, Malaise trap (D. A. H. Murray) (QDPI); 2♂, Brisbane, SEQ, 13.ix.1970 (J. Wilson) (QM); 1♂, Lake Broadwater nr Dalby, site A, 27°21'S 151°06'E, mv lamp, 27.ix.1986 (G. & A. Daniels) (UQIC); 1♀, Lake Broadwater nr Dalby, site B, 27°21'S 151°06'E, 8.xi.1986 (G. Daniels) (UQIC); 1♂, St Marys SF, Gympie, *Acacia falcata*, viii.2000 (N. Andrew) (ASCU); 1♂, Yeerongpilly, 4.x.1939 (W. A. Smith) (QDPI); 2♀, Gurgeena Plateau, 360 m, site 2, open forest, mv light, 14.x.2001 (Monteith & Cook) (QM); 2♀, Pine Creek, c. 19 km S of Bundaberg, 5.ix.1975 (H. Frauca) (ANIC); 1♀, St George, on river bank, 11.x.1974 (I. D. Galloway) (QDPI); 1♀, Woody I[island] SEQ, 9.ix.1953 (P. Thomsen) (QM). **SA:** 5♂, 2♀, Oratunga Ck, 11 km E of Parachilna, 4.x.1975 (Z. Liepa) (ANIC); 1♀, Windy Ck, 22 km N of Beltana, 14.ix.1972 (Z. Liepa) (ANIC). **Vic:** 3♂, 2♀, Elmore, 30 km NE of Bendigo, 10.xi.1982 (J. Osmelak) (ASCU); 1♀, Rochester, 50 km NE of Bendigo, ex stand predominantly of mallows, 6.xi.1980 (J. Osmelak) (ASCU). **NT:** 2♂, Glen Helen, 16.viii.1959 (E. M. Exley) (UQIC Reg. ♂ 54208, 54206); 2♀, Todd River 9 km N by E of Alice Springs, 23°38'S 133°53'E, 28.ix.1978 (Upton & Barrett) (ANIC); 1♀, Amadeus Basin, 14–16.ix.1962 (P. Ranford) (ANIC). **NSW:** 1♀, Ophir, NE of Orange, 20.xi.1985, by sweeping (G. R. Brown) (ASCU); 1♀, Plateau Killarney, 4.xi.1932 (H. Hacker) (BMNH); 1♀, Broken Hill, St Ck Resvr, Euc. Leaves, 29.x.1944 (C. E. Chadwick) (ASCU).

*Description**Morphology*

*Body length.* ♂ 3.6–4.4 mm, ♀ 3.7–5.4 mm.

*Head.* Median carina of vertex incomplete, less than 1/2 as long as vertex. Median carina of frons incomplete, ~1/3 as long as frons; lateral carinae s-shaped or convex.



*Thorax.* Hind margin of pronotum right, obtusely or, more rarely, acutely angled. Forewing 3.0–3.5× longer than wide; costa with 11–18 tubercles; position of *icu* at CuP distad of or at same level as apex of clavus; 9–10 (eight, on one wing in one specimen) apical cells. Hind leg: tibia with 0–3 small lateral spines (without large lateral spines); 1st tarsomere with seven apical teeth and 0–1 platella; 2nd tarsomere with eight apical teeth and six platellae.

*Male genitalia.* Anal tube as in Fig. 52C, D; genital styles as in Fig. 52E, F. Aedeagus (Fig. 52A, B): phallosome

with a very long moderately curved spine arising left lateral above midlength; one spine at apex of flagellum.

*Remarks*

Most specimens lacked platellae on the 1st tarsomere but a single platella was found on two specimens.

*Etymology*

‘Pulcher’ is the Latin term for ‘beautiful’.

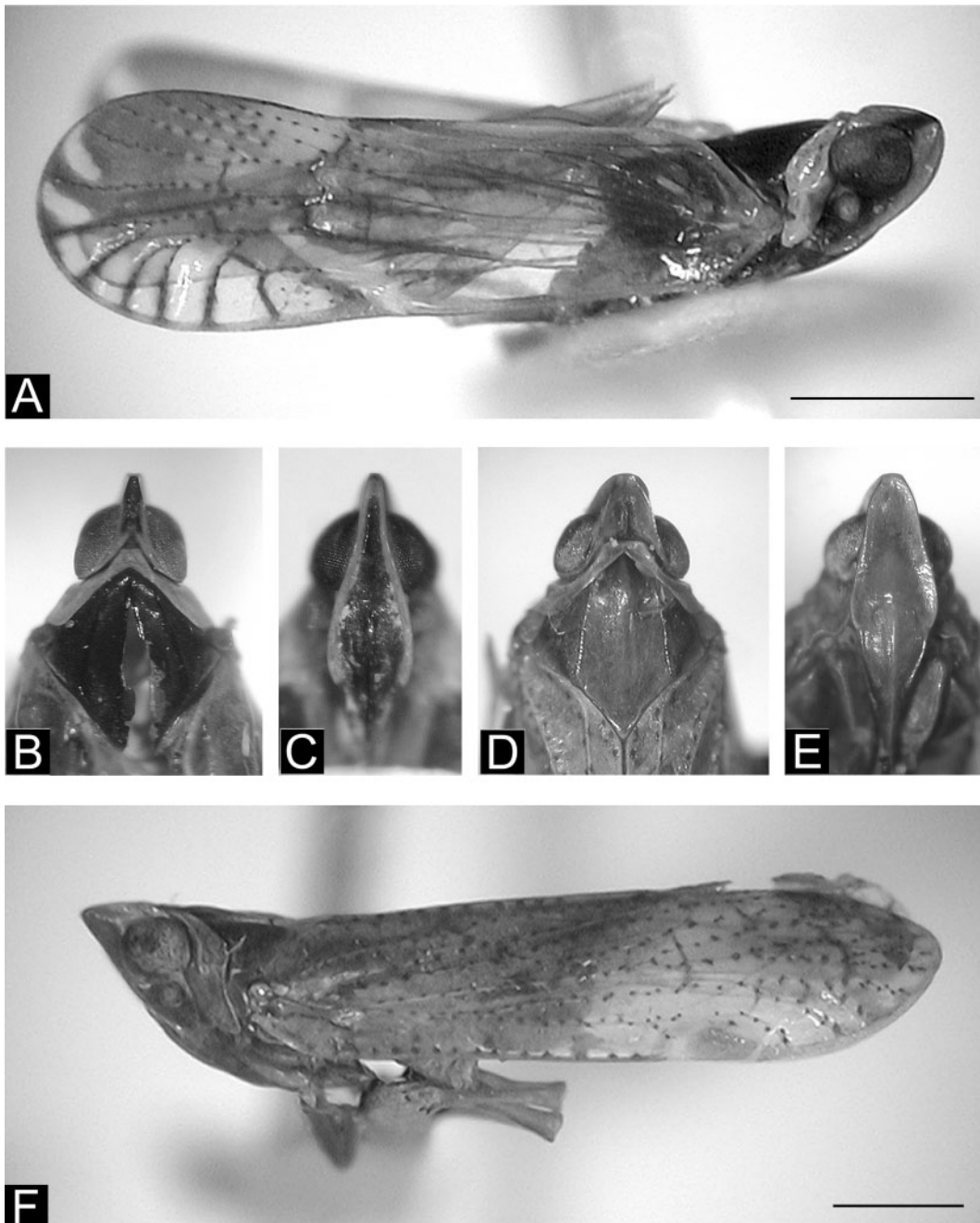


Fig. 18. *Candicarina geroldi*: A, habitus; B, C, head. *Carolus crispus*: D, E, head; F, habitus.

***Candicarina geroldi*** Löcker & Larivière, sp. nov.

(Figs 18A–C, 53)

*Material examined*

*Holotype*. ♂, Australia: WA: Kimberley, B. M. R. Camp, SW of Bedford Downs, nr Landsdowne HS, 15.viii.1964 (K. Plumb) (ANIC).

*Paratype*. **Australia**: NT: 1♂, 60 km ENE of Limbunya, 29.viii.1969 (M. Mendum) (ANIC) (head of specimen missing).

*Description**Morphology*

*Body length*. ♂ 4.9 mm.

*Head*. Median carina of vertex incomplete, 1/4–1/2 as long as vertex. Median carina of frons incomplete, ~1/4 as long as frons; lateral carinae s-shaped.

*Thorax*. Hind margin of pronotum more or less rectangular. Forewing 3.5–4.0× longer than wide; costa with 0–5 tubercles; position of icu at CuP distad of apex of clavus; 10 apical cells. Hind leg: tibia with 1–2 small lateral spines (without large lateral spines); 1st tarsomere with seven apical teeth and no platellae; 2nd tarsomere with seven apical teeth and five platellae.

*Male genitalia*. Anal tube as in Fig. 53D, E; genital styles as in Fig. 53F–G. Aedeagus (Fig. 53A–C): phallosome with a long, moderately curved spine arising ventrally above midlength; flagellum with three spines.

*Etymology*

Named in honour of the first author's friend Gerold Eder.

Genus ***Carolus*** Kirkaldy

*Carolus* Kirkaldy, 1906: 401.

Type species *Carolus crispus* Kirkaldy, 1906, by monotypy.

*Description**Colour*

Head orange to brown, lateral carinae slightly paler; pronotum yellow brown; mesonotum orange brown to mid brown; legs light brown to mid brown; forewing hyaline grey with light brown areas and row of light to mid brown marks starting around nodus of Y-vein and extending obliquely across wing to distad third of costa, veins concolorous with cells, tubercles mid brown; abdominal sternites mid to dark brown, intersegmental membranes orange.

*Morphology*

*Body length*. ♂ 6.3–6.6 mm, ♀ 5.56–7.61 mm.

*Head*. Tip of head acutely angled in lateral view. Vertex produced before eyes by 1/2–3/4 of an eye length; apex broadly rounded; caudal border u-shaped; lateral carinae strongly elevated; median carina ~1/2 as long as vertex. Frons with its maximum width around centre of frontoclypeal suture;

lateral carinae double s-shaped, slightly elevated, lateral margins foliaceous, concealing base of antennae; median carina incomplete. Frontoclypeal suture semicircular, median part reaching almost to lower margin of antennal scape; post-clypeus with well developed lateral carinae and median carina.

*Thorax*. Pronotum with sinuate carinae; hind margin rectangular. Forewing 3.5–4.0× longer than wide; concavity at costal border present; Sc+R+M forming common stem; r-m1 distad of fork of MA–MP. Hind tibia with six apical teeth in row interrupted by a wide gap; 1st tarsomere with seven apical teeth and no platellae.

*Male genitalia*. Anal tube as in Figs 54C, D; 55–56B, C; genital styles variable; pair of spines (*a*) and moderately to strongly curved spine (*b*) present on base of phallosome (Figs 54A, B; 55–56A).

*Remarks*

A clade consisting of *Carolus crispus* and the two new species *C. stiriae*, sp. nov. and *C. carinatus*, sp. nov. was retrieved by all weightings, except for the successive approximations weighting of dataset *A* where a potential synapomorphy for *Carolus*, a pair of basal spines on the phallosome, was downweighted to zero. The reason for this is that a basal pair of spines also exists in two other unrelated species, namely '*Cixius*' *sidnicus* and *Rokebia australis*, sp. nov. The shape of the spines, especially in *Rokebia*, gen. nov. (Fig. 93A), differs from that in *Carolus*, so it might be an analogy, which then would suggest that the pair of spines in *Carolus* represents a synapomorphy. Other characters supporting the *Carolus*-clade are the acutely angled tip of head in lateral view, the shape of the head in facial view (Figs 18E, 19C, 19E), the shape of the frontoclypeal suture (slightly semicircular, bent upwards, median part reaching almost to lower margin of antennal scape), the chaetotaxy of the 1st tarsomere (seven apical teeth, no platellae) and the presence of the moderately to strongly curved spine, *b*, on the phallosome (Figs 54–56A).

*Distribution*

NSW, Qld.

**Key to species of *Carolus***

- Median carina on frons incomplete, but more than 5/6 as long as frons; aedeagus with spines *b* and *e* long, and spine *d* missing (Fig. 55A) . . . . . *C. carinatus*, sp. nov.  
Median carina on frons incomplete, 1/2–3/4 as long as frons, evanescent or absent in apical 1/3; aedeagus with a spine *b*, short; spine *e*, either short or missing, and spine *d* present (Figs 54A, B; 56A) . . . . . 2
- Second hind tarsomere with seven apical teeth and five platellae; genital styles as in Fig. 54E, F; aedeagus with spine (*c*) long and s-shaped, and spine (*d*) very short (Fig. 54A, B) . . . . .  
. . . . . *C. crispus* Kirkaldy  
Second hind tarsomere with 9–11 apical teeth and 7–9 platellae; genital styles as in Fig. 56D, E; aedeagus with spines (*c*) and (*d*) long and straight (Fig. 56A) . . . . . *C. stiriae*, sp. nov.

*Carolus crispus* Kirkaldy

(Figs 18D–F, 54)

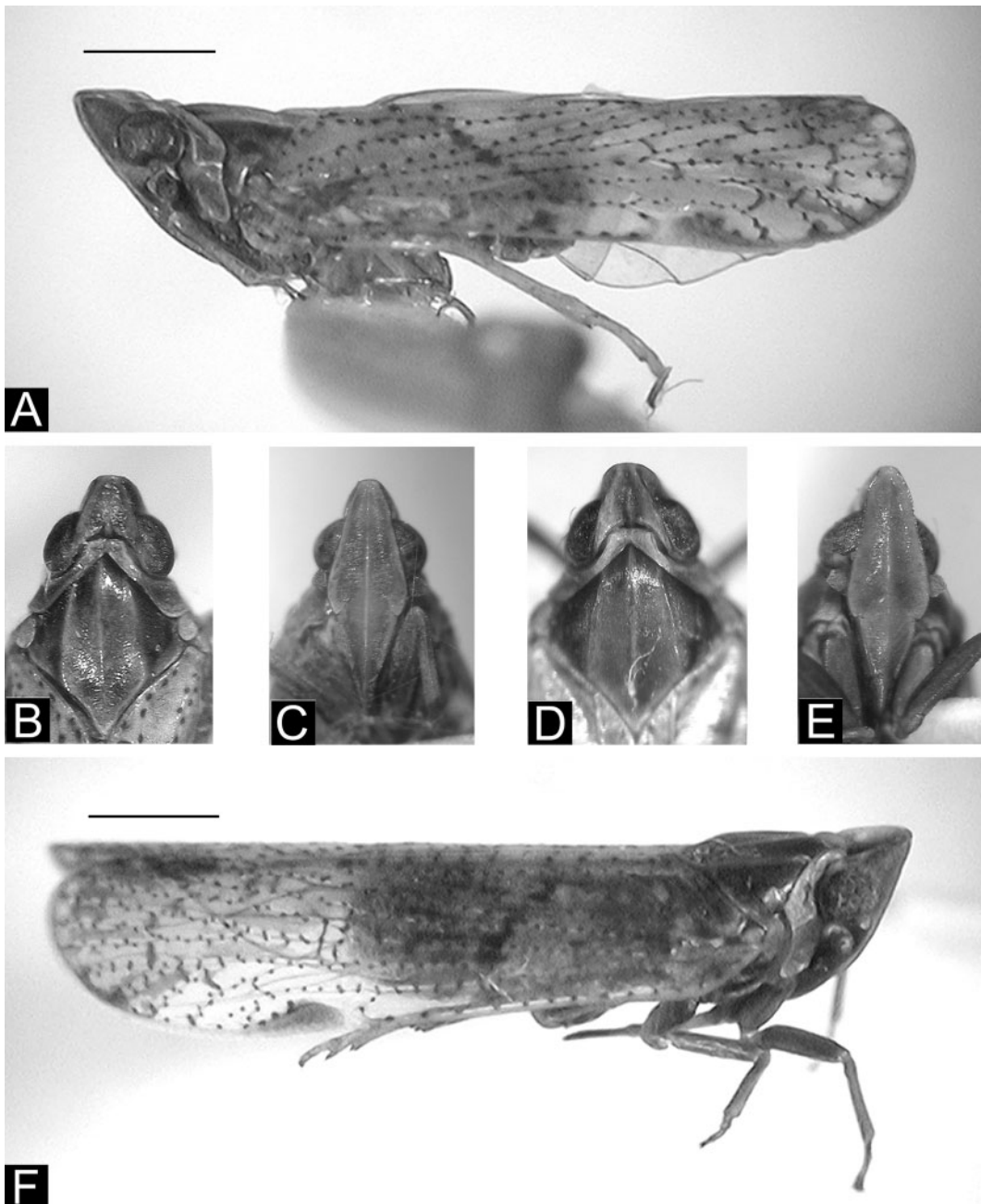
*Carolus crispus* Kirkaldy, 1906: 401.*Material examined**Lectotype.* (here designated), ♂ (examined), Australia: NSW: Sydney, i.1905 (Koebele) (BPBM).*Description**Morphology**Body length.* ♂ 6.6 mm.*Head.* Vertex 1.1× as long as wide. Frons 1.1–1.5× longer than wide; median carina incomplete, 1/2–3/4 as long as frons. Anteclypeus with well developed median carina.*Thorax.* Costa with 13–16 tubercles; Sc+R+M forming common stem; fork of Sc+R slightly basad of fork of CuA1+CuA2; position of icu at CuP at same level as apex of

Fig. 19. *Carolus carinatus*: A, habitus; B, C, head. *Carolus stiriae*: D, E, head; F, habitus.

clavus; 10 apical cells. Hind leg: tibia with 0–1 small lateral spine (without large lateral spines); 2nd tarsomere with seven apical teeth and five platellae.

*Male genitalia.* Anal tube as in Fig. 54C, D; ventro-median process of pygofer and genital styles as in Fig. 54E, F. Aedeagus (Fig. 54A, B): phallotheca with a pair of very small spines (a) ventrally near base, one short strongly curved spine (b) left lateral about midlength, one long s-shaped spine (c) right lateral near apex, and two very short spines (d, e) ventrally also near apex; flagellum unarmed.

#### Remarks

In the original description, Kirkaldy (1906) did not indicate how many males he examined. One male specimen carrying a holotype label, was obtained from the BPBM. It is here designated as lectotype in order to provide a comparative basis for this species.

Kirkaldy (1906: 401) stated, 'Radial and cubital veins forked about the same place', but in the lectotype the fork of Sc+R is slightly basad of the fork of CuA1+CuA2.

### *Carolus carinatus* Löcker & Larivière, sp. nov.

(Figs 19A–C, 55)

#### Material examined

*Holotype.* ♂, Australia: Qld: Dunwich area, Stradbroke I., 24–26.ix.1985, sweeping open forest (QM T123595, originally from QDPI).

*Paratypes.* **Australia:** **NSW:** 1 ♀, Myall Lakes NP, 32°29'22"S 152°23'53"E, ex: *Leptospermium laevigatum*, 15.xi.1996 (L. Wilkie) (AM); 1 ♀, Doyalson, nr Wyong, mv light, 4.ii.1979 (G. R. Brown) (ASCU).

#### Description

##### Morphology

*Body length.* ♂ 6.3 mm, ♀ 5.56–7.39 mm.

*Head.* Vertex 0.9× as long as wide. Frons 1.1–1.5× longer than wide; median carina incomplete, more than 5/6 as long as frons. Anteclypeus with well developed median carina.

*Thorax.* Costa with 14–15 tubercles; Sc+R+M forming short common stem; fork of Sc+R basad of fork of CuA1+CuA2; position of icu at CuP distad of or at same level as apex of clavus; 10–11 apical cells. Hind leg: tibia with two small lateral spines (without large lateral spines); 2nd tarsomere with nine apical teeth and seven platellae.

*Male genitalia.* Anal tube as in Fig. 55B, C; ventro-median process of pygofer and genital styles as in Fig. 55D, E. Aedeagus (Fig. 55A): phallotheca with a pair of very small spines (a) ventrally near base, one long moderately curved spine (b) left lateral about midlength, one long strongly curved spine (c) right lateral above midlength and very long spine (e) right lateral near apex; flagellum unarmed.

#### Etymology

Named after the well developed carinae on the face, that are less developed in other species of *Carolus*.

### *Carolus stiriae* Löcker & Larivière, sp. nov.

(Figs 19A–C, 56)

#### Material examined

*Holotype.* ♂, Australia: Qld: L. Broadwater, via Dalby, 19.–22.xi.1985, sweeping (QM T123594, originally from QDPI).

*Paratypes.* **Australia:** **Qld:** 2 ♀, Wondai, 10.ii.1922 (SAM); 1 ♀, Brisbane, 1.iii.1926 (H. Hacker) (QM). **NSW:** 1 ♀, N end of Bells Fire Trail Lake Innes Nature Res. S of Port Macquarie, 19.xii.2000 (Fletcher & Glover) (ASCU).

#### Description

##### Morphology

*Body length.* ♂ 6.6 mm, ♀ 7.22–7.61 mm.

*Head.* Vertex 0.9× as long as wide. Frons 1.5–1.9× longer than wide; median carina incomplete, 1/2–3/4 as long as frons. Anteclypeus lacking carinae.

*Thorax.* Costa with 14–16 tubercles; Sc+R+M forming very short common stem; fork of Sc+R at same level as fork of CuA1+CuA2; position of icu at CuP at same level as apex of clavus; 11 apical cells. Hind leg: tibia with 3–4 small lateral spines (without large lateral spines); 2nd tarsomere with (9–) 10–11 apical teeth and (7–) 8–9 platellae.

*Male genitalia.* Anal tube as in Fig. 56B, C; ventro-median process of pygofer and genital styles as in Fig. 56D, E. Aedeagus (Fig. 56A): phallotheca with a pair of very small spines (a) ventrally near base, one short strongly curved spine (b) left lateral about midlength, one long straight spine (c) dorsally above midlength and one long straight spine (d) ventrally above midlength; flagellum unarmed.

#### Etymology

'Stiria' is the Latin term for 'frozen drop' or 'icicle'. Named after the icicle-shaped spines on the phallotheca.

### Genus *Corylonga* Löcker & Fletcher, gen. nov.

Type species *Corylonga loisae* Löcker & Fletcher, sp. nov.

#### Description

##### Colour

Head yellowish brown, central part of vertex and clypeus sometimes darker, carinae straw coloured; pronotum in central part straw coloured, lateral parts darker; mesonotum orange to mid brown, carinae paler; legs straw coloured to light brown; forewing hyaline straw coloured sometimes with few light brown marks, veins straw coloured, tubercles mid brown; abdominal sternites yellowish brown to mid brown, intersegmental membranes pale yellowish.

### Morphology

*Body length.* ♂ 4.9–6.4 mm, ♀ 5.2–7.3 mm.

*Head.* Vertex more than 1.7× longer than wide; produced before eyes by (1/2–) 3/4–1× eye length; apex narrowly rounded or truncate; lateral carinae strongly elevated. Frons at least 2.2× longer than wide; position of maximum width around centre of frontoclypeal suture; lateral carinae double s-shaped, strongly elevated apically; median carina incomplete. Frontoclypeal suture semicircular, median part not reaching lower margin of antennal scape; postclypeus with well developed lateral carinae and median carina; anteclypeus with well developed median carina.

*Thorax.* Pronotum with strongly undulating carinae. Concavity at costal border of forewing absent; r–m1 distad of fork of MA–MP. Hind tibia with six apical teeth in a row interrupted by a wide gap.

*Male genitalia.* Anal tube as in Figs 57–63D, E and ventromedian process of pygofer and genital styles as in Figs 57–63F, G, with inner side of basal arm bearing small tooth. Aedeagus with 3–4 spines (*a, b, c, d*) (Figs 57–63A–C).

### Distribution

NSW, NT, Qld, WA.

### Remarks

Females could only be identified to genus level. The measurements of females given above are derived from 19 specimens from WA, Qld, NT and NSW.

A minimal branch length of 3785 (baseweight = 420) in the modified scaled weighting regime of dataset *A* (Fig. 5) clearly sets apart the *Corylonga*-clade, a monophyletic group that was retrieved by all different weighting regimes. Some of the characters defining the genus are the arrangement of spines on the phallosome (Figs 57–63A–C), the shape of the genital styles (Figs 57–63F, G) including a small tooth on the inner side of the basal arms, the very long and narrow vertex (more than 1.7× longer than wide), strongly produced before the eyes, the long and narrow frons (at least 2.2× longer than wide) and strongly undulating postocular carinae. The most parsimonious trees retrieved in each analysis varied only in the relationships of the seven species in *Corylonga* relative to each other. Very short branch lengths (minimal = 0–490; maximal = 0–840) within the genus reflect their great resemblance in external morphology. The main differences between the species are found in the male genitalia (three spines *v.* four spines, rounded *v.* lobiform spines and the orientation of the spines), characters that have not all been included in the phylogenetic analysis.

### Etymology

Name derived from the long vertex (= *coryphe sensu* Emeljanov). Gender: feminine.

### Key to species of *Corylonga*

1. Aedeagus with three spines ..... 2  
Aedeagus with four spines ..... 6
- 2(1). Spines lobiform (Fig. 61A–C) ..... *C. lobata*, sp. nov.  
Spines not lobiform (Figs 57–60A–C, 62–63A–C) ..... 3
- 3(2). Spines (*a*) and (*b*) with triangular foliaceous enlargements (Fig. 63A–C); spine (*c*) short (Fig. 63B) ... *C. triangula*, sp. nov.  
Spines (*a*) and (*b*) without or with very small triangular enlargements (Figs 57–60A–C; 62A–C); spine (*c*) long (Figs 57, B; 62C) ..... 4
- 4(3). Spine (*c*) long, arising on the right side and ending dorsal of the phallosome (Fig. 60B) ..... *C. leighi*, sp. nov.  
Spine (*c*) very long, arising on the right side, passing the phallosome dorsally and ending at the left side of the phallosome (Figs 57B, 59B, 62C) ..... 5
- 5(4). Spine (*b*) curved sinuate in two planes, arising right lateral below midlength (Fig. 57B, C) ..... *C. loisae*, sp. nov.  
Spine (*b*) moderately curved in one plane, arising ventrolaterally below midlength (Fig. 62A–C) ..... *C. mahmudae*, sp. nov.
- 6(1). Aedeagus with a spine (*d*) arising left lateral (Fig. 58B); without a ventral spine ..... *C. aaroni*, sp. nov.  
Aedeagus lacking spine (*d*), but with a ventral spine (*e*) (Fig. 59B) ..... *C. krottendorfi*, sp. nov.

### *Corylonga loisae* Löcker & Fletcher, sp. nov.

(Figs 20A–C, 57)

### Material examined

*Holotype.* ♂, Australia: WA: Kimberley Research Station via Wyndham, NW Aust., 5.ix.1956 (E. C. B. Langfield) (ANIC).

*Paratypes.* **Australia: WA:** 7♂, same locality and collector as holotype, 23.viii.1956 (ANIC).

### Description

#### Morphology

*Body length.* ♂ 5.1–5.7 mm.

*Head.* Vertex 1.7–2.8× longer than wide; produced before eyes by 3/4–1× eye length; caudal border u-shaped; median carina ~1/3 as long as vertex. Frons at least 2.2× longer than wide; median carina incomplete, ~1/3 as long as frons.

*Thorax.* Hind margin of pronotum right or acutely angled. Forewing 3.5–4.0× longer than wide; costa with 16–18 tubercles; Sc+R forming common stem, with M emerging separately from basal cell (rarely Sc+R+M forming very short common stem); fork of Sc+R distad of fork of CuA1+CuA2; position of icu at CuP distad of or at same level as apex of clavus; 10 apical cells. Hind leg: tibia with 3–4 small lateral spines (without large lateral spines); 1st tarsomere with 10–12 apical teeth and (4–)5 or 7 platellae; 2nd tarsomere with 9–10(–11) apical teeth and 7–8 platellae.

*Male genitalia.* Anal tube as in Fig. 57D, E; ventromedian process of pygofer and genital styles as in Fig. 57F, G. Aedeagus (Fig. 57A–C): phallosome with a long strongly curved spine (*c*) arising on right side above midlength, passing phallosome dorsally and ending at left side of phallosome, a second moderately curved spine (*a*) on left side above midlength and a third, shorter spine (*b*), curved sinuate

in two planes, arising right lateral below midlength; flagellum unarmed.

*Remarks*

The chaetotaxy of the hind leg is variable in this species, even between the legs of one specimen.

*Etymology*

Named in honour of the first author's friend and colleague Lois O'Brien.

*Corylonga aaroni* Löcker & Fletcher, sp. nov.

(Figs 20D–F, 58)

*Material examined*

*Holotype.* ♂, Australia: WA: Kimberley Research Station via Wyndham, NW Aust., 28.xii.1956 (E. C. B. Langfield) (ANIC).

*Description*

*Morphology*

*Body length.* ♂ 5.0 mm.

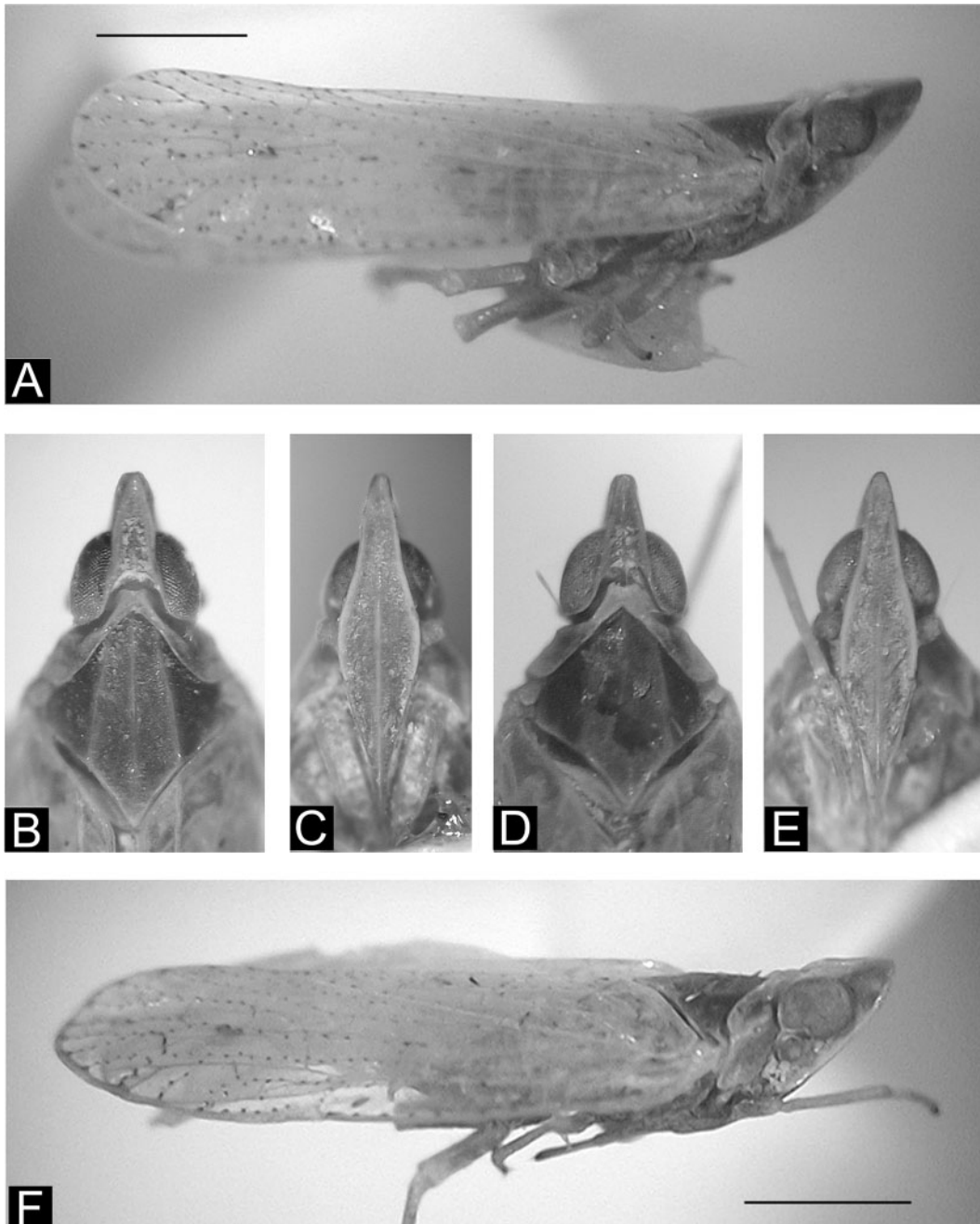


Fig. 20. *Corylonga loisae*: A, habitus; B, C, head. *Corylonga aaroni*: D, E, head; F, habitus.

*Head.* Vertex  $1.8\times$  longer than wide; produced before eyes by  $1/2\text{--}3/4$  of an eye length; caudal border u-shaped; median carina  $1/4\text{--}1/3$  as long as vertex. Frons more than  $2.3\times$  longer than wide; median carina incomplete,  $\sim 1/3\times$  as long as frons.

*Thorax.* Hind margin of pronotum rectangular. Forewing  $3.5\text{--}4.0\times$  longer than wide; costa with  $\sim 14$  tubercles; Sc+R forming common stem, M emerging separately from basal cell; fork of Sc+R basad of fork of CuA1+CuA2; position of icu at CuP distad of apex of clavus; 10 apical cells. Hind leg: tibia with three small lateral spines (without large lateral spines); 1st tarsomere with 11 apical teeth and six platellae; 2nd tarsomere with nine apical teeth and seven platellae.

*Male genitalia.* Anal tube as in Fig. 58D, E; ventro-median process of pygofer and genital styles as in Fig. 58F, G. Aedeagus (Fig. 58A–C): phallosome with a long strongly curved spine (c) arising on right side above midlength, passing phallosome dorsally and ending at left side of phallosome, a second, long, moderately curved spine (a) on left side above midlength, a third, shorter spine (b), curved sinuate in two planes, arising right lateral about midlength, and a fourth, short, slightly curved spine (d) with enlarged base on left side above midlength; flagellum unarmed.

#### *Etymology*

Named in honour of the first author's friend and colleague Aaron Simmons.

#### *Corylonga krottendorfi* Löcker & Fletcher, sp. nov.

(Figs 21A–C, 59)

#### *Material examined*

*Holotype.* ♂, Australia: NSW: Moree (W. W. F[rogatt]) (ASCU ASCTHE016810).

#### *Description*

##### *Morphology*

*Body length.* ♂ 6.4 mm.

*Head.* Vertex  $2.1\times$  longer than wide; produced before eyes by  $3/4\text{--}1\times$  eye length; caudal border u-shaped; median carina  $1/4\text{--}1/3$  as long as vertex. Frons at least  $2.3\times$  longer than wide; median carina incomplete,  $\sim 1/3$  as long as frons.

*Thorax.* Hind margin of pronotum rectangular. Forewing  $3.5\text{--}4.0\times$  longer than wide; costa with  $\sim 18$  tubercles; Sc+R forming common stem, with M emerging separately from basal cell; fork of Sc+R basad of fork of CuA1+CuA2; position of icu at CuP at same level as apex of clavus; 10 apical cells. Hind leg: tibia with four small lateral spines (without large lateral spines); 1st tarsomere with 10 apical teeth and five platellae; 2nd tarsomere with 10 apical teeth and eight platellae.

*Male genitalia.* Anal tube as in Fig. 59D, E; ventro-median process of pygofer and genital styles as in Fig. 59F,

G. Aedeagus (Fig. 59A–C): phallosome with a slightly curved spine (c) arising on right side near apex, a second slightly curved spine on left side above midlength (a), a third, moderately curved spine (b) ventrally about midlength, and a fourth, moderately curved spine (e) more basally; flagellum unarmed.

#### *Etymology*

Named in honour of Krottendorf, Austria, where the first author acknowledges her volleyball team colleagues.

#### *Corylonga leighi* Löcker & Fletcher, sp. nov.

(Figs 21D–F, 60)

#### *Material examined*

*Holotype.* ♂, Australia: Qld: Langi Lagoon, Mungkan Kandju NP,  $13^{\circ}27'S$   $142^{\circ}42'E$ , 29.vi–5.vii.1998, at light, open forest (T. Weir) (ANIC).

#### *Description*

##### *Morphology*

*Body length.* ♂ 5.8 mm.

*Head.* Vertex  $2\times$  longer than wide; produced before eyes by  $3/4\text{--}1\times$  eye length; caudal border u-shaped; caudal border v-shaped; median carina less than  $1/4$  as long as vertex. Frons more than  $2.3\times$  longer than wide; median carina incomplete,  $1/3\text{--}1/2$  as long as frons.

*Thorax.* Hind margin of pronotum rectangular. Forewing more than  $4\times$  longer than wide; costa with 11–14 tubercles; Sc+R+M forming very short common stem or Sc+R forming common stem, with M emerging separately from basal cell; fork of Sc+R distad of fork of CuA1+CuA2; position of icu at CuP at same level as apex of clavus; 10 apical cells. Hind leg: tibia with  $\sim 3$  small lateral spines (without large lateral spines); 1st tarsomere with 11–12 apical teeth and 6–7 platellae; 2nd tarsomere with 10 apical teeth and eight platellae.

*Male genitalia.* Anal tube as in Fig. 60D, E; ventro-median process of pygofer and genital styles as in Fig. 60F, G. Aedeagus (Fig. 60A–C): phallosome with a long moderately curved spine (c) arising on right side above midlength and ending dorsal of phallosome, a second moderately curved spine (a) on left side above midlength and a third, shorter spine (b) moderately curved in one plane arising ventrolaterally about midlength; flagellum unarmed.

#### *Etymology*

Named in honour of the first author's friend and colleague Leigh Pilkington.

***Corylonga lobata*** Löcker & Fletcher, sp. nov.

(Figs 22A–C, 61)

**Material examined**

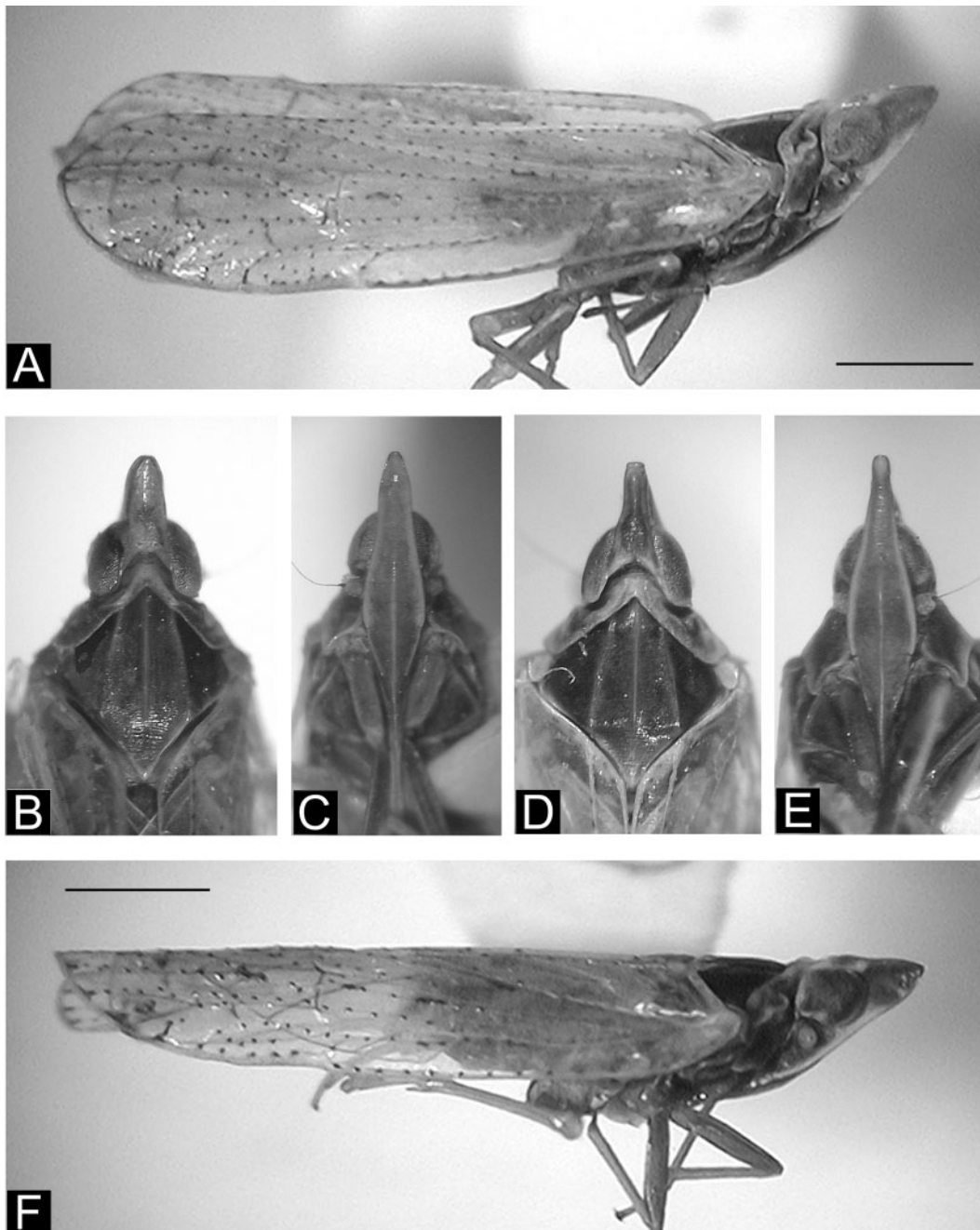
**Holotype.** ♂, Australia: Qld: 4 km NE Batavia Downs, 12°39'S 142°42'E, 24.x–23.xi.1992, Malaise Trap (P. Zborowski & A. Calder) (ANIC).

**Paratype.** **Australia: Qld:** 1♂, 7 km S Batavia Downs, 12°43'S 142°42'E, 23.xi.–11.xii.1992, Malaise Trap (P. Zborowski & W. Dressler) (ANIC).

**Description****Morphology**

**Body length.** ♂ 4.9–5.6 mm.

**Head.** Vertex 2.3–2.4× longer than wide; produced before eyes by 1/2–3/4 of an eye length; caudal border v-shaped; median carina 1/4–1/2 as long as vertex. Frons more than 2.4× longer than wide; median carina incomplete, 1/4–1/3 as long as frons; lateral margins sometimes foliaceous, concealing base of antennae.



**Fig. 21.** *Corylonga krottendorfi*: A, habitus; B, C, head. *Corylonga leighi*: D, E, head; F, habitus.



*Thorax.* Hind margin of pronotum right or acutely angled. Forewing 3.5–4.0× longer than wide; costa with 14–16 tubercles; Sc+R+M forming very short common stem or Sc+R forming common stem, with M emerging separately from basal cell; fork of Sc+R at same level as fork of CuA1+CuA2; position of icu at CuP slightly distad of apex of clavus; 10–11 apical cells. Hind leg: tibia with 2–3 small lateral spines (without large lateral spines); 1st tarsomere with 10 apical teeth and five platellae; 2nd tarsomere with (8–)10 apical teeth and (6–)8 platellae.

*Male genitalia.* Anal tube as in Fig. 61D, E; ventro-median process of pygofer and genital styles as in Fig. 61F, G. Aedeagus (Fig. 61A–C): phallosome with a flattened, lobiform spines, a short bifurcated spine (c) arising on right side above midlength, a second, short, slightly curved lobiform spine (a) arising on left side above midlength and a third, short lobiform spine (e) arising ventrally about midlength; flagellum unarmed.

#### Etymology

Named after the lobiform spines on the phallosome.

#### *Corylonga mahmudae* Löcker & Fletcher, sp. nov.

(Figs 22D–F, 62)

#### Material examined

*Holotype.* ♂, Australia: Qld: Kowanyama, N Qld, (Red Lilly Lagoon), 27.vii.1982 (J. F. Donaldson, J. W. Turner), at light, wild rice swamp (QM T123596, originally from QDPI).

#### Description

##### Morphology

*Body length.* ♂ 5.5 mm.

*Head.* Vertex 1.8× longer than wide; produced before eyes by 3/4–1× eye length caudal border u-shaped; median carina 1/4–1/3 as long as vertex. Frons at least 2.2× longer than wide; median carina incomplete, ~1/3 as long as frons.

*Thorax.* Hind margin of pronotum rectangular. Forewing more than 4× longer than wide; costa with ~12 tubercles; Sc+R forming common stem, with M emerging separately from basal cell; fork of Sc+R distad of or at same level as fork of CuA1+CuA2; position of icu at CuP at same level as apex of clavus; 10 apical cells. Hind leg: tibia with three small lateral spines (without large lateral spines); 1st tarsomere with 10 apical teeth and five platellae; 2nd tarsomere with 10 apical teeth and eight platellae.

*Male genitalia.* Anal tube as in Fig. 62D, E; ventro-median process of pygofer and genital style as in Fig. 62F, G. Aedeagus (Fig. 62A–C): phallosome with one long strongly curved spine (c) arising on right side above

midlength, passing phallosome dorsally and ending at left side of phallosome, a second moderately curved spine (a) on left side about midlength and a third, shorter spine (b) moderately curved in one plane arising ventrolaterally below midlength; flagellum unarmed.

#### Etymology

Named in honour of the first author's friend and colleague Mahmuda Begum.

#### *Corylonga triangula* Löcker & Fletcher, sp. nov.

(Figs 23A–C, 63)

#### Material examined

*Holotype.* ♂, Australia: NT: Tindal, NT, 1–10.xii.1967, at light (W. Vestjens) (ANIC).

*Paratype.* Australia: NT: 1 ♂, same data as holotype (ANIC).

#### Description

##### Morphology

*Body length.* ♂ 5.3–5.4 mm.

*Head.* Vertex 1.9–2.1× longer than wide; produced before eyes by 3/4–1× eye length caudal border u-shaped; caudal border v-shaped; median carina 1/4–1/2 as long as vertex. Frons more than 2.3× longer than wide; median carina incomplete, 1/4–1/3 as long as frons; lateral margins sometimes foliaceous, concealing base of antennae.

*Thorax.* Hind margin of pronotum acutely angled. Forewing 3.5–4.0× longer than wide; costa with 15–20 tubercles; Sc+R forming common stem, with M emerging separately from basal cell; fork of Sc+R basad of or at same level as fork of CuA1+CuA2; position of icu at CuP at same level as apex of clavus. Hind leg: tibia with 3–4 small lateral spines (without large lateral spines); 1st tarsomere with 10–12 apical teeth and 5–6 platellae; 2nd tarsomere with 10 apical teeth and eight platellae.

*Male genitalia.* Anal tube as in Fig. 63D, E; ventro-median process of pygofer and genital styles as in Fig. 63F, G. Aedeagus (Fig. 63A–C): phallosome with a short slightly curved spine (c) arising on right side above midlength, a second moderately curved spine (a) arising on left side above midlength and a third, shorter spine (b) moderately curved in one plane arising ventrolaterally about midlength, the latter two bearing triangular foliaceous enlargements; flagellum unarmed.

#### Etymology

Named after the triangular enlargements on the spines of the phallosome.

Genus *Fletcherolus* Löcker & Larivière, gen. nov.

Type species *Fletcherolus monospinosus* Löcker & Larivière, sp. nov.

*Description**Colour*

Vertex brown with white mark along lateral carinae, median carina paler; frons dark brown with yellow carinae;

clypeus light brown with yellow carinae; pronotum brown, carinae and adjacent areas pale yellowish; mesonotum brown, central area and carinae paler; legs yellow to brown; forewing hyaline white with light brown marks, veins concolorous with cells, tubercles dark brown; abdominal sternites brown, intersegmental membranes pale yellowish.

*Morphology*

*Body length.* ♂ 4.7–5.3 mm, ♀ 5.8–6.4 mm.

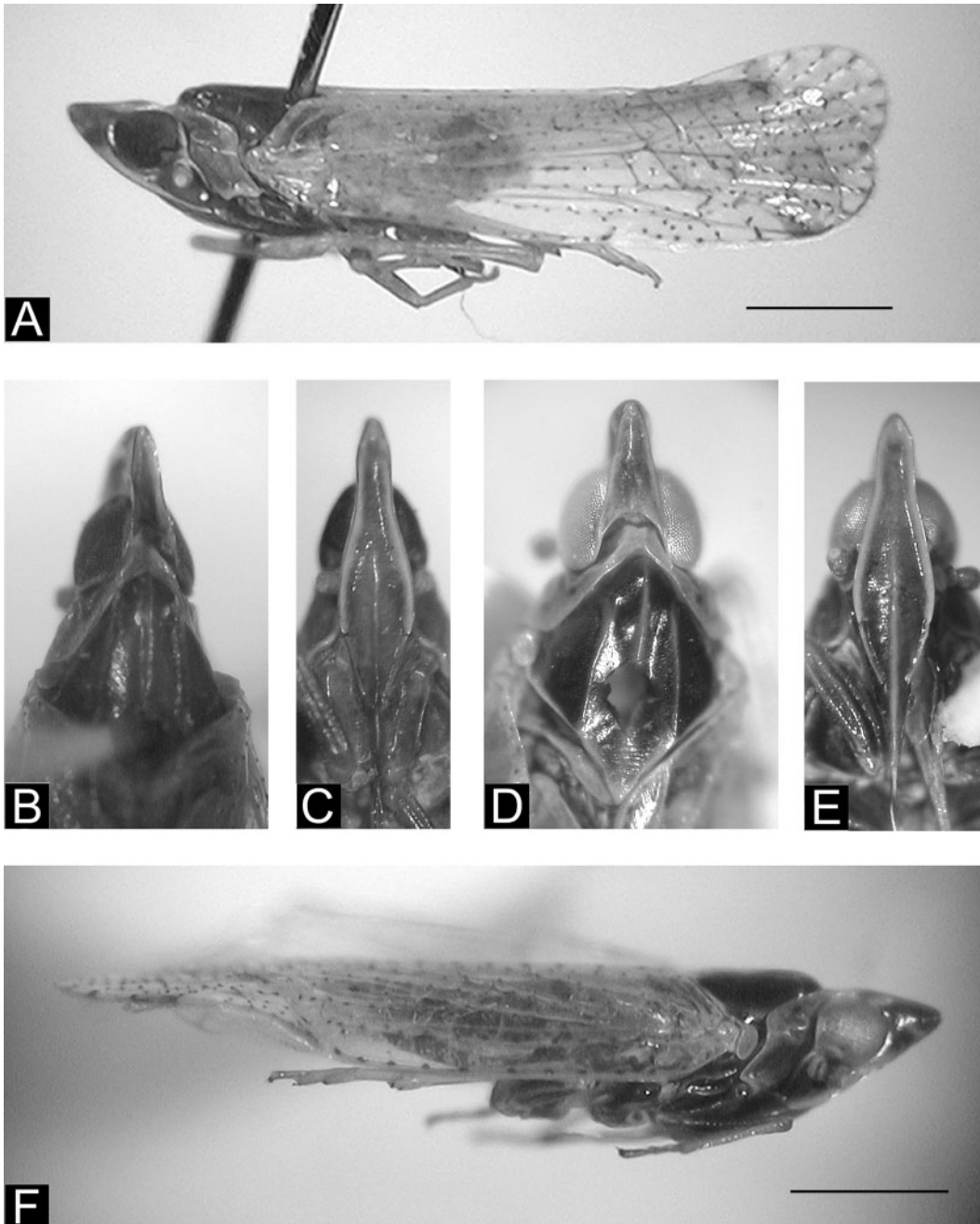


Fig. 22. *Corylonga lobata*: A, habitus; B, C, head. *Corylonga mahmudae*: D, E, head; F, habitus.

*Head.* Vertex 0.8–0.9× as long as wide; apex broadly pointed; caudal border u- or v-shaped; lateral carinae strongly elevated; median carina 1/3–1/2 as long as vertex. Lateral carinae of frons slightly elevated; median carina complete. Frontoclypeal suture semicircular, median part not reaching lower margin of antennal scape; postclypeus with well developed lateral carinae and median carina.

*Thorax.* Pronotum with sinuate carinae. Concavity at costal border absent; Sc+R forming common stem with M

emerging separately from basal cell; r–m1 distad of fork of MA–MP; position of icu at CuP at same level as apex of clavus; 10 apical cells. Hind tibia with row of six apical teeth interrupted by narrow gap; 1st tarsomere with 7(–8) apical teeth and no platellae; 2nd tarsomere with nine apical teeth and seven platellae.

*Male genitalia.* Anal tube as in Figs 64–65B, C, in dorsal view ovoid-shaped with a pointed tip; genital styles as in Figs 64–65D, E. Aedeagus ventrally with a large sclero-

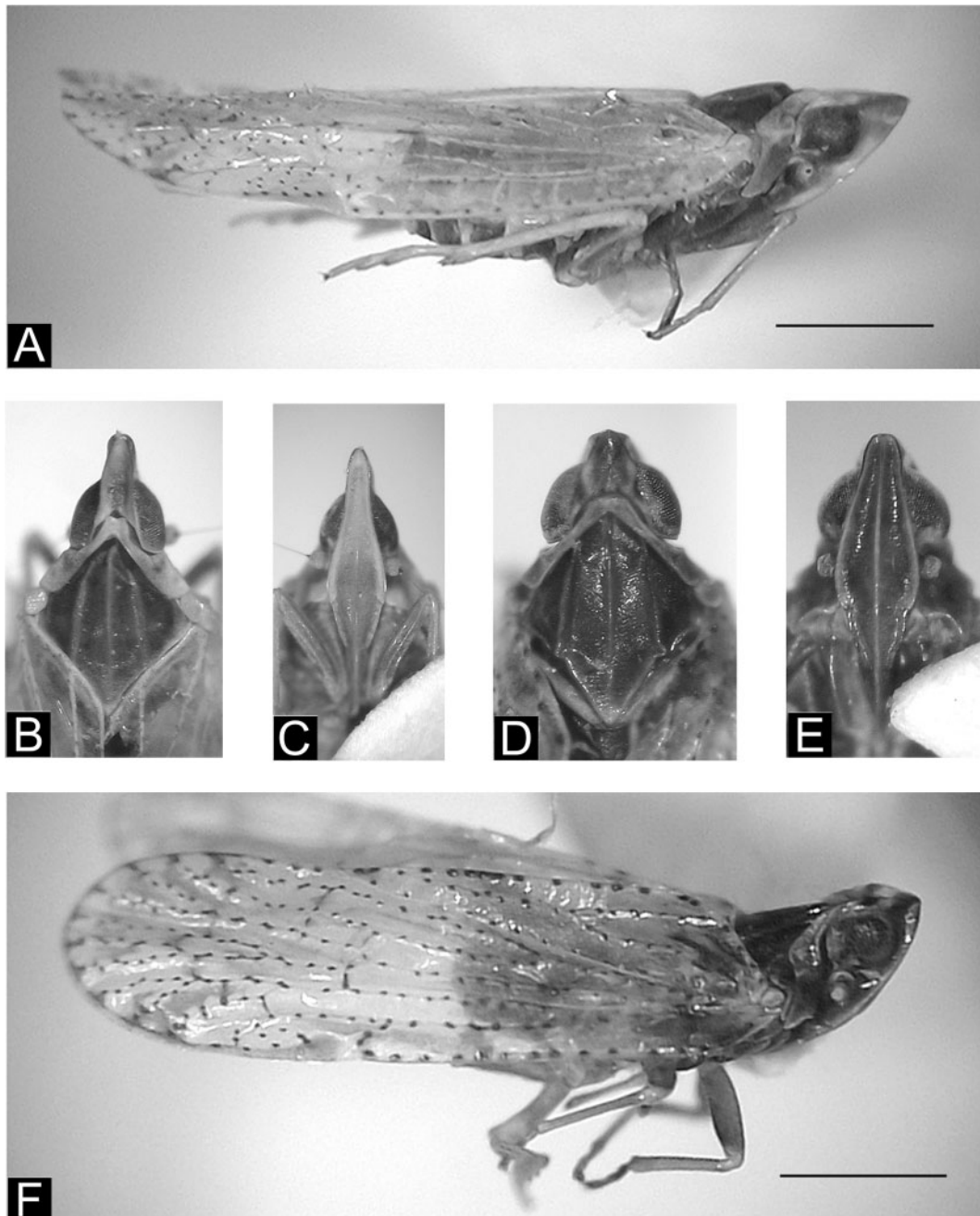


Fig. 23. *Corylonga triangula*: A, habitus; B, C, head. *Fletcherolus monospinosus*: D, E, head; F, habitus.

tised triangular ridge bearing another small ridge in 90° angle ending in small tooth. Spine (*a*) present. Spine (*b*) present or absent.

#### *Distribution*

NT, Qld.

#### *Remarks*

Females could only be identified to genus level. The measurements of females given above are derived from three specimens from Qld and NT.

The presence of a large sclerotised triangular ridge bearing another small ridge in 90° angle ending in small tooth is a synapomorphy for the *Fletcherolus*-clade, which was retrieved by all analyses. Other characters shared by both species of this genus are the ovoid-shaped anal tube with its pointed tip in dorsal view (Figs 64–65*B*), the presence of a spine (*a*) arising right lateral near the apex of the phallotheca, genital styles shaped as in Figs 64–65*D, E*, the narrow gap in the row of apical spines on the hind tibia, the broadly pointed apex of vertex and a distinctive shape and carination of the face as in Figs 23*E, 24C*. These and other characters account for a relatively long branch length (minimal = 2100, maximal = 3220) under the modified scaled weighting regime of dataset *A* (Fig. 5).

#### *Etymology*

Named in honour of our friend and colleague Murray Fletcher. Gender: masculine.

#### Key to species of *Fletcherolus*

1. Aedeagus with two spines: spine (*a*) slightly sinuate and spine (*b*) lance-shaped (Fig. 65*A*) . . . . . *F. lanceolatus*, sp. nov.  
Aedeagus with only one spine: spine (*a*) strongly sinuate (Fig. 64*A*) . . . . . *F. monospinosus*, sp. nov.

#### *Fletcherolus monospinosus* Löcker & Larivière, sp. nov.

(Figs 23*D–F, 64*)

#### *Material examined*

*Holotype*. ♂, Australia: Qld: Bamaga, Cape York, N Qld, 3.–6.vi.1969 (G. B. Monteith) (QM T123589, originally UQIC).

*Paratypes*. **Australia: Qld:** 1♂, same data as holotype (UQIC Reg. ♂ 551321). **Qld:** 1♂, Pat Ck, 11 km N of Archer Xing, via Coen, N Qld, 28–29.vi.1975 (G. B. Monteith) (QM).

#### *Description*

##### *Morphology*

*Body length*. ♂ 4.7–5.1 mm.

*Head*. Vertex produced before eyes by 1/4–1/2 of an eye length. Frons 1.9–2.3× longer than wide, position of

maximum width distinctly dorsad of centre of frontoclypeal suture; lateral carinae double s-shaped. Anteclypeus with well developed median carina.

*Thorax*. Hind margin of pronotum right or obtusely angled. Forewing 3.0–3.5× longer than wide; costa with 13–17 tubercles; fork of Sc+R basad of fork of CuA1+CuA2. Hind leg: tibia with 1–3 small lateral spines (without large lateral spines).

*Male genitalia*. Anal tube as in Fig. 64*B, C*; ventro-median process of pygofer and genital styles as in Fig. 64*D, E*. Aedeagus (Fig. 64*A*): phallotheca with a strongly sinuate spine arising right lateral near apex; flagellum unarmed.

#### *Etymology*

Named after the presence of a single spine on the phallotheca.

#### *Fletcherolus lanceolatus* Löcker & Larivière, sp. nov.

(Figs 24*A–C, 65*)

#### *Material examined*

*Holotype*. ♂, Australia: Qld: Statton R. nr Inkerman HS, N Qld, at light, 29.vii.1982 (J. F. Donaldson, J. W. Turner) (QM T123600, originally from QDPI).

*Paratype*. **Australia: Qld:** 1♂, same data as holotype (spine *b*, broken at base, glued onto card) (QDPI).

#### *Description*

##### *Morphology*

*Body length*. ♂ 5.0–5.3 mm.

*Head*. Vertex produced before eyes by 1/2–3/4 of an eye length. Frons 1.5–1.9× longer than wide, position of maximum width around centre of frontoclypeal suture; lateral carinae convex (although rectilinear apically) or double s-shaped. Anteclypeus with evanescent median carina.

*Thorax*. Hind margin of pronotum obtusely angled. Forewing 3.5–4.0× longer than wide; costa with 14–16 tubercles; fork of Sc+R basad of, or at same level as, fork of CuA1+CuA2. Hind leg: tibia with 3–4 small lateral spines (without large lateral spines).

*Male genitalia*. Anal tube as in Fig. 65*B, C*; ventro-median process of pygofer and genital styles as in Fig. 65*D, E*. Aedeagus (Fig. 65*A*): phallotheca with a long, slightly sinuate spine (*a*) arising right laterally near apex and straight, flattened and a bifurcated lance-shaped spine (*b*) right laterally above midlength; flagellum unarmed.

#### *Etymology*

Named after the lance-shaped spine on the phallotheca.

Genus *Gelastocaledonia* Löcker & Larivière, gen. nov.

Type species *Gelastocaledonia monteithi* Löcker & Larivière, sp. nov.

*Description*

*Morphology*

*Head.* Vertex  $0.6\times$  as long as wide (about as long as transverse carina), produced before eyes by less than  $1/4$  of an eye length; apex broadly truncate; caudal border

u-shaped; lateral carinae strongly elevated; median carina  $1/4$ – $3/4$  as long as vertex. Frons  $1.6$ – $1.8\times$  longer than wide, position of maximum width around centre of frontoclypeal suture; lateral carinae convex (although rectilinear apically) or s-shaped, moderately elevated, lateral margins foliaceous, concealing base of antennae; median carina incomplete, only present in middle part of frons. Frontoclypeal suture semi-circular, median part not reaching lower margin of antennal scape; postclypeus with well developed lateral carinae and

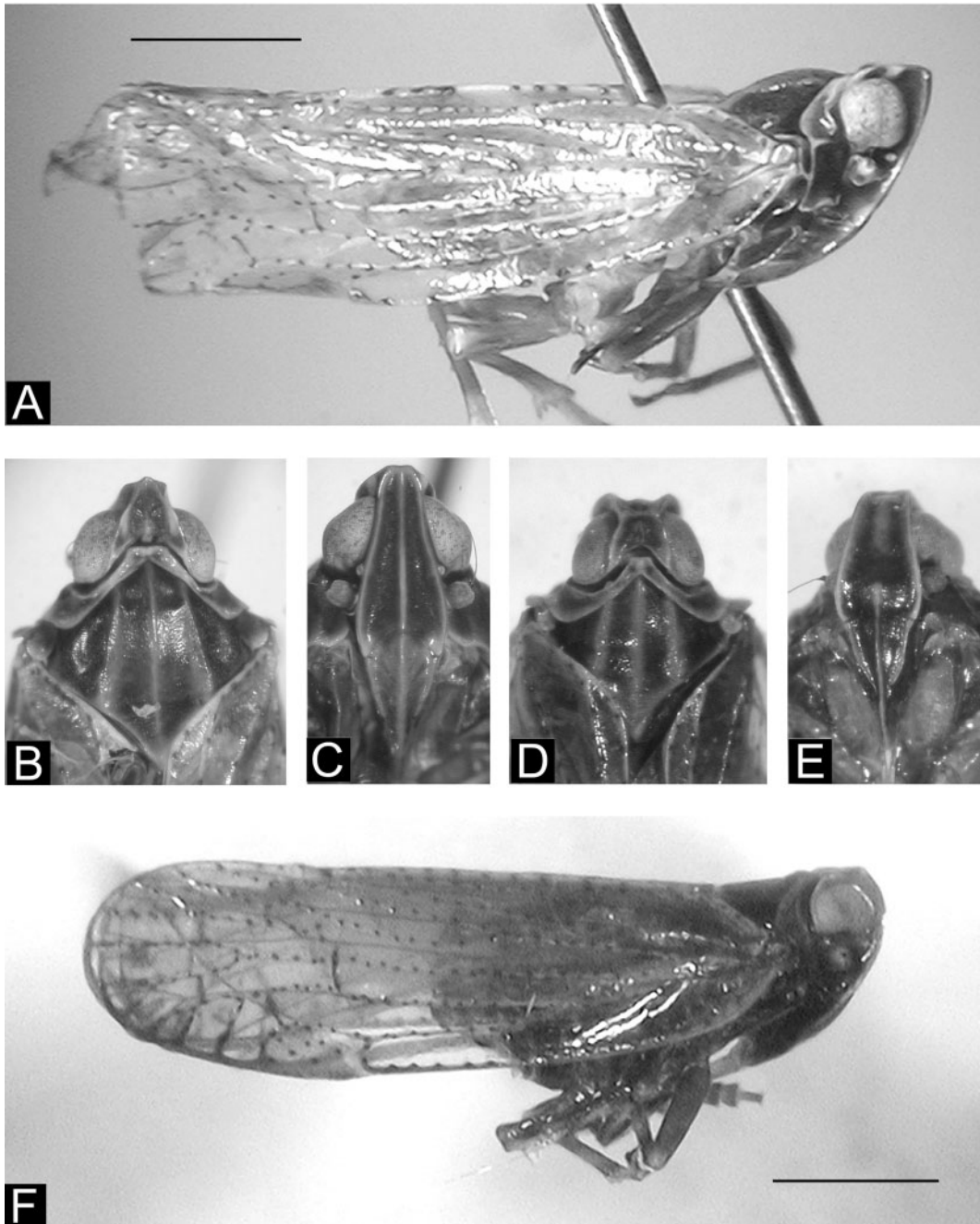


Fig. 24. *Fletcherolus lanceolatus*: A, habitus; B, C, head. *Gelastocaledonia monteithi*: D, E, head; F, habitus.

median carina; anteclypeus with well developed median carina.

*Thorax.* Pronotum with arched (rarely sinuate) carinae; hind margin right or obtusely angled. Forewing 3.0–3.5× longer than wide; costa with 16–19 tubercles; concavity at costal border absent; Sc+R+M forming common stem; fork of Sc+R basad or distad of fork of CuA1+CuA2; r-m1 basad, distad of or at same level as fork of MA–MP; position of icu at CuP distad of apex of clavus; (8–)9(–10) apical cells. Hind leg: tibia without lateral spines; six apical teeth in row interrupted by small or wide gap; 1st tarsomere with 9–10(–11) apical teeth and 2–4 platellae; 2nd tarsomere with 9–11 apical teeth and 7–9 platellae.

#### *Distribution*

New Caledonia.

#### *Remarks*

The following combination of characters is diagnostic for this species: shape of the face in facial view (Fig. 24E) and shape of vertex (about as long as transverse carina, Fig. 24D).

#### *Etymology*

This genus is only known from New Caledonia. Gender: feminine.

#### *Gelastocaledonia monteithi* Löcker & Larivière, sp. nov.

(Figs 24D–F, 66)

#### *Material examined*

*Holotype.* ♂, New Caledonia: Mt Humboldt, source, 21°53'S 166°25'E, 1300 m, sweeping, 8.xi.2002 (C. J. Burwell), 11127, (MNHN).

*Paratypes.* **New Caledonia:** 2♂, same data as holotype; 2♂, 3♀, Mt Humboldt, refuge, 21°53'S 166°25'E, 1350 m, beating, 5–8.xi.2002 (S. Wright), (1♂ genitalia damaged), (2♂, 2♀ QM, 1♀ MNHN); 2♀, Mt Humboldt, refuge, 21°53'S 166°25'E, 1350 m, 5–8.xi.2002 (Monteith, Wright & Burwell) (QM); 1♀, Mt Humboldt, summit track base, 21°53'S 166°25'E, 1350 m, sweeping, 7.xi.2002 (C. J. Burwell), (QM).

#### *Description*

##### *Colour*

Vertex mid brown, lateral carinae paler; face mid to dark brown, carinae light brown; pronotum mid brown, carinae paler; mesonotum dark brown, central part orange brown, carinae paler; legs straw coloured to dark brown; forewing hyaline light brown, veins light brown, mid brown tubercles; abdominal sternites dark brown, intersegmental membranes yellow or white.

##### *Morphology*

*Body length.* ♂ 4.4–4.8 mm; ♀ 5.2–5.8 mm.

*Male genitalia.* Anal tube as in Fig. 66B, C; ventro-median process of pygofer and genital styles as in Fig. 66D, E, genital styles broadly spoon-shaped. Aedeagus (Fig. 66A): phallosome with a very long, curved spine (*a*) arising ventral near apex and a very thin spine (*b*) arising left laterally above midlength; flagellum bearing a spine near apex.

#### *Etymology*

Named in honour of our colleague Geoff Monteith, who provided support for this project, particularly with material from New Caledonia.

#### Genus *Gelastocephalus* Kirkaldy

*Gelastocephalus* Kirkaldy, 1906: 402.

*Tarberus* Jacobi, 1928, synonymised by Fennah, 1969: 8.

Type species *Gelastocephalus ornithoides*, by monotypy.

#### *Description*

##### *Colour*

Vertex yellow to brown; face pale yellowish, lateral carinae sometimes darker, anteclypeus light brown, apical portion of anteclypeus black or brown; pronotum yellow brown to mid brown; mesonotum dark brown to black; forewing hyaline light to dark brown, with or without grey areas, with one whitish spot basad of pterostigma and one or two distad of pterostigma, veins concolorous with cells, tubercles mid to dark brown.

#### *Morphology*

*Body length.* ♂ 3.0–4.3 mm, ♀ 4.2–5.3 mm.

*Head.* Apex of vertex narrowly rounded or truncate; caudal border v-shaped; lateral carinae strongly elevated. Frons with strongly elevated lateral carinae; median carina absent. Postclypeus and anteclypeus with well developed, distinctly elevated median carina; postclypeus with absent or evanescent lateral carinae.

*Thorax.* Concavity at costal border of forewing present; Sc+R+M forming common stem; fork of Sc+R basad of fork of CuA1+CuA2. Hind tibia with row of six apical teeth.

#### *Distribution*

NSW, Qld, SA, Vic.

#### *Remarks*

Fennah (1969) synonymised the type species of *Tarberus*, *T. semicarinatus*, with *Gelastocephalus ornithoides* thereby making *Tarberus* a junior objective synonym of *Gelastocephalus*.

Females could only be identified to genus level. The measurements of females given above are derived from 20 specimens from NSW, Qld, SA and Vic.

Except for very few analyses, including the successive approximations weighting regimes of both datasets, *G. ornithoides* and *G. velifer* always formed a monophyletic group. The male genitalia of both species do not have any obvious similarities, though it is imaginable that they may have been derived from a common ancestor. The external morphology, however, makes it hard to distinguish between these two species. Both species show the same shape of head in lateral, dorsal and facial view (Fig. 25), a pale yellowish face without a median carina on the frons but a distinctly ele-

vated median carina on post- and anteclypeus and a postclypeus with absent or evanescent lateral carinae.

#### Key to species of *Gelastocephalus*

1. Male genital styles as in Fig. 67D, E; aedeagus with straight spine, turning 90° at its distal third (Fig. 67A), spine not concealed by a membranous lobe. . . . *G. ornithoides* Kirkaldy  
Male genital styles as in Fig. 68D, E; aedeagus with a completely straight spine that is almost entirely concealed by a large membranous lobe (Fig. 68A). . . . *G. velifer*, sp. nov.

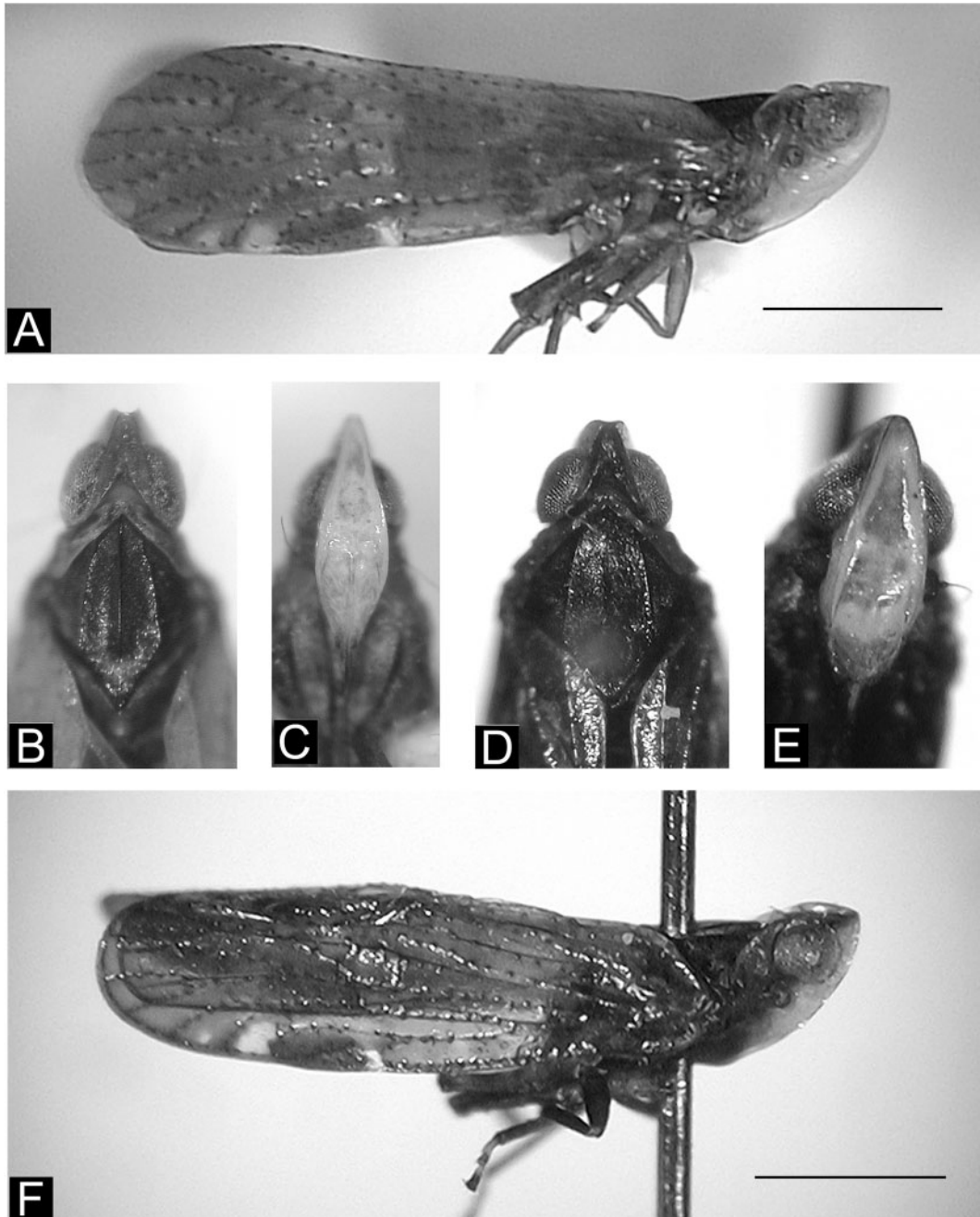


Fig. 25. *Gelastocephalus ornithoides*: A, habitus; B, C, head. *Gelastocephalus velifer*: D, E, head; F, habitus.

***Gelastocephalus ornithoides* Kirkaldy**

(Figs 25A–C, 67)

*Gelastocephalus ornithoides* Kirkaldy, 1906: 402, (plate XXXII, figs 6–7).*Tarberus semicarinatus* Jacobi, 1928, synonymised by Fennah, 1969: 8.**Material examined***Syntype* of *G. ornithoides*. ♀ (examined), Australia: NSW: Sydney, i.1905 (Koebele) (BPBM).*Holotype* (by monotypy) of *T. semicarinatus*. ♀ (examined), Australia: Qld: Malanda (Mjöberg) (NRS).*Other material examined*. **Australia:** **NSW:** 1♂, Boonoo Boonoo, 24.xi.1980, (M. A. Schneider, G. Daniels) (UQIC Reg. ♂ 55349); 1♂, 5 km N of Berry, 7.i.1980, (M. J. Fletcher) (ASCU); 1♂, Booti Booti NP, jct Lakes Way and Green Point, 32°20'S 152°32'E, site 95–8, from *Melaleuca nodosa*, 21.x.1995, (Schuh & Cassis) (AM). **Qld:** 2♂, Dunwich area, Stradbroke I., sweeping open forest, 24–26.ix.1985 (QDPI); 1♂, Moreton Island NP, Middle Rd, 27°10'01"S 153°24'06"E, 137 m, malaise trap in open Eucalyptus shrub, 5–8.x.2002, (C. Lambkin, N. Starick, N. Power, D. White, G. Kampmaier) (ANIC).**Description****Colour**

Legs light brown; abdominal sternites mid brown, intersegmental membranes pale yellowish.

**Morphology***Body length.* ♂ 3.0–4.3 mm.*Head.* Vertex 1.3–1.5× longer than wide, produced before eyes by 1/2–3/4 of an eye length; median carina incomplete, less than 1/4 as long as vertex. Frons 1.5–1.9× longer than wide, position of maximum width around or distinctly ventrad of centre of frontoclypeal suture; lateral carinae slightly s-shaped or convex (although rectilinear apically). Frontoclypeal suture semicircular, median part not reaching lower margin of antennal scape; lateral carinae on postclypeus absent or evanescent.*Thorax.* Pronotum with slightly sinuate carinae; hind margin right or acutely angled. Forewing 3–3.5× longer than wide; costa with 18–25 tubercles; r–m1 basad of or at same level as fork of MA–MP; position of icu at CuP distad of or at same level as apex of clavus; 10 (rarely nine) apical cells. Hind leg: tibia with 2–4 small lateral spines (without large lateral spines); six apical teeth in row interrupted by a wide gap; 1st tarsomere with 7(–9) apical teeth and 2(–3) platellae; 2nd tarsomere with seven apical teeth and five platellae.*Male genitalia.* Anal tube as in Fig. 67B, C; ventromedian process of pygofer and genital styles as in Fig. 67D, E. Aedeagus (Fig. 67A): phallosome with a long spine, straight and thickened in basal 2/3, then turning 90° and narrowing towards apex, and a broad, ventral sclerotised ridge bearing a triangular extension about midlength (Fig. 67A); flagellum unarmed.**Remarks**Kirkaldy (1906) indicated that his description was based on at least one male with no reference to females. However, the specimen in BPBM labelled as 'holotype' is a female that nonetheless matches the description of *G. ornithoides*. It is therefore possible either that Kirkaldy made an error regarding the gender of the specimen or that a male syntype exists. Because of this possibility, the female examined remains as syntype only. The holotype of *T. semicarinatus* is missing apart from the apices of the tarsi embedded in glue.The following combination of characters is diagnostic for this genus: pale yellow face without a median carina on the frons, with a distinctly elevated median carina on the clypeus and with absent or evanescent lateral carinae on the postclypeus. Completely absent or evanescent lateral carinae on the postclypeus are unusual within the Gelastocephalini. This feature occurs only in this species and in *Wernindia bubalis*, sp. nov.***Gelastocephalus velifer* Löcker & Larivière, sp. nov.**

(Figs 25D–F, 68)

**Material examined***Holotype.* ♂, Australia: NSW: Orange, Cadia Valley Gold Mine, Tunbridge Wells Farm, Four Mile Creek Road, 33°38'S 149°12'E, sticky trap, 21.xi.2003 (Löcker & Pilkington) (ASCU ASCTHE026730).*Paratype.* **Australia:** **Vic:** 1♂, Montmorency, 24.xii.1966 (SAM).**Description****Colour**

Legs dark brown with yellow 1st and 2nd tarsal segments, or legs yellow to mid brown; abdominal sternites mid to dark brown, intersegmental membranes orange.

**Morphology***Body length.* ♂ 4.0 mm.*Head.* Vertex as long as wide, produced before eyes by 1/4–1/2 of eye length; median carina incomplete, ~1/4 as long as vertex. Frons with lateral carinae convex (although rectilinear apically). Lateral carinae on postclypeus evanescent.*Thorax.* Pronotum with sinuate carinae; hind margin rectangular. Forewing 3.5–4.0× longer than wide; costa with 23–24 tubercles; r–m1 distad of or at same level as fork MA–MP; position of icu at CuP distad of apex of clavus; nine apical cells. Hind leg: tibia with 1–2 small lateral spines (without large lateral spines); six apical teeth in row interrupted by small or wide gap; 1st tarsomere with seven apical teeth and no platellae; 2nd tarsomere with eight apical teeth and six platellae.*Male genitalia.* Anal tube as in Fig. 68B, C; ventromedian process of pygofer and genital styles as in Fig. 68D, E. Aedeagus (Fig. 68A): phallosome with a long sclerotised completely straight spine concealed almost in its entire length by large membranous lobe; flagellum unarmed.



*Etymology*

Named after the large sail-shaped membranous lobe of the phallotheca; 'velifer' being the Latin term for 'sail-bearing'.

Genus *Gurrundus* Löcker & Larivière, gen. nov.

Type species *Gurrundus fuscomarginatus* Löcker & Larivière, sp. nov.

*Description**Morphology*

*Body length.* ♂ 4.5–5.1 mm, ♀ 5.4 mm.

*Head.* Vertex produced before eyes by less than 1/2–3/4 of an eye length; apex broadly rounded; caudal border u-shaped; median carina incomplete, 1/4–1/2 as long as vertex. Frons 1.9–2.3× longer than wide, position of maximum width around centre of frontoclypeal suture; lateral carinae convex (although rectilinear apically), moderately elevated; median carina incomplete. Frontoclypeal suture semicircular, median part not reaching lower margin of antennal scape; postclypeus with well developed lateral carinae and median carina; anteclypeus with well developed median carina.

*Thorax.* Hind margin of pronotum rectangular. Forewing 3.0–3.5× longer than wide; costa with 12–14 tubercles; Sc+R+M forming common stem; position of icu at CuP at same level as apex of clavus. Hind tibia with six apical teeth in row interrupted by a wide gap; 1st tarsomere with seven apical teeth and no platellae; 2nd tarsomere with eight apical teeth and six platellae.

*Male genitalia.* Anal tube as in Figs 69–70B, C; ventromedian process of pygofer and genital styles as in Figs 69–70D, E.

*Distribution*

NSW, NT, Qld.

*Remarks*

Most of the weighting regimes applied regard *G. nectostylus* and *G. fuscomarginatus* as closely related, but some of the analyses support a monophyletic genus *Gurrundus*. These two species share a similar shape and carination of the head (Fig. 26A, C, E, F), a long face (frons 1.9–2.3× longer than wide), the chaetotaxy of the hind tarsomeres (1st tarsomere with seven apical teeth and no platellae, 2nd tarsomere with eight apical teeth and six platellae) and similar types of genital styles (Fig. 69–70D, E) and anal tube (Figs 69–70B, C). Based on these characters the two species are primarily put in one genus, but additional material is needed to clarify whether they should not be placed in two different genera.

*Etymology*

Named in honour of our friend and colleague Geoff Gurr. Gender: masculine.

**Key to species of *Gurrundus***

- Head dark brown with pale yellow lateral carinae; pygofer mid brown, ventromedian process triangular (Fig. 70E) with a dark brown border; flagellum apically with a spine (Fig. 70A) . . . . . *G. nectostylus*, sp. nov.  
Head light to mid brown with light brown lateral carinae; pygofer light brown, ventromedian process truncate (Fig. 69E) with a black border; flagellum without spines but with a long sclerotised blade (Fig. 69A) . . . . .  
. . . . . *G. fuscomarginatus*, sp. nov.

*Gurrundus fuscomarginatus* Löcker & Larivière, sp. nov.

(Figs 26A–C, 69)

*Material examined*

*Holotype.* ♂, Australia: Qld: West Claudie River, 4.5 km SW road junction, 12°44'S 143°15'E, 5.xii.1986, mv lamp (G. Daniels, M. A. Schneider) (QM T123591, originally from UQIC, Reg. ♂ 55329).

*Paratypes.* **Australia: NSW:** 1♀, Gloucester River, Barrington Tops SF, 19.i.1981 (C. N. Smithers) (AM).

*Description**Colour*

Vertex light brown; face mid brown with light brown carinae; pronotum light brown; mesonotum dark brown, central part mid brown; legs straw coloured to mid brown; forewing hyaline grey with light brown to mid brown areas, veins concolorous with cells, tubercles mid brown; abdominal sternites brown, intersegmental membranes pale yellow.

*Morphology*

*Body length.* ♂ 4.5 mm; ♀ 5.4 mm.

*Head.* Vertex 1.5× longer than wide; lateral carinae strongly elevated. Median carina of frons incomplete, 1/2–3/4 as long as frons.

*Thorax.* Pronotum with slightly undulating carinae. Concavity at costal border present or absent; Sc+R+M forming common stem; fork of Sc+R basad of (almost at same level as) fork of CuA1+CuA2; r-m1 distad of fork MA–MP; 10 apical cells. Hind leg: tibia with 2–3 small lateral spines (without large lateral spines).

*Male genitalia.* Anal tube as in Fig. 69B, C; ventromedian process of pygofer and genital styles as in Fig. 69D, E. Aedeagus (Fig. 69A): phallotheca with a long slightly curved spine (a) arising on right side above midlength and a long almost straight spine (b) arising ventrolaterally above midlength; flagellum without spines but with long sclerotised blade.

*Etymology*

Named after the dark brown to black margin of the ventromedian process of the pygofer; 'fuscus' being the latin term for 'dark'.

***Gurrundus nectostylus* Löcker & Larivière, sp. nov.**

(Figs 26D–F, 70)

*Material examined*

*Holotype.* ♂, Australia: NT: 33 km WNW of Alice Springs, 23°36'S 133°34'E, 30.ix.1978 (Upton & Barret) (ANIC).

*Description*

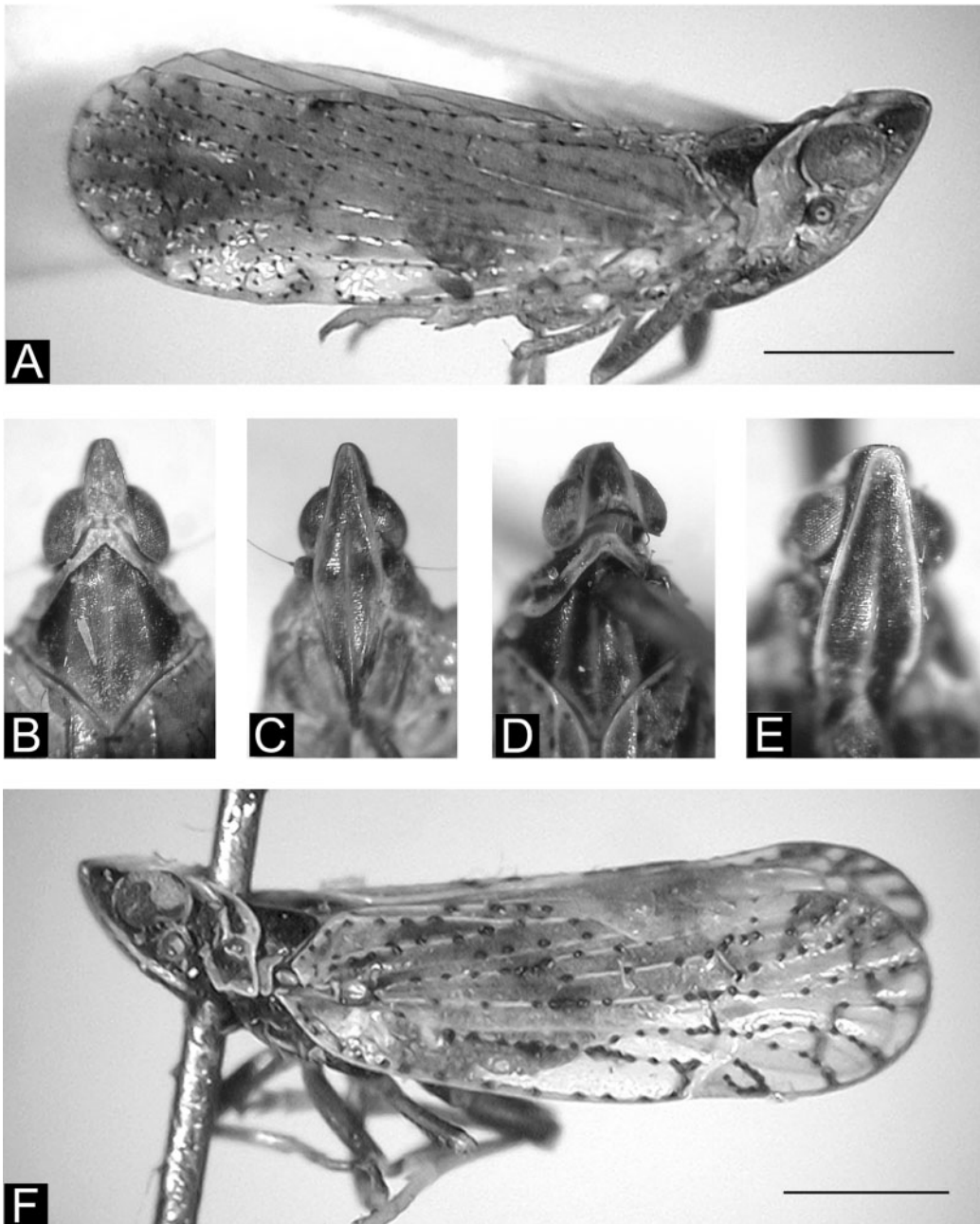
*Colour*

Vertex pale yellow, central part dark brown, median carina yellow to brown, lateral carinae yellow; face dark

brown, lateral carinae pale yellow, median carina orange; pronotum yellow with dark brown marks; mesonotum dark brown to black, central part orange brown, carinae and hind border of mesonotum orange; legs yellow to brown; forewing hyaline white with a few mid brown marks especially along crossveins, veins white, tubercles dark brown; abdominal sternites mid to dark brown, intersegmental membranes yellow to orange.

*Morphology*

*Body length* ♂ 5.1 mm.



**Fig. 26.** *Gurrundus fuscomarginatus*: A, habitus; B, C, head. *Gurrundus nectostylus*: D, E, head; F, habitus.

**Head.** Vertex as long as wide; lateral carinae moderately elevated. Median carina of frons incomplete, ~3/4 as long as frons.

**Thorax.** Pronotum with interrupted carinae, apically integrated with lateral carinae to form circular carinal loop. Concavity at costal border absent; Sc+R+M forming very short common stem; fork of Sc+R distad of fork of CuA1+CuA2; r-m1 basad of or at same level as fork MA-MP; eight apical cells. Hind leg: tibia without lateral spines.

**Male genitalia.** Anal tube as in Fig. 70B, C; ventromedian process of pygofer and genital styles as in Fig. 70D, E. Aedeagus (Fig. 70A): phallosome with a long bent spine (a) arising ventrally above midlength and a long, slightly curved spine (b) arising ventrolaterally above midlength; flagellum apically with spine.

#### Etymology

Named after the paddle-shaped genital styles; 'nektos' being the Greek term for 'swimming'.

#### Genus *Guttala* Löcker & Larivière, gen. nov.

Type species *Guttala mona* Löcker & Larivière, sp. nov.

#### Description

##### Colour

Frons dark brown with yellow lateral carinae, clypeus mid brown, or entire face orange except for yellow lateral carinae; mesonotum mid brown or orange; legs straw coloured to light brown; forewing hyaline light brown except for large colourless area along costa, colourless marks in apical cells, brown stripes apically on Sc and R, dark (mostly bullate) spots or streaks apically on MA1 and MA2 and sometimes on MP1, one more or less distinctive brown mark at apex of clavus, with or without brown marks apically on CuA1 and CuA2, veins concolorous with cells, tubercles in some areas light brown in others dark brown; abdominal sternites yellow, intersegmental membranes yellow.

##### Morphology

**Body length.** ♂ 5.1–5.4 mm, ♀ 5.6–6.0 mm.

**Head.** Vertex produced before eyes by less than 1/4–1/2 of an eye length; apex broadly truncate; caudal border u-shaped; lateral carinae moderately to strongly elevated. Frons 1.1–1.5× longer than wide, position of maximum width distinctly ventrad of centre of frontoclypeal suture; lateral carinae (slightly) s-shaped, moderately to strongly elevated, lateral margins foliaceous, concealing base of antennae; median carina absent. Frontoclypeal suture semi-circular, median part reaching at least lower margin of antennal scape; anteclypeus lacking carinae.

**Thorax.** Hind margin of pronotum rectangular. Forewing 3.5–4.0× longer than wide; concavity at costal border absent; Sc+R+M forming common stem (sometimes very short); r-m1 basad of or at same level as fork MA-MP; position of icu at CuP distad of apex of clavus; nine apical cells. Hind tibia with six apical teeth in a row interrupted by a wide gap; 1st tarsomere normally with 11 apical teeth and five platellae; 2nd tarsomere normally with 10 apical teeth and eight platellae.

**Male genitalia.** Anal tube as in Figs 71–72B, C; 73C, D; 74B, C; ventromedian process of pygofer and genital styles as in Figs 71–72D, E; 73E, F; 74D, E. Aedeagus with a similar configuration of spines in all species.

#### Distribution

NT.

#### Remarks

Females could only be identified to genus level. The measurements of females given above are derived from six specimens from NT. The dentition of the tarsomeres is constant throughout the genus except for *G. nickeli* that varies as given in the species description. The number of apical cells of the forewing is unknown in *G. nickeli* because the tegmina of the only known specimen are apically damaged.

The 2–3 three dark (mostly bullate) spots or streaks on the apex of the forewing represent a synapomorphy for this clade, retrieved by most of the analyses. Due to the chaetotaxy of the tarsomeres and the carination of the postclypeus, which differ from all other species in *Guttala*, a few analyses placed *G. nickeli* outside the *Guttala*-clade. Additional insect material may show if that this is just an aberration. Characters such as the shape of genital styles (Figs 71–72D, E; 73E, F; 74D, E), the ovoid-shaped anal tube in dorsal view (Figs 71–72B, 73C, 74B) and the synapomorphy named above leave no doubt that all four species are part of one monophyletic genus.

#### Etymology

This genus is named after the bullate spots on the apex of the forewing. In Latin 'gutta' means 'drop' and 'ala' is the 'wing'. Gender: feminine.

#### Key to species of *Guttala*

1. Aedeagus with spine (d) short, slightly curved, cylindrical2  
Aedeagus with spine (d) long, strongly curved, blade-like. . . . . 3
- 2(1). Aedeagus ventrally with spine (a) bifurcated (Fig. 73A) . . . . .  
. . . . . *G. nickeli*, sp. nov.  
Aedeagus ventrally spine (a) not bifurcated (Fig. 72A) . . . . .  
. . . . . *G. bernhardtae*, sp. nov.
- 3(1). Spine (b) bifurcated in its basal third (Fig. 74A) . . . . .  
. . . . . *G. robierae*, sp. nov.  
Spine (b) not bifurcated (Fig. 71A) . . . . . *G. mona*, sp. nov.

***Guttala mona*** Löcker & Larivière, sp. nov.

(Figs 27A–C, 71)

*Material examined*

*Holotype.* ♂, Australia: NT: 60 km SSW of Victoria R. Downs, 18.vii.1969 (M. Mendum) (ANIC).

*Description**Colour*

Vertex mid brown, with yellow stripe on each side ranging from lateral carina to caudal border of vertex. Three dark brown slightly bullate spots on the apex of forewing.

*Morphology*

*Body length.* ♂ 5.4 mm.

*Head.* Vertex 0.7× as long as wide; median carina incomplete, less than 1/4 as long as vertex. Postclypeus with well developed lateral carinae and evanescent median carina.

*Thorax.* Pronotum with sinuate carinae. Costa of forewing with 15–16 tubercles; fork of Sc+R distinctly basad of fork of CuA1+CuA2; r–m1 basad of fork MA–MP; position of icu at CuP distad of apex of clavus, nine apical cells. Hind leg: tibia with one small lateral spine (without large lateral spines); six apical teeth in row interrupted by a wide gap; 1st tarsomere with 11 apical teeth and five platellae; 2nd tarsomere with 10 apical teeth and eight platellae.

*Male genitalia.* Anal tube as in Fig. 71B, C; ventro-medial process of pygofer and genital styles as in Fig. 71D, E. Aedeagus (Fig. 71A): phallosome with a strongly curved bifurcated spine (a) ventrally, a short strongly curved spine (b) ventrolaterally, and a long, strongly curved, blade-like spine (d) dorsally; flagellum unarmed.

*Etymology*

Derived from the name of first author's friend Monika Klaisner.

***Guttala bernhardtae*** Löcker & Larivière, sp. nov.

(Figs 27D–F, 72)

*Material examined*

*Holotype.* ♂, Australia: NT: 25 km S of Wave Hill Police Stn, 17°39'S 130°52'E, 13.viii.1969 (M. Mendum) (ANIC).

*Paratype.* Australia: NT: 1♂, 55km NW of Victoria R. Downs, 16°03'S 131°22'E, 19.vi.1969 (M. Mendum) (ANIC) (head missing).

*Description**Colour*

Vertex light brown, central part mid brown.

*Morphology*

*Body length.* ♂ 5.2 mm.

*Head.* Vertex as long as wide; median carina incomplete, 1/4–1/2 as long as vertex. Postclypeus with well developed lateral carinae and evanescent median carina.

*Thorax.* Pronotum with sinuate to arched carinae. Costa of forewing with 15–17 tubercles; fork of Sc+R basad of fork of CuA1+CuA2; r–m1 basad of or at same level as fork MA–MP; position of icu at CuP distad of apex of clavus; nine apical cells. Hind leg: tibia with 1–2 small lateral spines (without large lateral spines); six apical teeth in row interrupted by a wide gap; 1st tarsomere with 11 apical teeth and five platellae; 2nd tarsomere with 10 apical teeth and eight platellae.

*Male genitalia.* Anal tube as in Fig. 72B, C; ventro-medial process of pygofer and genital styles as in Fig. 72D, E. Aedeagus (Fig. 72A): phallosome with a moderately curved spine (b) arising ventrolaterally, a second long moderately curved spine (c) left laterally, and a third short, slightly curved, cylindrical spine (d) dorsally (all spines arising near apex); flagellum unarmed.

*Remarks*

The two dark brown spots on the apex of the forewing are not bullate and are therefore less distinctive than those in the other species of *Guttala*.

*Etymology*

Named in honour of the first author's friend Theresia Bernhardt.

***Guttala nickeli*** Löcker & Larivière, sp. nov.

(Figs 28A–C, 73)

*Material examined*

*Holotype.* ♂, Australia: NT: 22 mls. S of Alice Springs, 15.ii.1966 (E. Britton) (ANIC).

*Description**Colour*

Vertex brownish yellow, lateral carinae paler.

*Morphology*

*Body length.* ♂ 5.1 mm.

*Head.* Vertex 0.7× as long as wide; median carina incomplete, 1/4–1/2 as long as vertex. Postclypeus with well developed lateral carinae and median carina.

*Thorax.* Pronotum with sinuate carinae. Costa of forewing with 1–3 tubercles; fork of Sc+R basad of or at same level as fork of CuA1+CuA2; r–m1 basad of or at same level as fork MA–MP; position of icu at CuP only slightly distad of apex of clavus. Hind leg: tibia without lateral spines; six apical teeth in row interrupted by a wide gap; 1st tarsomere with 13 or 16 apical teeth and seven or nine platellae; 2nd tarsomere with 13 apical teeth and 11 platellae.

*Male genitalia.* Anal tube as in Fig. 73C, D; ventro-medial process of pygofer and genital styles as in Fig. 73E, F. Aedeagus (Fig. 73A, B): phallosheca with a short bifurcated spine (a) ventrally, a short, slightly curved spine (b) ventrolaterally, a long moderately curved spine (c) left laterally, and a short, slightly curved, cylindrical spine (d) dorsally (all spines arising above midlength); flagellum unarmed.

#### Remarks

This species is characterised by the presence of three dark brown slightly bullate spots on the apex of forewing. The dentition of the tarsomeres is also more variable in this species than in other species of the genus. The number of apical cells of the forewing is unknown in *G. nickeli* because the tegmina of the only known specimen are apically damaged.

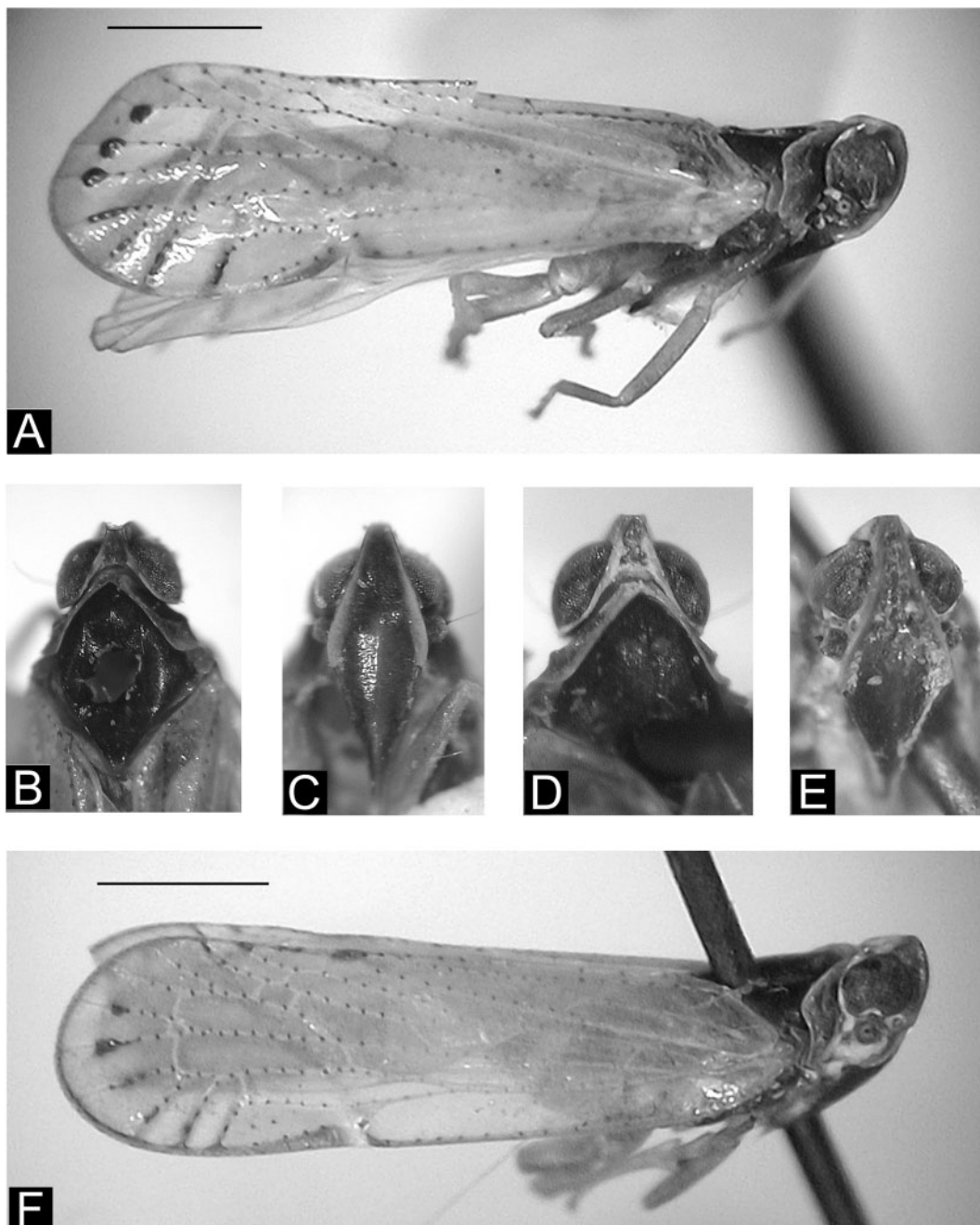


Fig. 27. *Guttala mona*: A, habitus; B, C, head. *Guttala bernhardtae*: D, E, head; F, habitus.

*Etymology*

Named in honour of the first author's friend and colleague Herbert Nickel.

***Guttala robierae*** Löcker & Larivière, sp. nov.

(Figs 28D–F, 74)

*Material examined*

*Holotype.* ♂, Australia: NT: 60 km SSW of Victoria R. Downs, 18.vii.1969 (M. Mendum) (ANIC).

*Description**Colour*

Vertex mid brown, with whitish stripe ranging from lateral carinae to caudal border of vertex. Three dark brown slightly bullate spots on the apex of forewing.

*Morphology*

*Body length.* ♂ 5.1 mm.

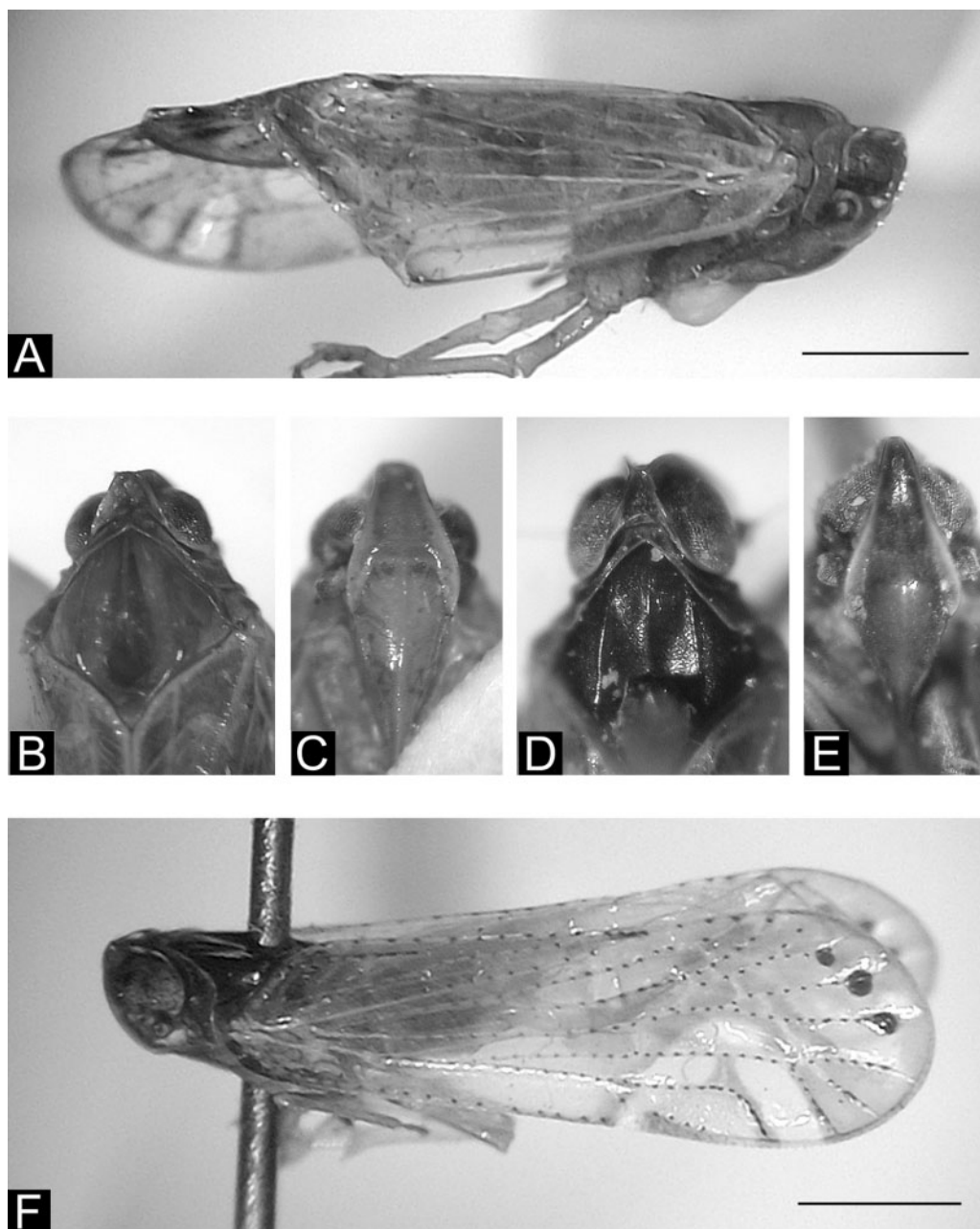


Fig. 28. *Guttala nickeli*: A, habitus; B, C, head. *Guttala robierae*: D, E, head; F, habitus.

*Head.* Vertex as long as wide; median carina incomplete, less than 1/4 as long as vertex. Postclypeus with evanescent lateral carinae and median carina.

*Thorax.* Pronotum with arched carinae. Costa of forewing with 18–19 tubercles; fork of Sc+R basad of fork of CuA1+CuA2; r-m1 basad of fork MA–MP; position of icu at CuP distad of apex of clavus, nine apical cells. Hind leg: tibia without lateral spines; six apical teeth in row interrupted by a wide gap; 1st tarsomere with 11 apical teeth and five platellae; 2nd tarsomere with 10 apical teeth and eight platellae.

*Male genitalia.* Anal tube as in Fig. 74B, C; ventro-median process of pygofer and genital styles as in Fig. 74D, E. Aedeagus (Fig. 74A): phallosome with a strongly curved, deeply bifurcated spine (a) ventrally, a shorter, in its basal third bifurcated spine (b) ventrolaterally, and a long, strongly curved, blade-like spine (d) dorsally; flagellum unarmed.

#### Etymology

Named in honour of the first author's friend Daniela Robier.

Genus *Hartliebia* Löcker & Larivière, gen. nov.

Type species *Hartliebia towinna* Löcker & Fletcher, sp. nov.

#### Description

##### Morphology

*Head.* Vertex 1.0–1.2× as long as wide, produced before eyes by 1/4–1/2 of an eye length; apex broadly rounded or truncate; caudal border u to v-shaped; lateral carinae strongly elevated; median carina incomplete, 1/2–3/4 as long as vertex. Frons 1.5–1.9× longer than wide, position of maximum width distinctly ventrad of the centre of the frontoclypeal suture; lateral carinae slightly s-shaped or convex (although rectilinear apically), slightly elevated, lateral margins foliaceous, concealing base of antennae; median carina incomplete, almost as long as frons. Frontoclypeal suture semicircular, median part just reaching lower margin of antennal scape; postclypeus with well developed lateral carinae and median carina; anteclypeus with well developed median carina.

*Thorax.* Pronotum with arched carinae; hind margin rectangular. Forewing 3.0–3.5× longer than wide; costa with 20–23 tubercles; concavity at costal border present; Sc+R+M forming common stem; fork of Sc+R basad, distad of or at same level as fork of CuA1+CuA2; r-m1 distad of fork MA–MP; position of icu at CuP at same level as apex of clavus, 10 apical cells. Hind leg: tibia with three small lateral spines (without large lateral spines); six apical teeth in row interrupted by narrow gap; 1st tarsomere with (6–)7 apical teeth and no platellae; 2nd tarsomere with seven apical teeth and five platellae.

#### Distribution

Qld.

#### Remarks

The 1st hind tarsomere normally has seven apical teeth although one leg of one specimen had six.

#### Etymology

Named in honour of the family of the first author's sister Astrid Hartlieb. Gender: feminine.

*Hartliebia towinna* Löcker & Larivière, sp. nov.

(Figs 29A–C, 75)

#### Material examined

*Holotype.* ♂, Australia: Qld: Victoria Pt, Brisbane, 11.ix.1954 (T. Woodward) (QM T123592, originally from UQIC).

*Paratypes.* **Australia: Qld:** 1♂, Baldwin Swamp Fauna Reserve, Bundaberg, 10.x.1972 (H. Frauca) (ANIC); 1♂, Brisbane, 30.ii.1952 (J. Letchford) (UQIC Reg. ♂ 54182); 1♀, Brisbane, 11.xii.1951 (Urquart) (UQIC Reg. ♂ 54184); 1♀, Victoria Pt, Brisbane, 11.ix.1954 (T. Woodward) (UQIC Reg. ♂ 55166); 1♀, Woodford, 26°55.6'S 152°46.1'E, collected on *Melaleuca quinquinervia*, 22.x.1990 (M. Purcell) (ASCU).

#### Description

##### Colour

Vertex yellow brown; face yellow brown, anteclypeus darker; pronotum yellow; mesonotum yellow brown or mid brown with paler carinae; legs yellow to brown; forewing hyaline white with light and mid brown areas, veins concolorous with cells, tubercles mid brown; abdominal sternites mid brown, intersegmental membranes yellow to orange.

##### Morphology

*Body length.* ♂ 4.4–4.6 mm; ♀ 4.8–5.5 mm.

*Male genitalia.* Anal tube as in Fig. 75B, C; ventro-median process of pygofer and genital styles as in Fig. 75D, E. Aedeagus (Fig. 75A): phallosome with a very long, slightly curved spine (a) arising near apex and a short spine (b) ventrally below midlength; flagellum unarmed.

#### Etymology

'Towinna' means 'long' in Kurna, a language spoken by Aboriginal people living in the Adelaide Plains (Thieberger and McGregor 1994). This species is named after the long spine on the phallosome.

Genus *Holgus* Löcker & Larivière, gen. nov.

Type species *Holgus liafredis* Löcker & Larivière, sp. nov.

#### Description

##### Colour

Legs yellow to orange brown; abdominal sternites mid brown, intersegmental membranes yellow to orange.

*Morphology*

*Body length.* ♂ 4.5 mm, ♀ 4.8–6.8 mm.

*Head.* Vertex produced before eyes by 1/4–1/2 of an eye length; apex broadly rounded or truncate; caudal border u-shaped. Frons 1.1–1.5× longer than wide, position of maximum width distinctly ventrad of centre of frontoclypeal suture; lateral carinae s-shaped; lateral margins foliaceous, concealing base of antennae. Postclypeus with well developed lateral carinae and median carina.

*Thorax.* Concavity at costal border of forewing absent; Sc+R+M forming common stem; r-m1 basad of, or almost at same level as, fork MA–MP; position of icu at CuP distad of apex of clavus. Hind tibia with six apical teeth in row interrupted by a wide gap.

*Male genitalia.* Genital styles broadly spoon-shaped, inner side of basal arm bearing very small tooth.

*Distribution*

NSW, Qld.

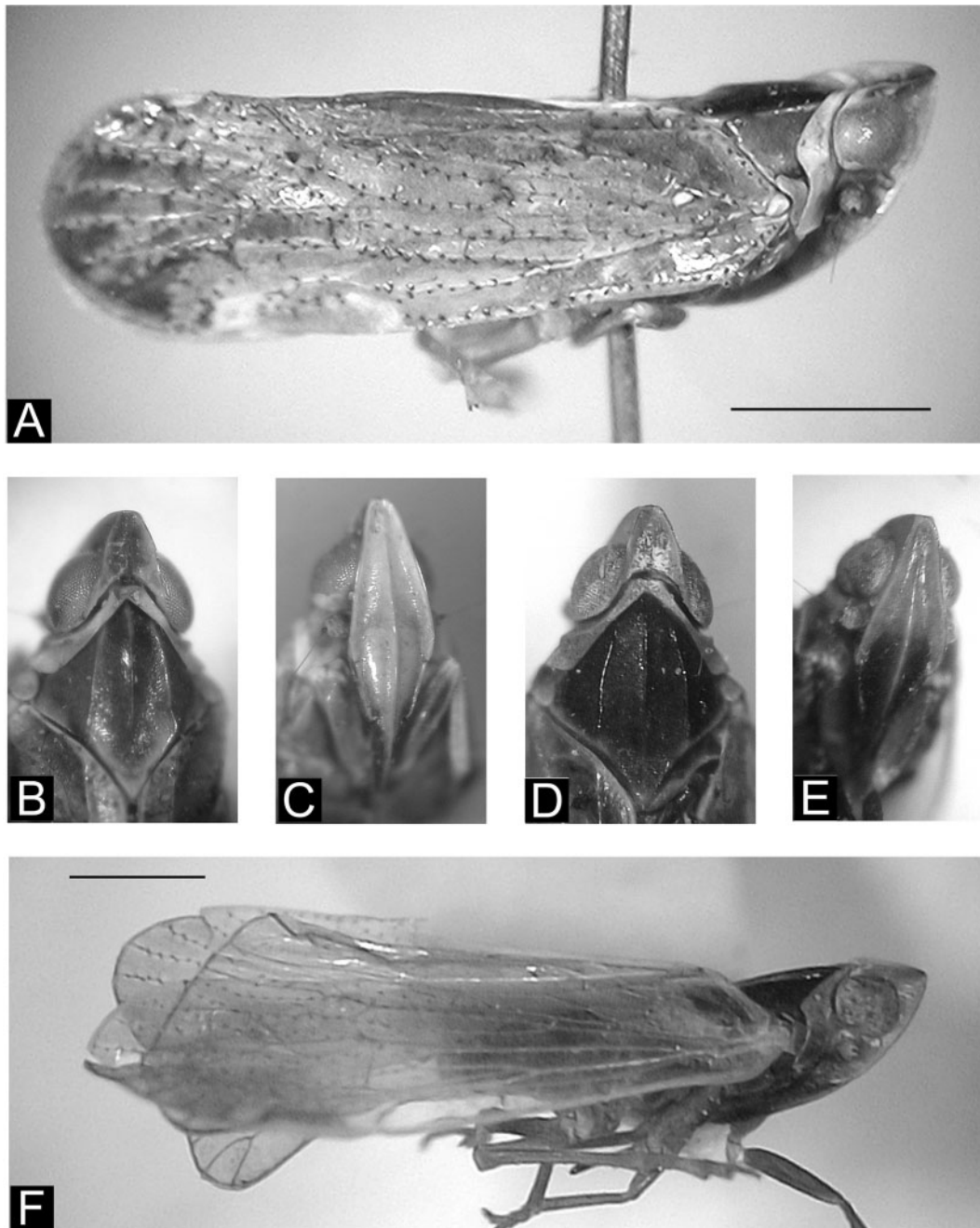


Fig. 29. *Hartliebina towinna*: A, habitus; B, C, head. *Holgus liafredis*: D, E, head; F, habitus.



**Remarks**

The position of maximum width of frons in *H. unispinosus*, sp. nov. is unknown.

The three species, *H. ancistrus*, sp. nov., *H. spiralis*, sp. nov. and *H. liafredis* clearly form a clade supported by characters such as the arrangement of spines on the aedeagus, the chaetotaxy of the 1st tarsomere (11 apical teeth and five platellae) and 2nd tarsomere (9–10 apical teeth and 7–8 platellae). Of uncertain placement is *H. unispinosus*, sp. nov. Not all of the analyses, e.g. equal and successive approximations weighting of dataset *A* place *H. unispinosus*, sp. nov. within the genus *Holgus*. Also the branches, that separate *H. unispinosus*, sp. nov. from the other three species in *Holgus* are relatively long (minimal = 1225, 1740; maximal = 2035, 2550) compared to the branches within these three species (minimal and maximal = 0–420). *H. unispinosus*, sp. nov. varies in several characters from the other species of this genus, e.g. chaetotaxy of hind tarsomeres. All of this supports the hypothesis that *H. unispinosus*, sp. nov. is not a true *Holgus*. However, character states present in all four species such as the presence of a small tooth on the inner side of the basal arm of the genital styles, the shape of the genital styles (spoon-shaped in ventral view, Figs 76F, 77G, 78H, 79F, triangular in lateral view, Figs 76E, 77F, 78G, 79E) justify a preliminary placement of *H. unispinosus*, sp. nov. in this genus. Additional material and the inclusion of additional characters (e.g. molecular data) are needed to clarify the affiliation of *H. unispinosus*, sp. nov.

**Etymology**

Named in honour of the first author's husband and colleague Holger Löcker. Gender: masculine.

**Key to species of *Holgus***

1. Frons with median carina complete; 1st hind tarsomere with seven apical teeth and no platellae; 2nd hind tarsomere with eight apical teeth and six platellae; aedeagus with only one spine . . . . . *H. unispinosus*, sp. nov.  
Frons with median carina incomplete (only 1/2–3/4 as long as frons); 1st hind tarsomere with 10 or more apical teeth and five or more platellae; 2nd hind tarsomere with 9–10 apical teeth and 7–8 platellae; aedeagus with more than one spine . . . . . 2
- 2(1). Shape of head in lateral view acutely angled (Fig. 11A); aedeagus with 2–3 spines, one of which (spine *c*) is bifurcate . . . . . 3  
Shape of head in lateral view obtusely angled (Fig. 11B); aedeagus with three spines (*a*, *b*, *c*) none of which is bifurcate (Fig. 77A–C) . . . . . *H. ancistrus*, sp. nov.
- 3(2). Spine (*c*) with both branches curving in the same direction (Fig. 78A–C); frons and clypeus uniformly orange brown, carinae paler . . . . . *H. spiralis*, sp. nov.  
Spine (*c*) with branches curving in different directions (Fig. 76A, B); frons orange brown or light brown, clypeus dark brown, carinae paler . . . . . *H. liafredis*, sp. nov.

***Holgus liafredis* Löcker & Larivière, sp. nov.**

(Figs 29D–F, 76)

**Material examined**

*Holotype*. ♂, Australia: Qld: Burbank, grasslands, 9.xi.1989 (C. W. & L. B. O'Brien) (ASCU ASCTHE026743).

*Paratypes*. **Australia: Qld:** 70♂, 80♀, same data as holotype (3♂, 3♀, ASCU; 3♂, 3♀, AM; 3♂, 3♀, ANIC; 3♂, 3♀, QM; 58♂, 68♀, LOB); 1♂, Cleveland, 18.v.1959 (W. Varrow) (UQIC Reg. ♂55187); 1♀, Brisbane, 20.x.1961, light trap (UQIC Reg. ♂55077); 1♀, Karawatha Forest, site 6, 51678, 27°37.6'S 153°05.4'E, sweeping eucalypt woodland, 5.xi.2003 (S. Wright) (QM). **NSW:** 1♂, 1♀, Upper Richmond R., 8 mls from Woodenborg, 6.xi.1958 (F. A. Perkins) (UQIC Reg. ♂55367).

**Description****Colour**

Vertex yellow to light brown, central part mid brown; frons orange brown (rarely light brown), median carina paler, lateral carinae yellow, postclypeus dark brown, median carina orange; pronotum yellow in central part, darker in lateral parts; mesonotum orange brown sometimes dark brown or black, hind border sometimes orange; forewing hyaline yellow, cell adjacent to pterostigma brown, apical cells sometimes with brown tinge, veins yellow, tubercles light brown.

**Morphology**

*Body length*. ♂ 5.4–5.9 mm; ♀ 5.8–6.8 mm.

*Head*. Tip of head acutely angled in lateral view. Vertex 1.0–1.2× as long as wide; apex broadly rounded; lateral carinae strongly elevated; median carina incomplete, 1/2–3/4 (rarely less than 1/2) as long as vertex. Lateral carinae of frons slightly to moderately elevated; median carina incomplete, 1/2–3/4 as long as frons. Frontoclypeal suture semicircular, median part reaching at least lower margin of antennal scape. Anteclypeus with well developed median carina.

*Thorax*. Pronotum with sinuate or arched carinae; hind margin rectangular. Forewing 3.5–4× longer than wide; costa with 2–7 tubercles; fork of Sc+R basad, distad of or at same level as fork of CuA1+CuA2; 10 apical cells. Hind leg: tibia with 0–2 small lateral spines (without large lateral spines); 1st tarsomere with 10–12 apical teeth and 5–6 platellae; 2nd tarsomere with 10 apical teeth and eight platellae.

*Male genitalia*. Anal tube as in Fig. 76C, D; ventro-median process of pygofer and genital styles as in Fig. 76E, F, inner side of basal arm bearing small tooth (Fig. 23). Aedeagus (Fig. 76A, B): phallosome with a long, slightly curved spine (*a*) arising ventrally near apex and a short, bifurcated spine (*c*) arising laterally above midlength, branches of spine curving in different directions (Fig. 76A, B); flagellum unarmed.

*Remarks*

The hind tarsomere normally has 11 apical teeth and five platellae. The variations given above are uncommon.

*Etymology*

Derived from the names of the first author's parents-in-law Liane and Manfred Löcker.

***Holgus ancistrus* Löcker & Larivière, sp. nov.**

(Figs 30A–C, 77)

*Material examined*

*Holotype.* ♂, Australia: Qld: Tewah Ck, via Tin Can Bay, 17.x.1970 (T. Weir) (QM T123586, originally from UQIC).

*Paratypes.* **Australia: Qld:** 5♂, 4♀, same data as holotype (UQIC); 1♂, Searys Creek Rainforest, via Tin Can Bay, 17–18.x.1970 (G. B. Monteith) (UQIC).

*Description**Colour*

Vertex orange brown, lateral carinae yellow to orange; face orange, carinae paler except for lateral carinae on postclypeus; pronotum yellow in central part, orange in lateral parts, hind border of pronotum yellow; mesonotum orange brown, darker than rest of body; forewing hyaline yellow, veins and tubercles concolorous.

*Morphology*

*Body length.* ♂ 4.5–4.6 mm; ♀ 4.8–5.4 mm.

*Head.* Tip of head obtusely angled in lateral view. Vertex 0.8–1.2× as long as wide; apex broadly rounded or truncate; lateral carinae moderately to strongly elevated; median carina incomplete, 1/2–3/4 as long as vertex. Lateral carinae of frons slightly to moderately elevated; median carina incomplete, ~1/2 as long as frons. Frontoclypeal suture semicircular, median part reaching at least lower margin of antennal scape. Anteclypeus with well developed median carina.

*Thorax.* Pronotum with sinuate carinae; hind margin right or acutely angled. Forewing more than 4× longer than wide; costa with 0–8 tubercles; fork of Sc+R distad of fork of CuA1+CuA2; 10 (sometimes nine) apical cells. Hind leg: tibia with 2–3 small lateral spines (without large lateral spines); 1st tarsomere with 11 apical teeth and five platellae; 2nd tarsomere with 9–10 apical teeth and 7–8 platellae.

*Male genitalia.* Anal tube as in Fig. 77D, E; ventro-median process of pygofer and genital styles as in Fig. 77F, G, inner side of basal arm bearing very small tooth. Aedeagus (Fig. 77A–C): phallosome with a long, moderately curved spine (a) arising ventrally near apex, a long, slightly curved spine (b) arising ventrally above midlength and a short, strongly sinuate spine (c) arising laterally above midlength; flagellum unarmed.

*Etymology*

'Ankistron' is the Greek term for 'fishhook'. It refers to the shape of a spine on the phallosome.

***Holgus spiralis* Löcker & Larivière, sp. nov.**

(Figs 30D–F, 78)

*Material examined*

*Holotype.* ♂, Australia: Qld: 20 ml. S of Gayndah, SE Qld, 16.x.1972 (B. K. & J. A. Cantrell) (QM T123587, originally from UQIC).

*Paratypes.* **Australia: Qld:** 1♂, same data as holotype (UQIC Reg. ♂55125).

*Description**Colour*

Vertex yellow to light brown lateral carinae paler; face orange brown, carinae paler except for lateral carinae on postclypeus; pronotum yellow in central part, darker in lateral parts, hind border yellow; mesonotum orange brown, darker than rest of body; forewing hyaline white, some parts yellow, apical part of wing with brown margin, cell adjacent to pterostigma brown, sometimes apical cells with brown tinge, veins yellow, tubercles light brown.

*Morphology*

*Body length.* ♂ 5.3–5.9 mm.

*Head.* Tip of head acutely angled in lateral view. Vertex 1.1× as long as wide; apex broadly rounded; lateral carinae strongly elevated; median carina incomplete, 1/2–3/4 as long as vertex. Lateral carinae of frons slightly elevated; median carina incomplete, ~3/4 as long as frons. Frontoclypeal suture semicircular, median part reaching at least lower margin of antennal scape. Anteclypeus with well developed median carina.

*Thorax.* Pronotum with sinuate or arched carinae; hind margin rectangular. Forewing 3.5–4× longer than wide; costa with 0–5 tubercles; fork of Sc+R basad of or at same level as fork of CuA1+CuA2; 10 apical cells. Hind leg: tibia with 0–4 small lateral spines (without large lateral spines); 1st tarsomere with 11 apical teeth and five platellae; 2nd tarsomere with 10 apical teeth and eight platellae.

*Male genitalia.* Anal tube as in Fig. 78E, F; ventro-median process of pygofer and genital styles as in Fig. 78G, H, inner side of basal arm bearing small tooth. Aedeagus (Fig. 78A–D): phallosome with a long, moderately curved spine (a) arising ventrally near apex, a short, strongly curved bifurcated spine (c) arising laterally above midlength, branches of spine curving in the same direction (Fig. 78A–C), and with or without a short, slightly curved spine (b) arising ventrally above midlength; flagellum unarmed.

*Remarks*

A male specimen from Australia: Qld, Gatton, 10.x.1932, (BMNH), may be a variant form of this species. It carries an additional spine (*b*) on the phallotheca (Fig. 78C). Additional specimens are required in order to show if this specimen represents a distinct species.

*Etymology*

Named after strongly curved spines on the phallotheca.

*Holgus unispinosus* Löcker & Larivière, sp. nov.*Material examined*

*Holotype*. ♂, Australia: Qld: Rocky Creek Xing, 12°06'S 142°34'E, 10.xii.1992, beating open forest along Ck (W. Dressler, P. Zborowski) (ANIC).

*Description**Colour*

Vertex pale yellow, apical part light brown; face yellow; pronotum pale yellow in central part, darker in lateral parts;

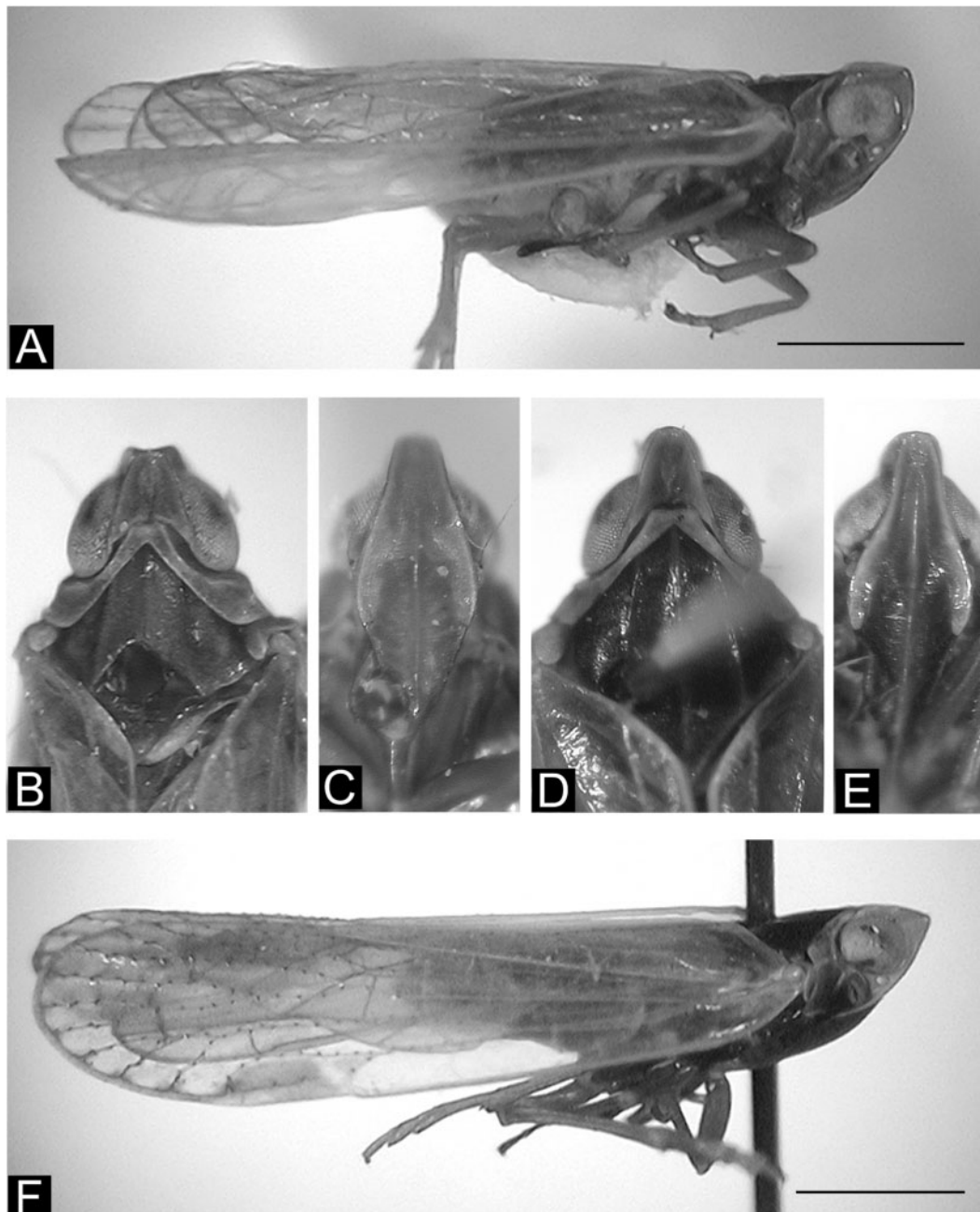


Fig. 30. *Holgus ancistrus*: A, habitus; B, C, head. *Holgus spiralis*: D, E, head; F, habitus.

mesonotum light to mid brown; forewing hyaline colourless, pterostigma and cell adjacent to pterostigma pale yellow to whitish, some apical cells with brown tinge, veins pale yellow, tubercles mid brown.

### Morphology

*Body length.* ♂ 4.6 mm.

*Head.* Vertex 1.2× longer than wide; apex broadly rounded (almost pointed); lateral carinae strongly elevated; median carina incomplete, less than 1/4 as long as vertex. Lateral carinae of frons moderately elevated; median carina complete. Anteclypeus lacking median carina.

*Thorax.* Pronotum with sinuate carinae; hind margin rectangular. Forewing more than 4× longer than wide; costa with 14–16 tubercles; fork of Sc+R distad of fork of CuA1+CuA2; 10 or 12 apical cells. Hind leg: tibia with 0–1 small lateral spines (without large lateral spines); 1st tarsomere with seven apical teeth and no platellae; 2nd tarsomere with eight apical teeth and six platellae.

*Male genitalia.* Anal tube as in Fig. 79C, D; ventro-medial process of pygofer and genital styles as in Fig. 79E, F, inner side of basal arm bearing small tooth. Aedeagus (Fig. 79A, B): phallosome with a single, long, slightly curved spine arising ventrally near apex; flagellum unarmed.

### Etymology

Named after a single spine on the phallosome.

### Genus *Lariviera* Löcker & Fletcher, gen. nov.

Type species *Lariviera yalhi* Löcker & Fletcher, sp. nov.

### Description

#### Colour

Vertex yellow, central part mid brown or black; face mid brown to black except for yellow lateral carinae on frons, sometimes median carina at level of frontoclypeal suture paler; pronotum yellow, sometimes with dark brown laterally; mesonotum mid brown to black, sometimes with yellow mark on each laterocaudal border.

### Morphology

*Body length.* ♂ 3.4–3.7 mm, ♀ 4.1–5.3 mm.

*Head.* Vertex 0.8–1.0× as long as wide, apex broadly truncate; caudal border u-shaped. Frons with its maximum width around centre of frontoclypeal suture; median carina incomplete, 1/2–3/4 as long as frons; lateral carinae convex (although rectilinear apically). Frontoclypeal suture semi-circular, median part not reaching lower margin of antennal scape; postclypeus with well developed lateral carinae and median carina; anteclypeus with well developed median carina.

*Thorax.* Pronotum with sinuate carinae; hind margin rectangular. Forewing 3.0–3.5× longer than wide; concavity at costal border absent; Sc+R+M forming common stem; fork of Sc+R distinctly basad of fork of CuA1+CuA2; r-m1 distinctly basad of fork MA–MP; position of icu at CuP distad of apex of clavus; C4 and C5 of equal length; 10 apical cells. Hind leg: tibia with 0–2 small lateral spines (without large lateral spines); six apical teeth in row interrupted by a narrow gap (almost forming uninterrupted row).

*Male genitalia.* Anal tube as in Figs 80–81B, C; ventro-medial process of pygofer and genital styles as in Figs 80–81D, E, with inner side of basal arm bearing small tooth; phallosome with a single spine arising left laterally.

### Distribution

NSW, Qld, SA, WA.

### Remarks

Most specimens of both species had eight apical teeth and six platellae on the 2nd hind tarsomere. One specimen of *L. yalhi* had seven apical teeth and five platellae.

The monophyly of the genus *Lariviera* is proven by two synapomorphies, the forewing bearing subapical cells C4 and C5 of equal length and genital styles shaped as in Figs 80–81D, E, the latter not being coded for the phylogenetic analysis. Other characters supporting this lineage are a distinct tooth on the inner side of the genital styles (Figs 80–81E), a single spine arising left lateral on the phallosome (Figs 80–81A) and the shape of the head in dorsal and lateral view (Figs 31D, F; 32A, B).

### Etymology

Named in honour of the first author's friend and colleague Marie-Claude Larivière. Gender: feminine.

### Key to species of *Lariviera*

1. Frons less than 1.5× longer than wide (Fig. 31E); aedeagus with a very long, almost straight spine (Fig. 80A) ..... *L. yalhi*, sp. nov.  
Frons more than 1.5× longer than wide (Fig. 32C); aedeagus with a short, strongly curved spine (Fig. 81A) ..... *L. yokunna*, sp. nov.

### *Lariviera yalhi* Löcker & Fletcher, sp. nov.

(Figs 31D–F, 80)

### Material examined

*Holotype.* ♂, Australia: WA: Arrowsmith River Wilson Reserve, 4.viii.1995 (R. P. McMillan) (WAM Reg no. 34380).

*Paratypes.* **Australia: WA:** 1 ♂, 2 ♀, same data as holotype (WAM Reg no. 34381, 34378, 34379). **SA:** 1 ♂, 1 ♀, Eyre Pen, 7 km S Mt Hope, low mallee sweep, 1.x.1979 (P. Greenslade) (SAM); 1 ♀, Scorpion Spr. CP along main NS track, 15.xii.1983 (D. Lacin, G. F. Gross, J. A. Forrest) (SAM); 1 ♀, Scorpion Springs Cons. Park, 100 m, 35°37'35"S 140°52'11"E, *Allocasuarina pusilla*, Casuarin-

aceae, 10.xi.1998 (Schuh, Cassis, Silveira), 98–40 (AM). NSW: 1 ♀, Conan, 4.xi.1962 (M. I. Nikitin) (BMNH).

### Description

#### Colour

Vertex yellow, central part black; face dark brown to black except for yellow lateral carinae on frons, median carina sometimes paler at level of frontoclypeal suture; pronotum yellow, lateral parts with dark brown areas; mesonotum black; legs yellow to dark brown; forewing hyaline yellow, veins yellow, occasionally darker apically, tubercles dark brown (in one specimen light brown); abdominal sternites dark brown, intersegmental membranes yellow to orange.

#### Morphology

*Body length.* ♂ 3.4–3.5 mm; ♀ 4.1–5.3 mm.

*Head.* Vertex produced before eyes by 1/4–1/2 of an eye length; lateral carinae slightly to strongly elevated; median carina incomplete, less than 1/4 as long as vertex. Frons 1.1–1.5× longer than wide; lateral carinae slightly elevated.

*Thorax.* Costa of forewing with 11–15 tubercles. Hind leg: 1st tarsomere with 8–9 apical teeth and 3–four platellae; 2nd tarsomere with 7–8 apical teeth and 5–6 platellae.

*Male genitalia.* Anal tube as in Fig. 80B, C; ventromedian process of pygofer and genital styles as in Fig. 80 D, E. Aedeagus (Fig. 80A): phallosome with a single, very long, almost straight spine arising left laterally near apex; flagellum unarmed.

#### Etymology

‘Yalthi’ means ‘straight’, ‘long’ in Paakantyi, a language spoken by Aboriginal people living along the Darling River (Thieberger and McGregor 1994). This species is named after the long, straight spine on the phallosome.

### *Lariviera yokunna* Löcker & Fletcher, sp. nov.

(Figs 32A–C, 81)

#### Material examined

*Holotype.* ♂, Australia: Qld: Tibrogargon, 26.viii.1960 (S. A. Thorburn) (QM T123590, originally from UQIC).

*Paratypes.* Australia: Qld: 1 ♀, same data as holotype (UQIC Reg. ♂ 54157); 1 ♂, Burrum Hds, at light, 23.viii.1977 (K. J. Lambkin) (QM); 1 ♂, Beerwah, 20.viii.1958 (I. C. Yeo) (UQIC Reg. ♂ 54209).

#### Description

#### Colour

Vertex yellow, central part mid brown; face mid brown to black except for yellow lateral carinae on frons, median carina sometimes paler at level of frontoclypeal suture; pronotum yellow; mesonotum mid brown to black with yellow mark on each laterocaudal border; legs yellow to light brown; forewing hyaline yellow, veins yellow, tubercles

yellow or light brown; abdominal sternites mid brown, intersegmental membranes pale yellowish.

#### Morphology

*Body length.* ♂ 3.6–3.7 mm; ♀ 4.3 mm.

*Head.* Vertex produced before eyes by less than 1/4 of an eye length; lateral carinae moderately elevated; median carina incomplete, 1/4–1/2 as long as vertex. Frons 1.5–1.9× longer than wide; lateral carinae slightly to moderately elevated.

*Thorax.* Costa of forewing with 14–21 tubercles. Hind leg: 1st tarsomere with nine apical teeth and four platellae; 2nd tarsomere with eight apical teeth and six platellae.

*Male genitalia.* Anal tube as in Fig. 81B, C; ventromedian process of pygofer and genital styles as in Figs 81D, E. Aedeagus (Fig. 81A): phallosome with a short, strongly curved thick spine arising left laterally above midlength; flagellum unarmed.

#### Etymology

‘Yokunna’ means, ‘bent’ in Kurna, a language spoken by Aboriginal people living in the Adelaide Plains (Thieberger and McGregor 1994). This species is named after the curved spine on the phallosome.

### Genus *Lipsia* Löcker & Fletcher, gen. nov.

Type species *Lipsia myrostylyus* Löcker & Fletcher, sp. nov.

#### Description

#### Morphology

*Head.* Vertex 0.7–1.0× as long as wide, produced before eyes by 1/2–3/4 of an eye length; apex broadly truncate; caudal border u-shaped; lateral carinae strongly elevated; median carina incomplete, 1/4× as long as vertex. Frons 1.5–1.9× longer than wide, position of maximum width about centre of frontoclypeal suture; lateral carinae convex (although rectilinear apically) or slightly s-shaped, strongly elevated; median carina absent. Frontoclypeal suture semicircular, median part almost reaching lower margin of antennal scape; postclypeus with well developed lateral carinae and median carina; anteclypeus with well developed median carina.

*Thorax.* Pronotum with arched, or slightly undulating carinae; hind margin right or obtusely angled. Forewing 3.0–3.5× longer than wide; costa with 14–20 tubercles; concavity at costal border absent or present; Sc+R+M forming common stem; fork of Sc+R basad of fork of CuA1+CuA2; r-m1 basad of or at same level as fork MA-MP; position of icu at CuP distad of or at same level as apex of clavus, 10 (rarely 11–12) apical cells. Hind leg: tibia with 0–3 small lateral spines (without large lateral spines); six apical teeth in a row interrupted by a wide gap; 1st tarsomere with 7–11

apical teeth and 2–3 platellae; 2nd tarsomere with 9–10 apical teeth and 7–8 platellae.

*Distribution*

NSW, Qld.

*Remarks*

Most species have 10 apical teeth and three platellae on the 1st hind tarsomere and 10 apical teeth and eight platellae on the 2nd hind tarsomere.

*Etymology*

Named in honour of the family of the first author's sister Ingrid Lips. Gender: feminine.

*Lipsia mystrostylus* Löcker & Fletcher, sp. nov.

(Figs 32D–F, 82)

*Material examined*

*Holotype*. ♂, Australia: NSW: Brookfield, 10.x.1926 (H. Hacker) (QM T123602).

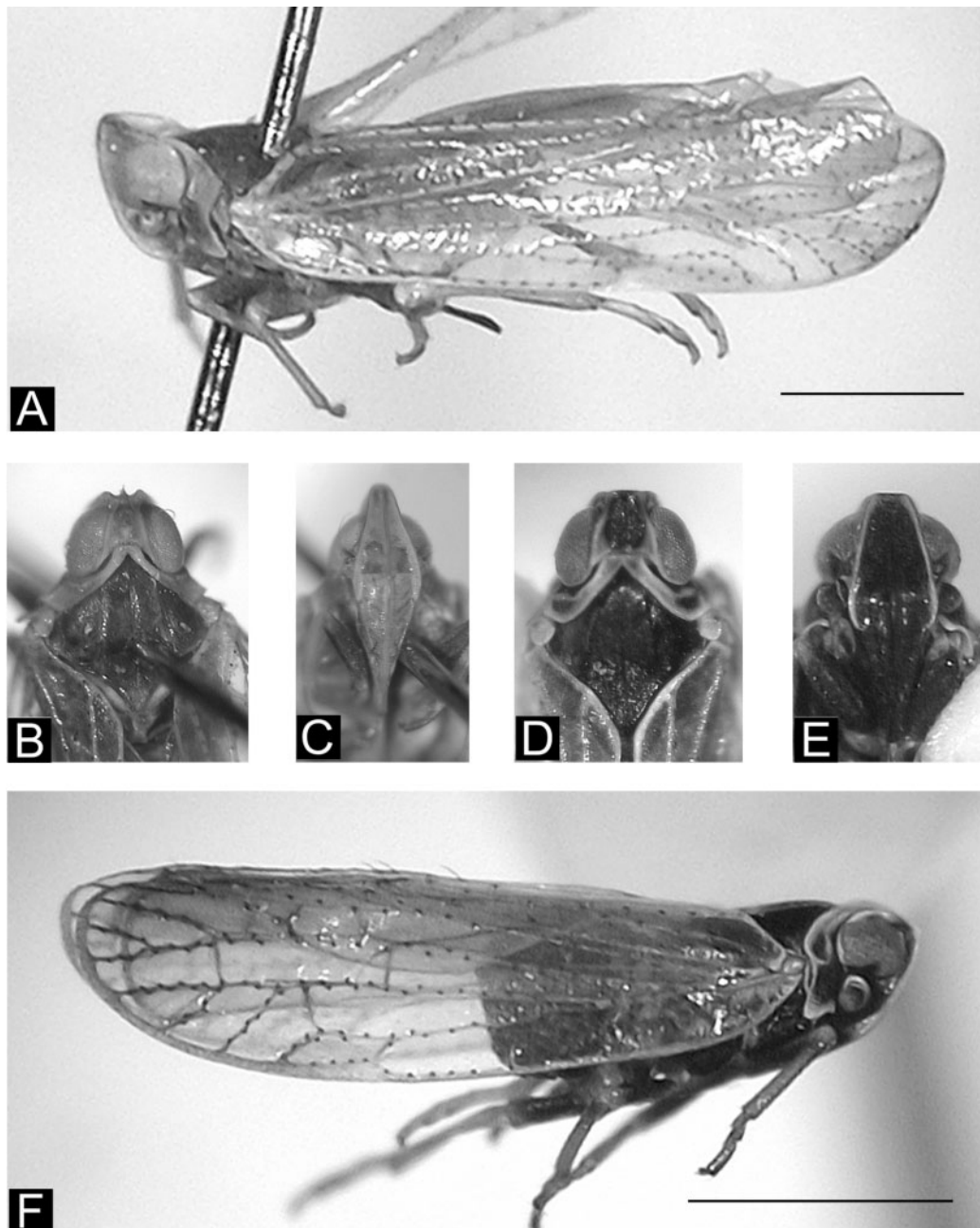


Fig. 31. *Holgus unispinosus*: A, habitus; B, C, head. *Larivierea yalthi*: D, E, head; F, habitus.

*Paratypes.* **Australia: NSW:** 1♂, same data as holotype (QM); 1♂, same locality as holotype, 1.xi.1926 (QM). **Qld:** 1♂, Gollard Ck, 21 ml. NE of Biloela, S Qld, 15.xi.1957 (T. E. Woodward) (UQIC Reg. ♂ 5412); 1♂, Rannes, 10.iv.1947 (K. R. Norris) (ANIC); 3♀, Rockhampton (MAMU); 3♀, Collard Ck, 21 ml. NE of Biloela, S Qld, 15.xi.1957 (T. E. Woodward) (UQIC Reg. ♂ 54119, ♂ 54120, ♂ 54122).

### Description

#### Colour

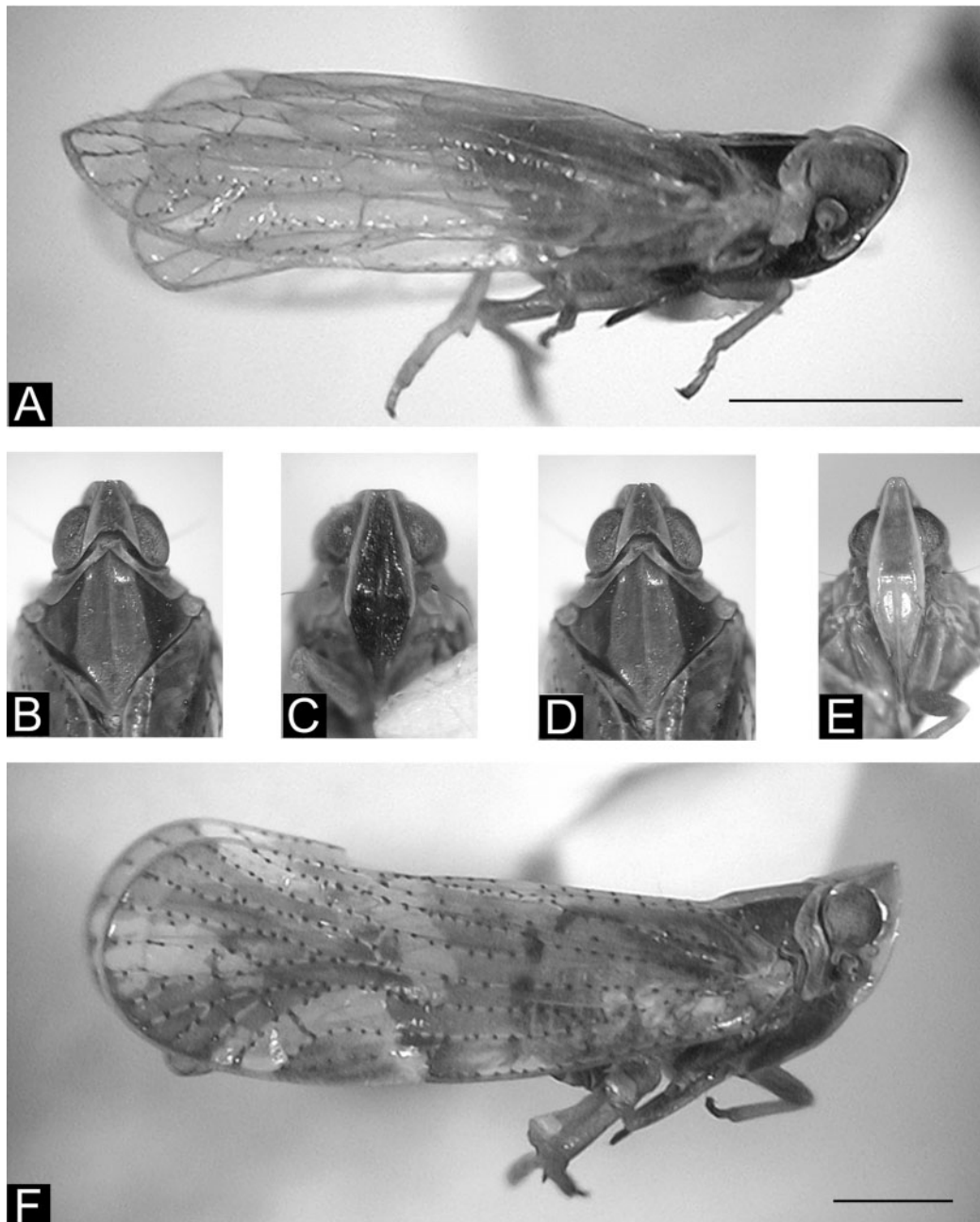
Vertex yellow, central part mid brown; face yellow, clypeus usually slightly darker; pronotum yellow to light

brown; mesonotum mid brown, lateral parts darker; legs yellow to brown; forewing hyaline white with light brown and mid brown areas, veins light brown, tubercles dark brown; abdominal sternites mid brown, intersegmental membranes yellow to orange.

### Morphology

*Body length.* ♂ 6.1–6.8 mm; ♀ 6.6–7.3 mm.

*Male genitalia.* Anal tube as in Fig. 82B, C; ventro-medial process of pygofer and genital styles as in Fig. 82D,



**Fig. 32.** *Lariviereea yokunna*: A, habitus; B, C, head. *Lipsia mystrostylus*: D, E, head; F, habitus.

*E.*, genital styles narrowly spoon-shaped. Aedeagus (Fig. 82A): phallosome with a long, sinuate spine (*a*) arising ventrolaterally near apex and a very short spine (*b*) ventrally below midlength; flagellum unarmed.

#### Etymology

'Mystron' is the Greek term for 'spoon'. The species name refers to the spoon-shaped genital styles.

Genus *Melanoclypeus* Löcker & Fletcher, gen. nov.

Type species *Melanoclypeus cristatus* Löcker & Fletcher, sp. nov.

#### Description

##### Colour

Vertex yellow to orange, central part mid brown; face pale yellow to orange, apical portion of anteclypeus dark brown; pronotum yellow; mesonotum dark brown to black; legs pale yellow to light brown; forewing hyaline light brown with mid brown, white and yellow areas often forming transverse band across wing at level of pterostigma, veins and tubercles concolourous with cells; abdominal sternites mid to dark brown, intersegmental membranes pale yellowish.

##### Morphology

*Body length.* ♂ 3.4–4.0 mm, ♀ 5.4 mm.

*Head.* Tip of head obtusely angled in lateral view. Vertex 1.1–1.6× longer than wide, produced before eyes by 1/4–1/2 of an eye length; apex narrowly rounded or truncate; caudal border v-shaped; lateral carinae strongly elevated; median carina incomplete, less than 1/4 as long as vertex. Frons 1.9–2.3× longer than wide, position of maximum width distinctly ventrad of centre of frontoclypeal suture; lateral carinae slightly s-shaped, strongly elevated; median carina absent. Frontoclypeal suture semicircular, median part reaching or not reaching lower margin of antennal scape; postclypeus and anteclypeus with well developed median carina.

*Thorax.* Hind margin of pronotum obtusely angled. Forewing 3.0–3.5× longer than wide; concavity at costal border absent; Sc+R+M forming common stem; position of icu at CuP at same level as apex of clavus. Hind with six apical teeth in row interrupted by a wide gap; 1st tarsomere with seven apical teeth and no platellae; 2nd tarsomere with eight apical teeth and six platellae.

*Male genitalia.* Anal tube as in Figs 83B, C; 84C, D; genital styles narrowly spoon-shaped (Figs 83E, 84F).

#### Distribution

NSW, Qld.

#### Remarks

Females could only be identified to genus level. The measurement given above is derived from one specimen from Qld.

A clade recovered by all weighting regimes is the genus *Melanoclypeus*. Characters supporting this clade are the narrow vertex (1.1–1.6× longer than wide), the obtusely angled tip of head in lateral view (Fig. 33A, F), the dark coloured apex of anteclypeus, an obtusely angled hind border of the pronotum, the position of icu at CuA (at same level as apex of clavus), the chaetotaxy of the hind tarsomeres (1st tarsomere with seven apical teeth and no platellae, 2nd tarsomere with eight apical teeth and six platellae) and narrowly spoon-shaped genital styles.

#### Etymology

Named after the dark apex of the anteclypeus. Gender: masculine.

#### Key to species of *Melanoclypeus*

1. Aedeagus with two very long spines, one slightly curved another strongly curved, and a large shield-like ventral ridge (Fig. 83A) . . . . . *M. cristatus*, sp. nov.  
Aedeagus with only one, short spine, but two ventral ridges, one forming a foliaceous hook-shaped process, the other forming a spine-like process (Fig. 84A, B) . . . *M. uncinatus*, sp. nov.

#### *Melanoclypeus cristatus* Löcker & Fletcher, sp. nov.

(Figs 33A–C, 83)

#### Material examined

*Holotype.* ♂, Australia: NSW: 500 m towards 'Caloola' Station from Gwydir Hwy turnoff, 29°46'38"S 148°18'26"E, ex *Eucalyptus largiflorens*, 13.xii.1999 (F. Christie, M. Elliott), DRRP131/03Bt, beating (AM K113774).

*Paratype.* **Australia: NSW:** 1♂, Mallee Scrub, Rankin Springs, 14.i.1963, at light (P. Aitken) (SAM).

#### Description

##### Morphology

*Body length.* ♂ 4.0 mm.

*Head.* Postclypeus with evanescent lateral carinae.

*Thorax.* Pronotum with undulating or sinuate carinae. Costa of forewing with ~20 tubercles; fork of Sc+R at same level as fork of CuA1+CuA2; r–m1 distad of fork MA–MP; nine apical cells. Hind leg: tibia without lateral spines.

*Male genitalia.* Anal tube as in Fig. 83B, C; ventro-median process of pygofer and genital styles as in Fig. 83D, E. Aedeagus (Fig. 83A): phallosome with a very long, slightly curved spine (*a*) arising ventrally above midlength, a very long strongly curved spine (*b*) arising right lateral near apex and a large shield-like sclerotised ridge ventrally; flagellum unarmed.



**Remarks**

The paratype male from Rankin Springs has damaged wings and genitalia, therefore some of the measurements given in the description only refer to the holotype.

**Etymology**

Named after the large ventral ridge on the phallotheca.

***Melanoclypeus uncinatus* Löcker & Fletcher, sp. nov.**

(Figs 33D–F, 84)

**Material examined**

**Holotype.** ♂, Australia: Qld: Gold Ck Reservoir, site 1, 27°27.9'S 152°52.5'E, 1.xii.2003–2.i.2004, 140 m, pitfall, 51801, spotted gum open forest (QM Party) (QM T123601).

**Paratype.** **Australia: Qld:** 1♂, Holroyd River, S of Coen, NQ, 29.xi.1974 (M. S. Moulds) (AM).

**Description****Morphology**

**Body length.** ♂ 3.4–3.6 mm.

**Head.** Lateral margins of frons sometimes foliaceous, concealing base of antennae. Postclypeus with well developed lateral carinae.

**Thorax.** Pronotum with arched carinae. Costa of forewing with 16–17 tubercles; fork of Sc+R basad of or at same level as fork of CuA1+CuA2; r–m1 basad, at same level or distad of fork MA–MP; 9–10 apical cells. Hind leg: tibia with two small lateral spines (without large lateral spines).

**Male genitalia.** Anal tube as in Fig. 84C, D; genital style as in Fig. 84E, F. Aedeagus (Fig. 84A, B): phallotheca with a single, short, slightly sclerotised spine ventrally near apex, a ventral ridge forming foliaceous hook-shaped process above midlength and another ventral ridge with a spine-like process extending from its basal corner; flagellum unarmed.

**Etymology**

The Latin term 'uncinatus' means 'hooked'. This species is named after the hook-shaped process of the phallotheca.

**Genus *Metaplacha* Emeljanov**

*Metaplacha* Emeljanov, 2000: 259.

Type species *Metaplacha tobiasi* Emeljanov, 2000, by original designation.

**Description****Morphology**

**Head.** Vertex 1.0–1.5× as long as wide, produced before eyes by 1/4–1/2 of an eye length; apex broadly pointed; caudal border u-shaped; lateral carinae strongly ele-

vated; median carina incomplete, 1/4–1/2 as long as vertex. Frons 1.1–1.5× longer than wide, position of maximum width distinctly ventrad of centre of frontoclypeal suture; lateral carinae slightly s-shaped, slightly elevated, lateral margins foliaceous, concealing base of antennae; median carina complete. Frontoclypeal suture semicircular, median part reaching at least lower margin of antennal scape; postclypeus with well developed lateral carinae and median carina; anteclypeus with well developed median carina.

**Thorax.** Pronotum with sinuate carinae; hind margin rectangular. Forewing less than 3× longer than wide; costa with 13–15 tubercles; concavity at costal border absent; Sc+R+M forming common stem; fork of Sc+R basad of fork of CuA1+CuA2; r–m1 basad of fork MA–MP; position of icu at CuP distad of or at same level as apex of clavus; eight apical cells. Hind leg: tibia with 1–2 small lateral spines (without large lateral spines); six apical teeth in row interrupted by narrow gap; 1st tarsomere with 8–9 apical teeth and 1–2 platellae; 2nd tarsomere with 9(–10) apical teeth and 7(–8) platellae.

**Distribution**

NSW.

***Metaplacha tobiasi* Emeljanov**

(Figs 34A–C, 85)

*Metaplacha tobiasi* Emeljanov, 2000: 260, figs 20–28.

**Material examined**

**Holotype.** ♂, Australia: NSW: Conargo, 17.iv.1978 (V. Tobias) (ANIC).

**Paratypes.** **Australia: NSW:** 3♂, 3♀ (1♂, 1♀ examined), same data as holotype (ZIN).

**Other material examined.** **Australia: NSW:** 1♂, 1♀, 18 km SE of Forbes, 10.iv.1977 (Z. Liepa) (ANIC).

**Description****Colour**

Vertex dark brown, median carina orange, lateral carinae white to yellow; face dark brown with yellow to orange carinae, except for mid brown lateral carinae on postclypeus; pronotum yellow medially with white carinae, dark brown laterally with orange and yellow hind border; mesonotum dark brown, with carinae, hind border and caudal part orange; legs yellow to mid brown; forewing milky white with light to mid brown marks, veins light brown, tubercles mid brown; abdominal sternites dark brown, intersegmental membranes yellow.

**Morphology**

**Body length.** ♂ 2.6–2.8 mm; ♀ 3.0–3.1 mm.

**Male genitalia.** Anal tube as in Fig. 85B, C; ventro-median process of pygofer and genital styles as in Fig. 85D,

*E.* Aedeagus (Fig. 85A): phallosome with a long, strongly curved robust spine (*a*) arising ventrally above midlength, and a long sinuate thick spine (*b*) arising ventrally near apex; flagellum unarmed.

*Remarks*

In his original description, Emeljanov (2000: 259) states, 'First segment of hind tarsus bearing 8–9 teeth without sub-

apical setae, second segment bearing 10 teeth with subapical setae, except for lateral teeth.' However, in the material examined in this study, 1–2 platellae (subapical setae) were observed on the 1st tarsomere and nine apical teeth on the 2nd tarsomere. The short forewing and the bright, yellow or orange carinae contrasting with the dark background on head and thorax, are distinctive for this species.

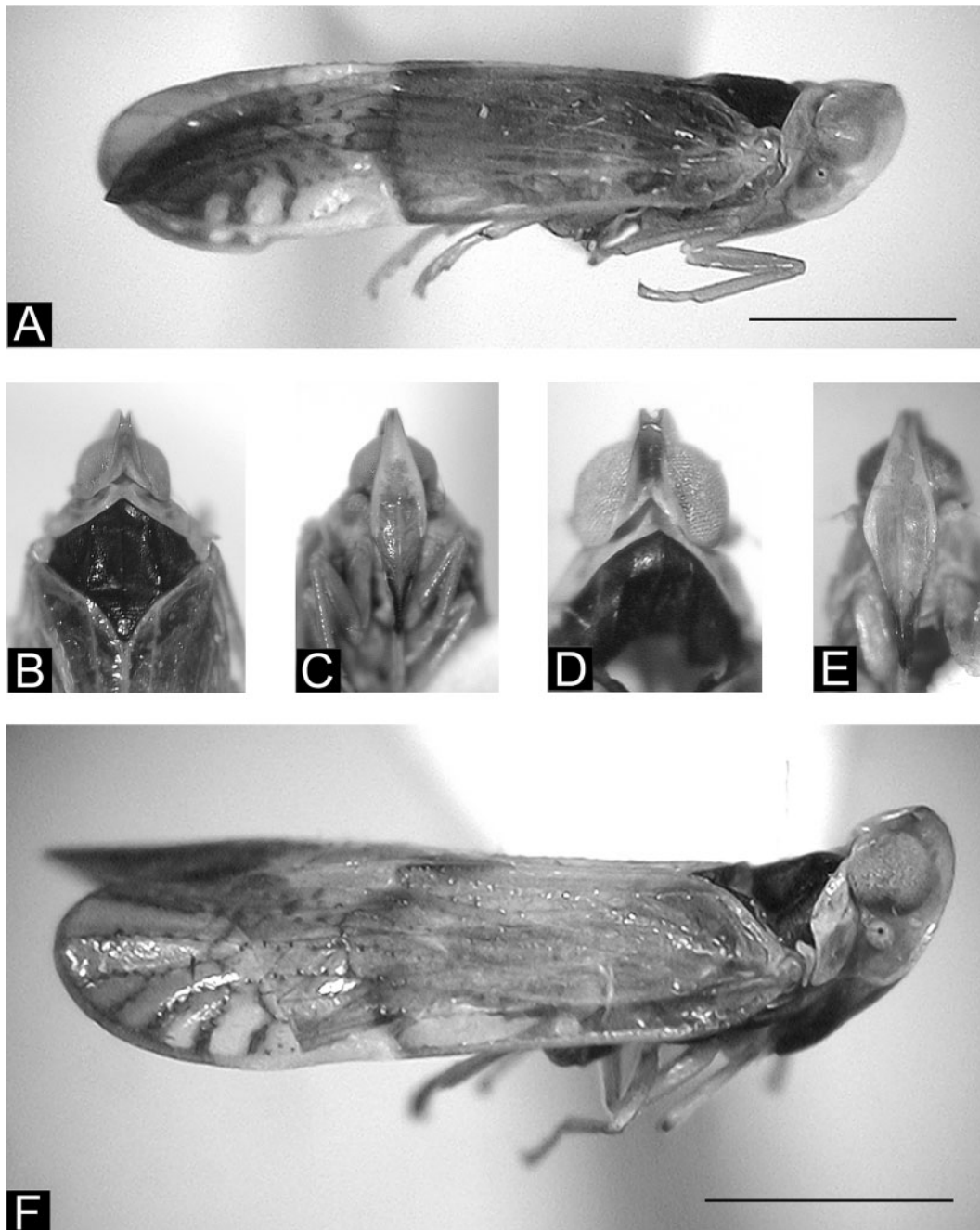


Fig. 33. *Melanoclypeus cristatus*: A, habitus; B, C, head. *Melanoclypeus uncinatus*: D, E, head; F, habitus.

Genus *Novotarberus* Löcker & Fletcher, gen. nov.Type species: *Tarberus jacobii* Muir*Description**Morphology**Body length.* ♂ 3.6–4.5 mm, ♀ 4.1–4.9 mm.*Head.* Vertex with lateral carinae strongly elevated. Frons with its maximum width distinctly ventrad of centre of frontoclypeal suture; median carina absent; postclypeus with well developed lateral carinae and median carina; anteclypeus with well developed median carina.*Thorax.* Pronotum with undulating or arched carinae. Concavity at costal border of forewing absent; Sc+R+M forming common stem. Hind tibia with six apical teeth in a row interrupted by a wide gap; 2nd tarsomere typically with nine apical teeth and seven platellae.*Male genitalia.* Genital styles as in Figs 86–87D, 86E, 87D. Aedeagus: phallosome with long strongly curved spine (a) arising right laterally near apex and. Spine (b) absent, rudimentary or long, sinuate and arising left laterally near apex. Spine (c) present or absent.*Distribution*

Australia: ACT, NSW, Vic, WA; New Caledonia.

*Remarks*

The position of maximum width of frons is unknown in *N. pseudorphninus*, sp. nov. Fennah (1969) synonymised the type species of *Tarberus*, *T. semicarinatus*, with *Gelastocephalus ornithoides* thereby making *Tarberus* a junior objective synonym of *Gelastocephalus*. *Tarberus jacobii* Muir, is not congeneric with *Gelastocephalus*, a new genus is thus required to accommodate it. *Novotarberus* and *Gelastocephalus* differ primarily in the number of spines on the hind tibiae and the degree of development of the lateral carinae on the postclypeus.

Most analyses performed show a clade consisting of the New Caledonian species *N. jacobii* and the three Australian species, *N. flagellospinosus*, sp. nov., *N. remanei*, sp. nov. and *N. pseudorphninus*, sp. nov. However, some analyses (e.g. the scaled weighting regime of both datasets and the equal weighting regime of dataset B) contradict the monophyly of this genus. *N. remanei*, sp. nov. and *N. jacobii* have a short ventral spine (b) at the base of phallosome in common, *N. pseudorphninus*, sp. nov. shows a reduced version of this spine, in *N. flagellospinosus*, sp. nov. spine (b) is completely absent. All species share a long strongly curved spine (a) right lateral on the phallosome (additional spines on the phallosome are present in some species), the shape of the anal tube in dorsal view as in Fig. 105D, E, and the absence of a median carina on the frons. Additional data, however, is needed to clarify whether all species included here are congeneric.

*Etymology*

Gender: masculine.

**Key to species of *Novotarberus***

1. Vertex at least 1.8× longer than wide; shape of head in lateral view as in Fig. 35F; aedeagus with two long spines on the phallosome (Fig. 88A, B); genital styles as in Fig. 88F . . . . . *N. pseudorphninus*, sp. nov.
- Vertex less than 1.3× longer than wide; shape of head in lateral view as in Figs 34F, 35–36A; aedeagus only one long spine on the phallosome (Figs 86–87A, 89A); genital styles different. . . . . 2
- 2(1). Forewings almost the same width throughout (Fig. 12A). . . . . *N. jacobii* (Muir)
- Forewings distinctly varying in width (Fig. 12B, C) . . . . . 3
- 3(2). Forewings distinctly decreasing in width over apical third (Fig. 12B); forewings more than 3.5× longer than wide; flagellum with one apical spine (Fig. 87A). . . . . *N. flagellospinosus*, sp. nov.
- Forewings distinctly decreasing in width in their basal third (Fig. 12C); forewings less than 3× longer than wide; flagellum lacking spines. . . . . *N. remanei*, sp. nov.

***Novotarberus jacobii* (Muir), comb. nov.**

(Figs 34D–F, 86)

*Tarberus jacobii* Muir 1931: 67, figs 6–7.*Gelastocephalus jacobii* (Muir), Fennah 1969: 8, figs 12–14.*Material examined**Holotype.* ♂ (examined), New Caledonia: Tontouta, 4.vi.1925 (P. A. Buxton) (BMNH).*Description**Colour*

Vertex light brown, with central part mid brown; face light to mid brown, with anteclypeus darker and carinae light brown; pronotum light brown, with dark brown areas laterally; mesonotum dark brown, with orange brown carinae and hind border; legs light to mid brown; forewing hyaline light brown with white areas, veins light brown, tubercles mid brown.

*Morphology**Body length.* ♂ 4.2 mm.*Head.* Vertex 1.2× longer than wide, produced before eyes by 1/4–1/2 of an eye length; apex broadly truncate; caudal border u-shaped; median carina ~1/2 as long as vertex. Frons 1.5–1.9× longer than wide; lateral carinae s-shaped, moderately elevated. Frontoclypeal suture semicircular, median part just reaching lower margin of antennal scape.*Thorax.* Hind margin of pronotum right to somewhat obtusely angled. Forewing 3.0–3.5× longer than wide, almost the same width throughout (Fig. 12A); costa with ~22 tubercles; fork of Sc+R distad of or at same level as fork of CuA1+CuA2; r–m1 basad of or at same level as fork of

MA–MP; position of icu at CuP distad of apex of clavus; nine apical cells. Hind leg: tibia without lateral spines; 1st tarsomere with nine apical teeth and two platellae; 2nd tarsomere with nine apical teeth and seven platellae.

*Male genitalia.* Anal tube as in Fig. 86B, C; ventro-median process of pygofer and genital styles as in Fig. 86D, E, genital styles broadly spoon-shaped. Aedeagus (Fig. 86A): phallosome with a long, strongly curved spine (a) near apex and a second short, moderately curved spine (b) ventrally below midlength; flagellum lacking spines.

*Novotarberus flagellospinosus* Löcker & Fletcher, sp. nov.  
(Figs 35A–C, 87)

*Material examined*

*Holotype.* ♂, Australia: WA: North Gingin, 29.viii.1969 (K. T. Richards) (WADA, 15698).

*Paratypes.* **Australia:** WA: 2♂, same data as holotype (WADA, 15698–9); 1♂, Gingin, 9.ix.1969 (P. J. Lawrence) (WADA 15701); 1♂, Stirling NP, 22.ix.1965 (E. Britton & Uther Baker) (ANIC); 7♀, Waroona, 25.x.1938, (A. J. Turner) (QM); 1♀, North Gingin, 17.ix.1969 (K. T. Richards) (WADA 15694); 1♀, Augusta, 34°20'S

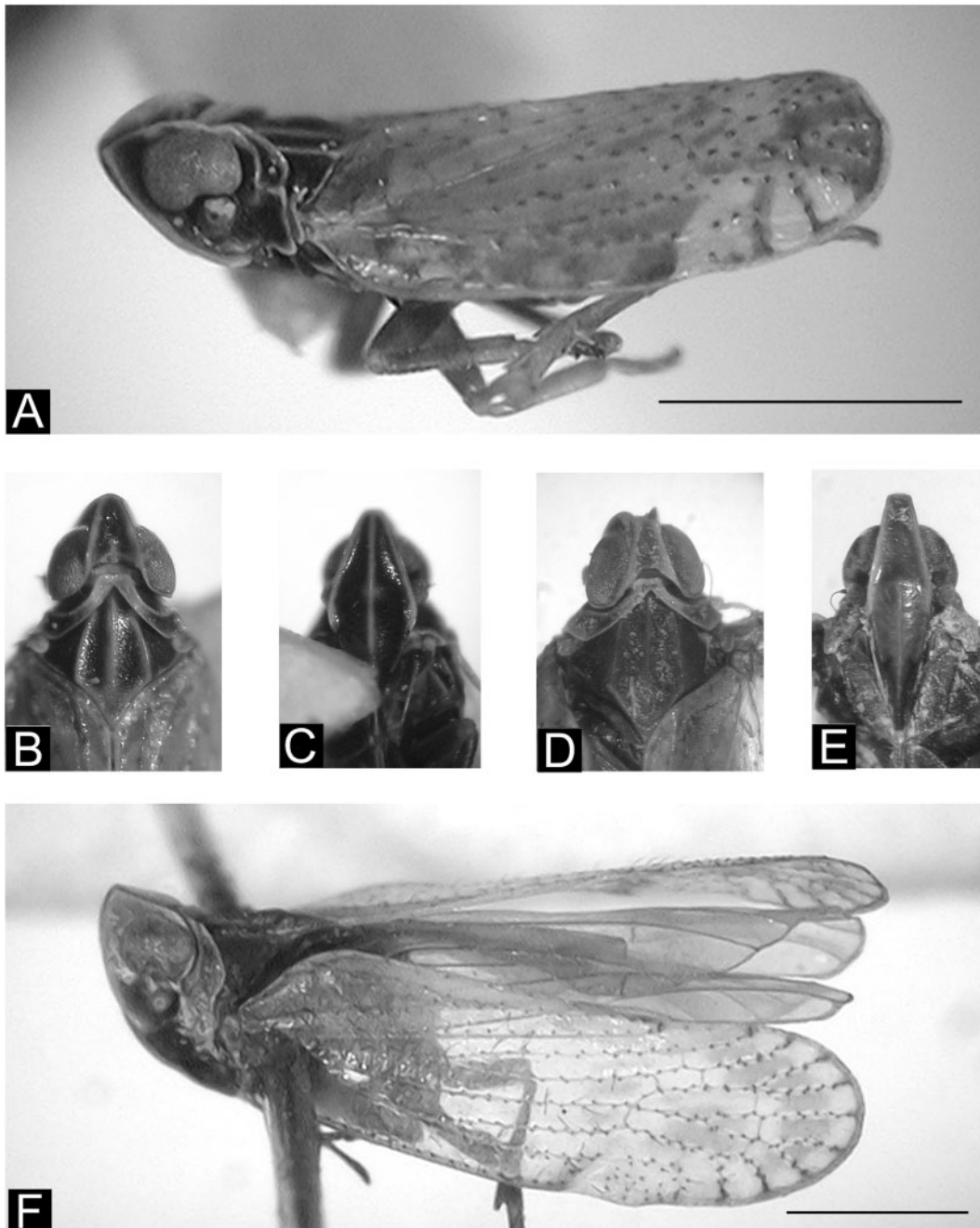


Fig. 34. *Metaplacha tobiasi*: A, habitus; B, C, head. *Novotarberus jacobii*: D, E, head; F, habitus.

15°9'E, 30 m, 4.xii.1999 (R. Schuh, G. Cassis, R. Silveira), 99–67, (AM); 1♀, 3.5 km N of Mt Chudalup, D'Entrecasteaux Nat. Pk., 34°44'00"S 116°05'20"E, 50 m, 15.xii.1997 (Schuh, Cassis, Brailovsky, Asquith), 97–52 (AM); 1♀, Albany, x.1966 (J. W. & F. Evans) (ASCU).

*Other material examined.* **Australia: WA:** 1♂, North Gingin, 29.viii.1969, (K. T. Richards) (WADA, 15689). (This male from North Gingin (Wada, 15689) is excluded from the type series because its genitalia are mutilated.)

### Description

#### Colour

Head dark brown with light brown carinae; pronotum dark brown, paler medially and on carinae; mesonotum dark brown to black; legs light to dark brown; forewing hyaline grey with yellow and brown marks, veins concolorous with cells, tubercles dark brown; abdominal sternites dark brown to black, intersegmental membranes orange.

#### Morphology

*Body length.* ♂ 3.6–4.1 mm; ♀ 4.1–4.9 mm.

*Head.* Vertex 1.0–1.2× as long as wide, produced before eyes by 1/2–3/4 of an eye length; apex broadly truncate; caudal border u-shaped; median carina less than 1/4 as long as vertex. Frons 1.5–1.9× longer than wide; lateral carinae s-shaped, strongly elevated. Frontoclypeal suture semicircular, median part reaching at least lower margin of antennal scape.

*Thorax.* Hind margin of pronotum right or acutely angled. Forewing 3.5–4.0× longer than wide, widest part half way between base of wing and apex of clavus, decreasing in width over apical third (Fig. 12B); costa with 21–25 tubercles; fork of Sc+R distinctly basad of fork of CuA1+CuA2; r-m1 basad of fork of MA–MP; position of icu at CuP distad of apex of clavus; nine apical cells. Hind leg: tibia with 3–4 very small lateral spines (without large lateral spines); 1st tarsomere with 9–11 apical teeth and 3–4 platellae; 2nd tarsomere with nine apical teeth and seven platellae.

*Male genitalia.* Anal tube as in Fig. 87B, C; ventro-median process of pygofer and genital styles as in Fig. 87D, E. Aedeagus (Fig. 87A): phallosome with a long strongly curved spine arising right lateral near apex; flagellum with short, curved spine near apex.

#### Remarks

*Novotarberus flagellospinus* is the only species in this genus bearing a spine on the flagellum, all other species in this genus lack spines on the flagellum. The 1st hind tarsomere normally has 9–10 apical teeth although one leg of one specimen had 11.

#### Etymology

Named after the sclerotised spine on the apex of the flagellum.

### *Novotarberus pseudorphninus* Löcker & Fletcher, sp. nov.

(Figs 35D–F, 88)

#### Material examined

*Holotype.* ♂, Australia: WA: Pilbara Dist, Rhodes Ridge Camp, 23°06'04.9"S 119°22'13.6"E, 694 m, 30.v.1999 (Cassis & Silveira), L36, (AM K113775).

*Paratypes.* **Australia: WA:** 6♂ 1♀, same data as holotype (AM).

#### Description

#### Colour

Vertex yellow, with central part black; face black, lateral carinae of frons yellow; pronotum yellow to orange, sometimes with brown marks; mesonotum black; legs yellow to dark brown; forewing hyaline colourless, patterned with white, light brown and dark brown areas, veins mainly dark brown, apical cells margined with dark brown; tubercles mid to dark brown; abdominal sternites black, intersegmental membranes yellow to orange.

#### Morphology

*Body length.* ♂ 3.9–4.2 mm; ♀ 4.3 mm.

*Head.* Vertex very long and narrow, 1.8–2.1× longer than wide, produced before eyes by 1/2–3/4 of an eye length; apex narrowly rounded; caudal border v-shaped, sometimes slightly u-shaped; median carina less than 1/4 as long as vertex. Lateral carinae of frons s- or double s-shaped, strongly elevated.

*Thorax.* Hind margin of pronotum rectangular. Forewing 3.0–3.5× longer than wide; costa with 10–16 tubercles; fork of Sc+R basad (almost at same level) as fork of CuA1+CuA2; r-m1 distad of fork MA–MP; nine apical cells; position of icu at CuP at same level as apex of clavus. Hind leg: tibia without lateral spines; 1st tarsomere with 8–9 apical teeth and 1–3 platellae; 2nd tarsomere with nine apical teeth and seven platellae.

*Male genitalia.* Anal tube as in Fig. 88C, D; ventro-median process of pygofer and genital styles as in Fig. 88E, F. Aedeagus (Fig. 88A, B): phallosome with a long strongly curved spine (a) arising right lateral, a second long, sinuate spine (c) arising left laterally near apex and a spine-like ventral process at the base; flagellum lacking spines.

#### Remarks

The normal dentition of the 1st hind tarsomere is eight apical teeth and two platellae. Other numbers given are uncommon.

#### Etymology

The produced head resembles that of *Orphninus mouldsi*.

***Novotarberus remanei* Löcker & Fletcher, sp. nov.**

(Figs 36A–C, 89)

*Material examined*

*Holotype*. ♂, Australia: ACT: Mt Gingera, 5.xii.1950 (H. M. Cane) (ANIC).

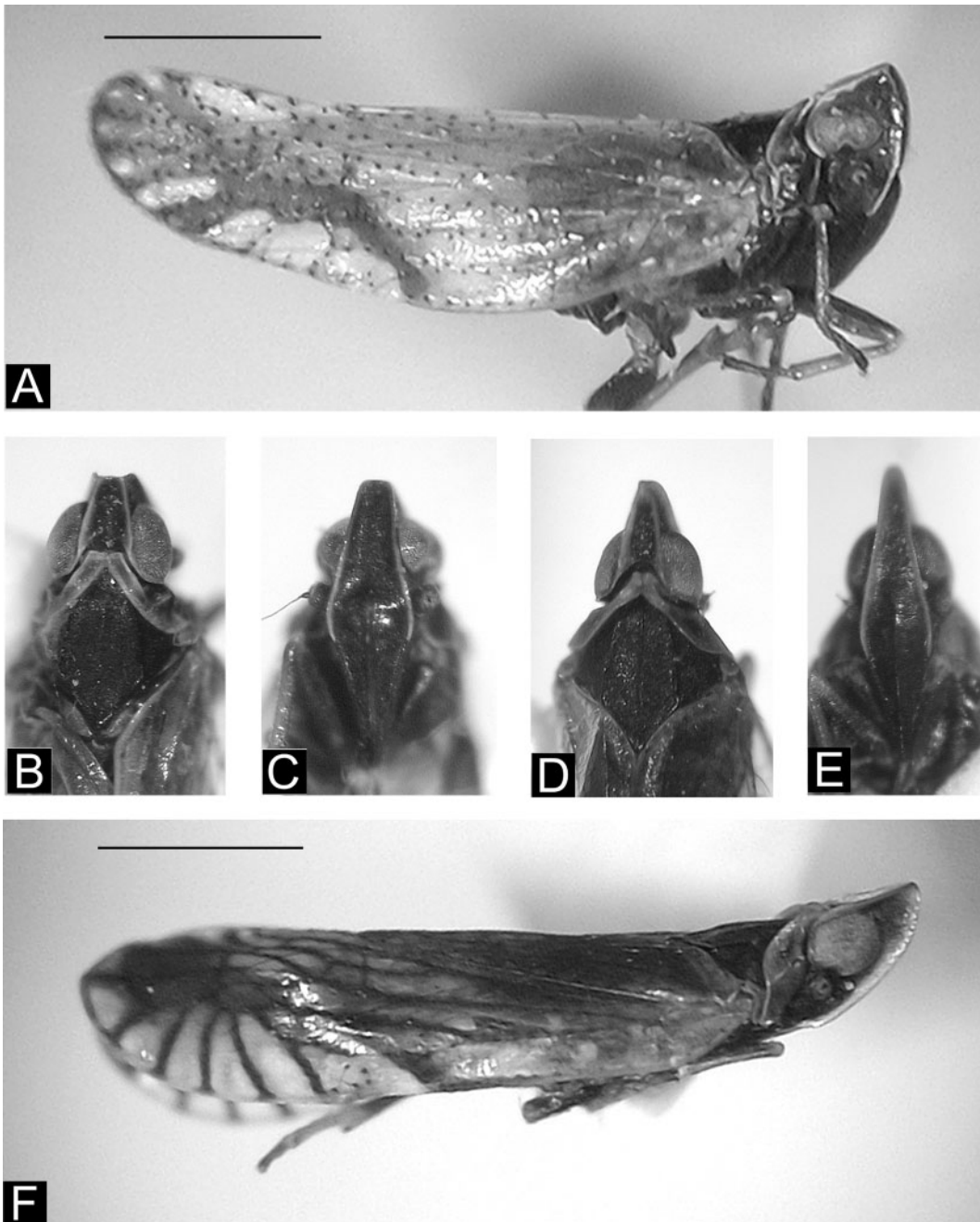
*Paratypes*. **Australia: ACT:** 1 ♀, Mt Gingera, 4.ii.1965 (D. H. Colless) (ANIC). **Vic.:** 2 ♂, 7 mi. W of Newmerella, by sweeping shrubs, 23.xi.1959 (G. F. Gross) (SAM). **NSW:** 2 ♀, Mt Kosciuszko, Wilsons Valley, 1966 (J. W. & F. Evans) (ASCU); 1 ♀, Mt Kosciuszko,

Rennex Gap, 1965 (J. W. & F. Evans) (ASCU); 1 ♀, Clyde Mtn, West slope, 1.ii.1973 (D. H. Colless) (ANIC).

*Description*

*Colour*

Head mid to dark brown, carinae light brown except for dark brown lateral carinae on postclypeus; pronotum mid brown, central carinae paler; mesonotum mid to dark brown, carinae sometimes paler; legs light to dark brown; forewing hyaline whitish with large light to dark brown areas, veins



**Fig. 35.** *Novotarberus flagellospinosus*: A, habitus; B, C, head. *Novotarberus pseudorphninus*: D, E, head; F, habitus.

concolorous with cells, tubercles dark brown; abdominal sternites dark brown, intersegmental membranes orange.

### Morphology

*Body length.* ♂ 4.0–4.5 mm; ♀ 4.4–4.7 mm.

*Head.* Vertex 1.1–1.3× longer than wide, produced before eyes by 1/2–3/4 of an eye length; apex broadly truncate; caudal border u-shaped; median carina ~1/4 as long as vertex. Frons 1.1–1.5× longer than wide; lateral carinae s-shaped, strongly elevated. Frontoclypeal suture semicircular, median part reaching at least lower margin of antennal scape.

*Thorax.* Hind margin of pronotum acutely angled. Forewing less than 3× longer than wide, distinctly decreasing in width in their basal third (Fig. 12C); costa with 16–27 tubercles; fork of Sc+R distinctly basad of fork of CuA1+CuA2; r-m1 basad, distad of or at same level as fork of MA-MP; position of icu at CuP distad apex of clavus; 10 apical cells. Hind leg: tibia with 0–3 small lateral spines (without large lateral spines); 1st tarsomere with 10 apical teeth and four platellae; 2nd tarsomere with 9–10 apical teeth and 7–8 platellae.

*Male genitalia.* Anal tube as in Fig. 89B, C; ventro-medial process of pygofer and genital styles as in Fig. 89D, E. Aedeagus (Fig. 89A): phallosome with a long strongly curved spine (a) arising right lateral near apex and a second short, slightly curved spine (b) ventrally below midlength; flagellum lacking spines.

### Remarks

The number of platellae on the 1st hind tarsomere appears to vary slightly; five platellae were observed on the leg of one specimen.

### Etymology

Named in honour of the authors' friend and colleague Reinhard Remane.

Genus *Payastylus* Löcker & Fletcher, gen. nov.

Type species *Payastylus gekiae* Löcker & Fletcher, sp. nov.

### Description

#### Morphology

*Body length.* ♂ 3.7–4.1 mm, ♀ 4.0–4.7 mm.

*Head.* Vertex produced before eyes by 1/4 to 1/2 of an eye length; caudal border broadly u-shaped. Frons 1.1–1.5× longer than wide; maximum width about centre of frontoclypeal suture; lateral carinae slightly elevated, lateral margins foliaceous, concealing base of antennae; median

carina complete. Frontoclypeal suture semicircular, median part not reaching lower margin of antennal scape. Median carina on post- and anteclypeus absent or evanescent; lateral carinae on postclypeus well developed.

*Thorax.* Concavity at costal border of forewing absent; position of icu at CuP distinctly distad of apex of clavus. First tarsomere of hind leg lacking platellae.

### Distribution

NSW, Qld, SA.

### Remarks

The monophyly of this genus is shown in every analysis. A few trees, such as the strict consensus tree obtained by successive approximations weighting of dataset A also allow the inclusion of *Yarnikada ulliae* in the genus *Payastylus*. Both genera share similarly shaped genital styles. Whether this represents a synapomorphy or is due to parallel evolution needs to be clarified. Based on the fact that most analyses place *Yarnikada* far apart from *Payastylus* and on characters such as a distinct median carina on the clypeus in *Yarnikada*, whereas in *Payastylus* the median carina is either absent or evanescent, *Yarnikada* was placed in a separate genus. The following combination of characters is diagnostic for the genus *Payastylus*: complete median carina on frons, absent or evanescent median carina on the postclypeus and genital styles in lateral view shaped as in Figs 90–92E.

### Etymology

'Paya' means 'bird' in Diyari, a language spoken by Aboriginal people in South Australia (Thieberger and McGregor 1994). The genus is named after the shape of the genital styles in lateral view, which resemble the head of a bird. Gender: masculine.

### Key to species of *Payastylus*

1. Apex of vertex narrowly pointed; forewing light in colour with contrasting dark brown tubercles; genital styles as in Fig. 90F; aedeagus with only one sclerotised spine, with or without a membranous spine (Fig. 90A, B) . . . . . *P. gekiae*, sp. nov.
- Apex of vertex broadly rounded or truncate; forewing and tubercles concolorous yellow to light brown; genital styles different; aedeagus with more than one sclerotised spine. . . . . 3
- 2(1). Hind tibia with three large lateral spines; colour of head black except for some paler carinae; genital styles as in Fig. 91F; aedeagus with three spines (Fig. 91A, B) . . . . . *P. brichrius*, sp. nov.
- Hind tibia with 1–4 small lateral spines; colour of head mid brown except for some paler carinae; genital styles as in Fig. 92F; aedeagus with two spines (Fig. 92A, B) . . . . . *P. kernaes*, sp. nov.

***Payastylus gekiae* Löcker & Fletcher, sp. nov.**

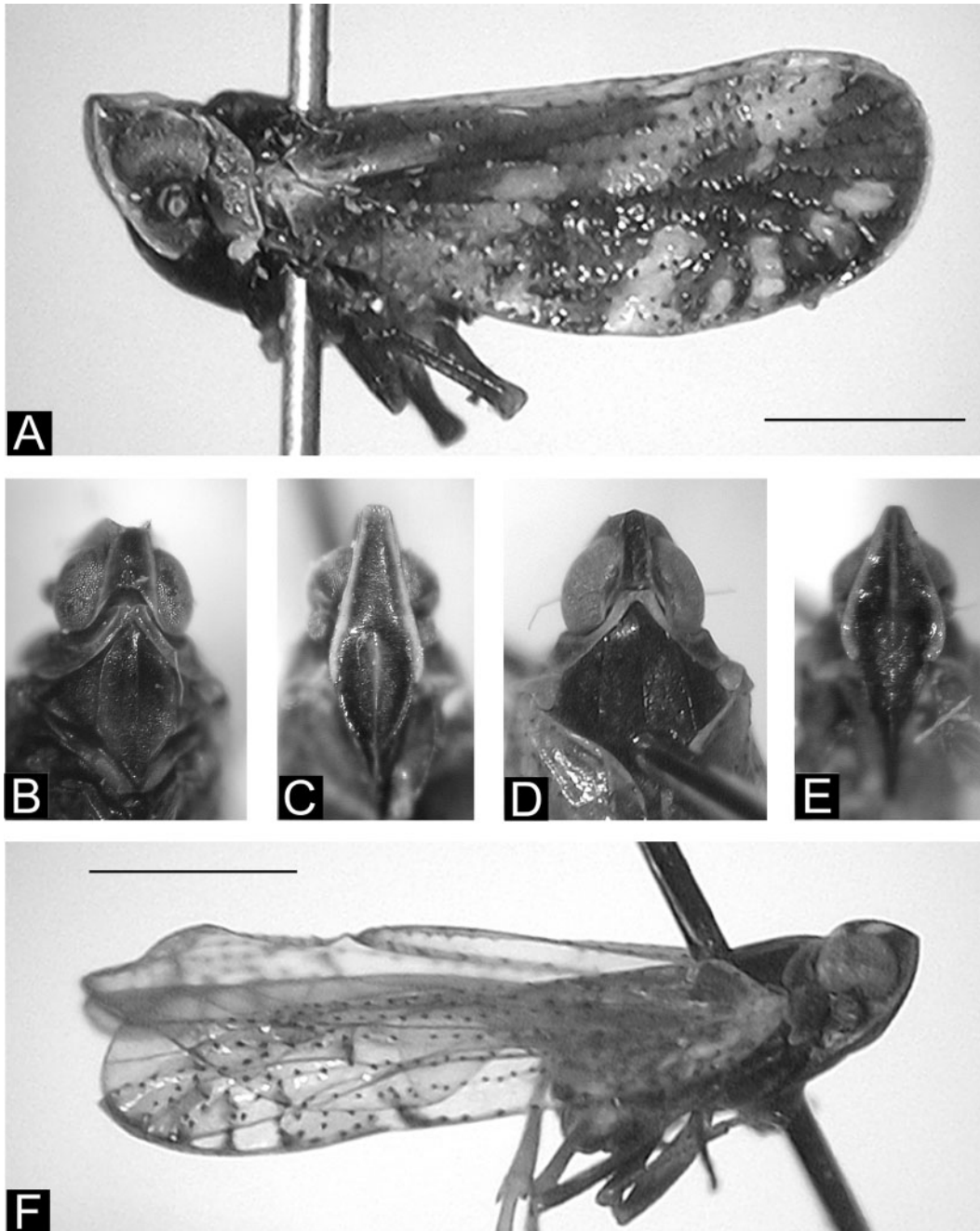
(Figs 36D–F, 90)

**Material examined**

**Holotype.** ♂, Australia: NSW: Cocopara NP, nr Griffith, NSW, 12.ii.1980, at mv. light (G. R. Brown) (ASCU ASCTHE026715).

**Paratypes.** **Australia:** **NSW:** 3♂, 2♀, Murda SF, 33°00'45"S 140° [sic.] [= 147°] 12'55"E, 10.ii.1999 (Aust. Mus., Terr. Ecol. Dept), Field No 9566 (AM); 1♂, 4♀, nr Murda SF, 33°00'56"S 147°14'57"E, 23.ii.1998 (Aust. Mus., Terr. Ecol. Dept), Field No 8787, K 116878 (AM); 2♀, nr Murda SF, 33°00'31"S 147°12'16"E, 23.ii.1998 (Aust.

Mus., Terr. Ecol. Dept), Field No 8786, K 116687 (AM); 1♀, nr Murda SF, 33°00'27"S 147°07'42"E, 9.ii.1999 (Aust. Mus., Terr. Ecol. Dept), Field No 9557, K 116289 (AM); 5♀, nr Murda SF, 33°00'50"S 147°15'23"E, 22.ii.1998 (Aust. Mus., Terr. Ecol. Dept), Field No 6025, K 116815 (AM); 2♂ 1♀, nr Corringale SF, 33°39'20"S 147°17'47"E, 10.iii.1998 (Aust. Mus., Terr. Ecol. Dept), Field No 12774, K117177 (AM); 1♂, nr Corringale SF, 33°42'58"S 147°07'00"E, 12.iii.1998 (Aust. Mus., Terr. Ecol. Dept), Field No 8796, K116890 (AM); 1♀, nr Corringale SF, 33°40'03"S 147°07'02"E, 12.iii.1998 (Aust. Mus., Terr. Ecol. Dept.), Field No 8805, K127878 (AM); 1♂, 12♀, Backyamma SF, 33°20'29"S 148°13'58"E, 7.iv.1999 (Aust. Mus. Terr. Ecol. Dept),



**Fig. 36.** *Novotarberus remanei*: A, habitus; B, C, head. *Payastylus gekiae*: D, E, head; F, habitus.



Field No 12948, K117738 (AM); 1♀, nr Backyamma SF, 33°08'33"S 148°13'26"E, 4.iv.1998 (Aust. Mus. Terr. Ecol Dept), Field No 6628, K 121845 (AM); 7♀, nr Backyamma SF, 33°08'33"S 148°13'25"E, 8.iv.1999 (Aust. Mus. Terr. Ecol Dept), Field No 12940 K 117783 (AM); 4♀, nr Backyamma SF, 33°20'26"S 148°13'21"E, 7.iv.1999 (Aust. Mus. Terr. Ecol Dept), Field No 12951, K 117655 (AM); 4♀, nr Backyamma SF, 33°18'21"S 148°11'02"E, 3.iv.1998 (Aust. Mus. Terr. Ecol Dept), Field No 6615, K 121831 (AM); 1♂, 1♀, Weddin Mtns NP, 14.ii.1980 (G. R. Brown) (ASCU); 1♂, Tottenham dist., Mallee country, 9.ii.1960 (T. E. Woodward) (UQIC Reg. ♂ 54150).

### Description

#### Colour

Vertex pale yellowish, with central part mid brown and brown mark along lateral carinae close to caudal border; face mid to dark brown, carinae light brown except for brown lateral carinae of postclypeus; pronotum mid brown, carinae and hind border light brown; mesonotum mid to dark brown; legs straw coloured to mid brown; forewing hyaline white with yellow and brown marks, veins whitish to yellowish, tubercles mid to dark brown.

#### Morphology

*Body length.* ♂ 3.7–4.0 mm; ♀ 4.0–4.6 mm.

*Head.* Vertex 0.9–1.4× as long as wide; apex narrowly pointed; lateral carinae strongly elevated; median carina incomplete, 1/4–1/2 as long as vertex. Lateral carinae of frons convex (although rectilinear apically) or s-shaped.

*Thorax.* Pronotum with arched or sinuate carinae; hind margin right or acutely angled. Forewing 3.5–4× longer than wide; costa with 11–19 tubercles; Sc+R+M forming very short common stem; fork of Sc+R basad of fork of CuA1+CuA2; r-m1 basad of or at same level as fork MA–MP; nine apical cells. Hind leg: tibia with 0–3 small lateral spines (without large lateral spines); six apical teeth in a row interrupted by a wide gap; 1st tarsomere with 7(–8) apical teeth and no platellae; 2nd tarsomere with 8–9 apical teeth and 6–7 platellae.

*Male genitalia.* Anal tube as in Fig. 90C, D; ventro-median process of pygofer and genital styles as in Fig. 90E, F. Aedeagus (Fig. 90A, B): phallosome with a long, slightly curved, sclerotised spine (a) and sometimes with a shorter, more membranous spine (c), both arising ventrally near apex; flagellum unarmed.

#### Remarks

In some specimens, including the holotype, an additional spine (c) is present. This spine is only slightly sclerotised and variable in size.

The longitude given on the data labels for the three paratypes from Murda SF in AM is 140° but this locality is actually at 147° of longitude.

#### Etymology

Named in honour of the first author's friend Angelika 'Geki' Jaklin.

### *Payastylus brichrius* Löcker & Fletcher, sp. nov.

(Figs 37A–C, 91)

#### Material examined

*Holotype.* ♂, Australia: NSW: Griffith turnoff, 15 km W of Rankins Springs, 5.iv.1997 (M. J. Fletcher & J. S. Mann) (ASCU ASCTHE025801).

*Paratypes.* **Australia: NSW:** 1♀, 7 km S of Dubbo, 4.ix.1982 (G. & A. Holloway) (AM). **Qld:** 1♀, Illaweena St, Drewvale, 27°38.6'S 153°03.8'E, 40 m, scribbly gum/heath, sweeping, 29.iv.2003 (E. Volschenk), 51185 (QM).

#### Description

##### Colour

Head black, carinae yellow to orange except for black lateral carinae on postclypeus; pronotum light brown, with carinae and hind border yellow; mesonotum mid brown, central part black with mid brown carinae; legs straw coloured to brown; forewing hyaline yellow with concolorous veins and tubercles (except apically, light brown).

##### Morphology

*Body length.* ♂ 4.0 mm; ♀ 4.7 mm.

*Head.* Vertex 0.8× as long as wide; apex broadly truncate; lateral carinae s-shaped, strongly elevated; median carina incomplete, 1/4–1/2 as long as vertex. Lateral carinae of frons sinuate.

*Thorax.* Pronotum with sinuate carinae; hind margin rectangular. Forewing 3.0–3.5× longer than wide; costa with 21–22 tubercles; Sc+R+M forming very short common stem or Sc+R forming common stem and M emerging separately from basal cell; fork of Sc+R distad of or at same level as fork of CuA1+CuA2; r-m1 basad of fork MA–MP. Hind leg: tibia with three large lateral spines; six apical teeth in row interrupted by a wide gap; 1st tarsomere with 6–7 apical teeth and no platellae; 2nd tarsomere with nine apical teeth and seven platellae.

*Male genitalia.* Anal tube as in Fig. 91C, D; ventro-median process of pygofer and genital styles as in Fig. 91E, F. Aedeagus (Fig. 91A, B): phallosome with a short, rather straight spine (a) arising ventrally about midlength, a long twisted spine (b) arising left laterally near apex and a long slightly curved spine (c) dorsally above midlength; flagellum unarmed.

#### Etymology

Derived from the names of the first author's friends and colleagues Brigitte and Christian Komposch.

### *Payastylus kerna* Löcker & Fletcher, sp. nov.

(Figs 37D–F, 92)

#### Material examined

*Holotype.* ♂, Australia: SA: 6 km N by W of Mt Sarah HS, N of Oodnadatta, 24.ix.1972 (Z. Liepa) (ANIC).

*Description**Colour*

Vertex mid brown, median carina orange-brown; face mid brown, carinae yellow to orange except for brown lateral carinae on postclypeus; pronotum orange, with carinae and hind border yellow; mesonotum orange, with central part mid brown; legs yellow to brown; forewing hyaline white to yellow with yellow veins and light brown tubercles.

*Morphology*

*Body length.* ♂ 4.1 mm.

*Head.* Vertex 0.9× as long as wide; apex broadly rounded; lateral carinae moderately elevated; median carina incomplete, ~3/4 as long as vertex. Lateral carinae of frons convex (although rectilinear apically).

*Thorax.* Pronotum with arched carinae; hind margin rectangular. Forewing 3.0–3.5× longer than wide; costa with

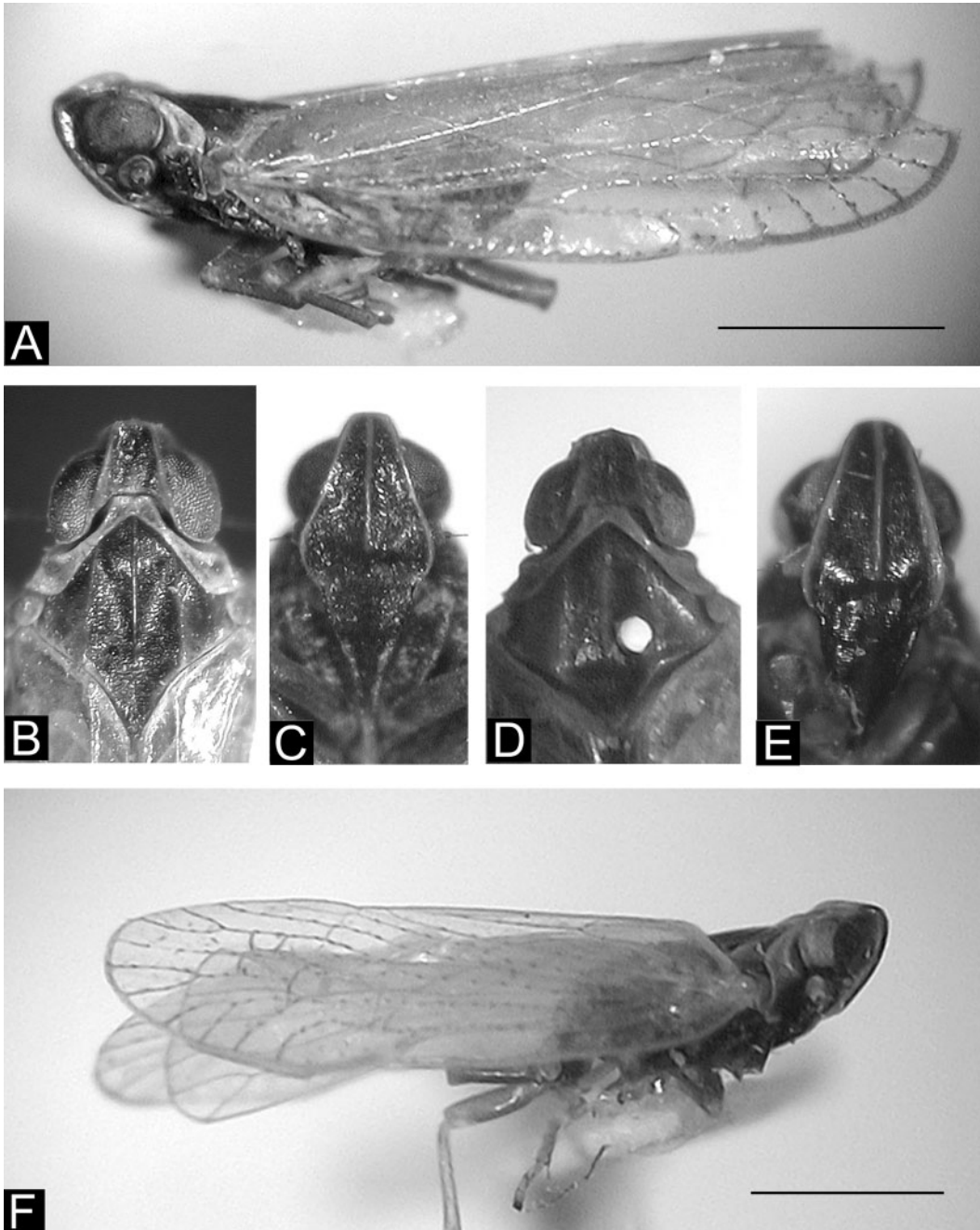


Fig. 37. *Payastylus brichrius*: A, habitus; B, C, head. *Payastylus kernaе*: D, E, head; F, habitus.

21–22 tubercles; Sc+R+M forming very short common stem or Sc+R forming common stem and M emerging separately from basal cell; fork of Sc+R basad of fork of CuA1+CuA2; r–m1 distad of fork MA–MP; 10 apical cells. Hind leg: tibia with 1–4 small lateral spines (without large lateral spines); five apical teeth in row interrupted by a wide gap; 1st tarsomere with six apical teeth and no platellae; 2nd tarsomere with eight apical teeth and six platellae.

*Male genitalia.* Anal tube as in Fig. 92C, D; ventro-medial process of pygofer and genital styles as in Fig. 92E, F. Aedeagus (Fig. 92A, B): phallosome with a long slightly sinuate spine (a) arising ventrally and a short, basally thickened spine (b) arising left laterally near apex; flagellum unarmed.

#### Remarks

Only five apical teeth were observed on the hind tibia of the only known specimen of this species. Since all other Gelastocephalini have at least six spines, this could be an aberration but further material is needed to confirm this.

#### Etymology

Named in honour of the first author's grandmother Maria Kern.

#### Genus *Rokebia* Löcker & Fletcher, gen. nov.

Type species *Rokebia australis* Löcker & Fletcher, sp. nov.

#### Description

##### Morphology

*Head.* Vertex 0.7× as long as wide, produced before eyes by 1/4–1/2 of an eye length; apex broadly truncate; caudal border v-shaped; lateral carinae strongly elevated; median carina incomplete, 1/2–3/4 as long as vertex. Frons with lateral carinae convex (although rectilinear apically), moderately elevated, lateral margins foliaceous, concealing base of antennae; median carina incomplete; postclypeus with well developed lateral carinae and median carina; anteclypeus with well developed median carina.

*Thorax.* Hind margin of pronotum obtusely angled. Forewing 3.5–4.0× longer than wide; costa with 4–5 tubercles; concavity at costal border absent; Sc+R+M forming short common stem; fork of Sc+R distad of or at same level as fork of CuA1+CuA2; r–m1 distad of fork MA–MP; position of icu at CuP distad of apex of clavus, 10 apical cells. Hind leg: tibia with two small lateral spines (without large lateral spines); six apical teeth in row interrupted by a wide gap; 1st tarsomere with seven apical teeth and no platellae; 2nd tarsomere with seven apical teeth and five platellae.

#### Distribution

Qld.

#### Etymology

Named after Rokeby, the type locality. Gender: feminine.

#### *Rokebia australis* Löcker & Fletcher, sp. nov.

(Figs 38A–C, 93)

#### Material examined

*Holotype.* ♂, Australia: Qld: 2 km N Rokeby, 13°39'S 142°40'E, 17.xii.1993–17.i.1994, Malaise Trap (P. Zborowski & M. Shaw) (ANIC).

#### Description

##### Colour

Body yellow; forewing hyaline yellow with concolorous veins and tubercles; abdominal sternites mid brown, inter-segmental membranes yellow.

##### Morphology

*Body length.* ♂ 3.6 mm.

*Male genitalia.* Anal tube as in Fig. 93C, D; ventro-medial process of pygofer and genital styles as in Fig. 93E, F. Aedeagus (Fig. 93A, B): phallosome with a long spine (a) arising ventrolaterally near apex and a sheet-like ventral ridge bearing a pair of slightly curved spines (b) near base; flagellum unarmed.

#### Genus *Ronaldia* Emeljanov

*Ronaldia* Emeljanov, 2000: 261.

Type species *Ronaldia fennahi* Emeljanov, 2000, by original designation.

#### Description

##### Colour

Head yellow; pronotum yellow, sometimes with brown areas; mesonotum dark brown to black; legs yellow.

##### Morphology

*Body length.* ♂ 3.9–4.6 mm, ♀ 3.6–5.1 mm.

*Head.* Vertex 0.7–0.9× as long as wide, produced before eyes by less than 1/4 of an eye length; apex broadly pointed; caudal border u- to v-shaped; lateral carinae slightly elevated. Frons 1.1–1.4× longer than wide, lateral carinae slightly elevated, lateral margins foliaceous, concealing base of antennae; median carina complete. Frontoclypeal suture semicircular, median part reaching at least lower margin of antennal scape; postclypeus with well developed lateral carinae and median carina; anteclypeus with well developed median carina, distinctly more elevated than that of postclypeus.

*Thorax.* Pronotum with sinuate carinae. Concavity at costal border of forewing absent; Sc+R+M forming common stem; r–m1 distad of fork MA–MP; position of icu

at CuP distad of apex of clavus. Row of apical teeth of hind tibia interrupted by a narrow gap; 1st tarsomere lacking platellae.

*Male genitalia.* Pygofer with truncate ventromedian process as in Figs 94–95E. Genital styles as in Figs 94–95D, E. Aedeagus (Figs 94–95A): phallosome with a straight or curved spine arising left laterally above midlength, and a foliaceous ventral ridge forming long spine-like process apically; flagellum with or without two apical teeth.

#### *Distribution*

ACT, SA.

#### *Remarks*

Females could only be identified to genus level. The measurements of females given above are derived from seven specimens from ACT, NSW, Qld, SA.

Two synapomorphies exist for the genus *Ronaldia*, an aedeagus with a foliaceous ventral ridge forming a long

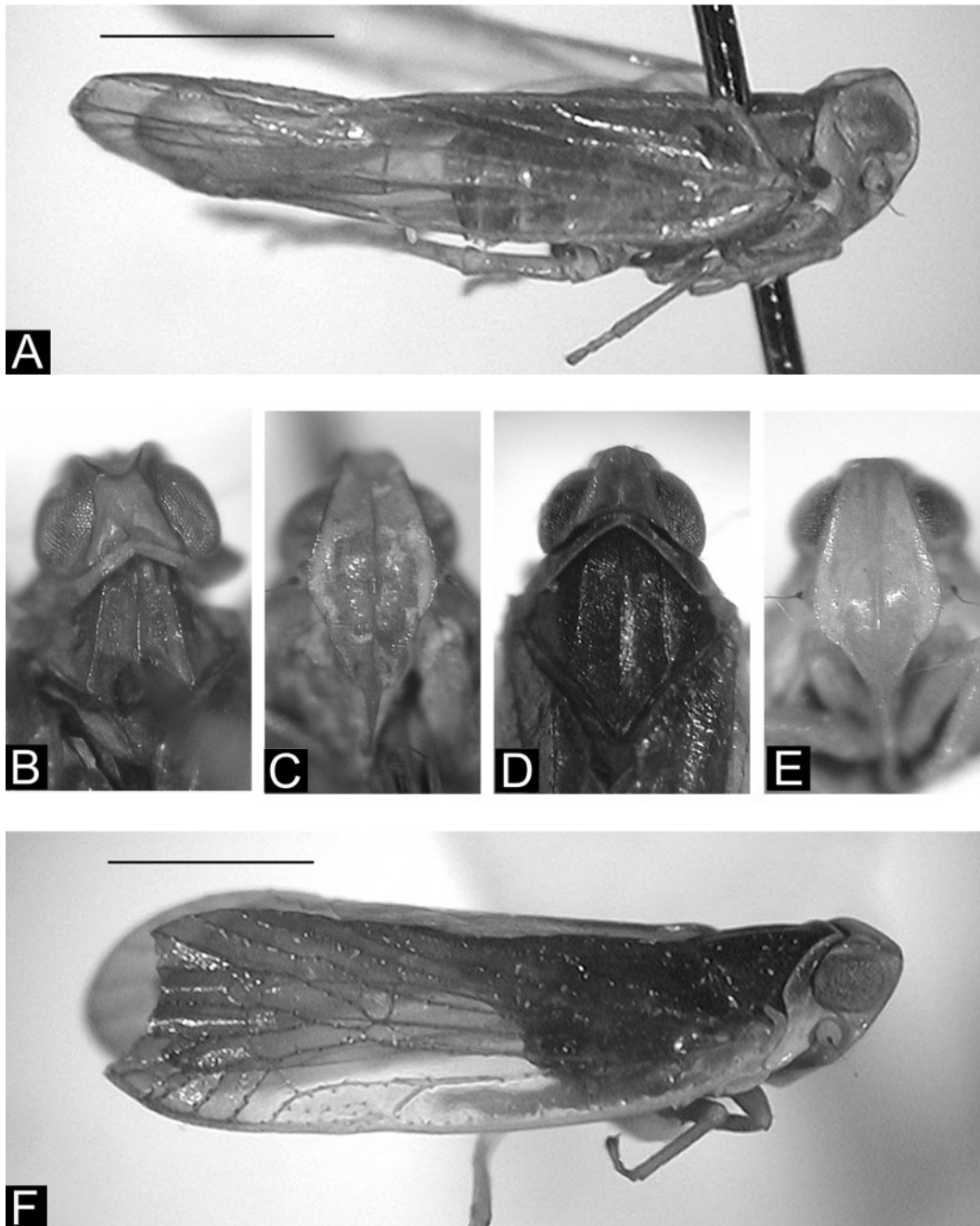


Fig. 38. *Rokebia australis*: A, habitus; B, C, head. *Ronaldia fennahi*: D, E, head; F, habitus.

spine-like process apically (Figs 94–95A) and a median carina, distinctly more elevated on the anteclypeus than on the postclypeus. The broad yellow face, and the shape of the head in dorsal, lateral and facial view and the narrow gap in the row of apical teeth, the 1st tarsomere lacking platellae, the shape of the anal tube in dorsal view as in Fig. 105D, E and the truncate apex of the ventromedian process are other characteristics of this clade, that was retrieved by all weighting regimes.

### Key to species of *Ronaldia*

- Phallotheca with a sinuate spine and a ventral ridge forming a spine-like process with a small base (Fig. 94A); flagellum with two apical spines (Fig. 94A) . . . *R. fennahi* Emeljanov  
Phallotheca with a straight spine, turned 90° in its apical third and a ventral ridge forming a spine-like process with a large base (Fig. 95A); flagellum lacking spines (Fig. 95A) . . . . .  
..... *R. emeljanovi*, sp. nov.

### *Ronaldia fennahi* Emeljanov

(Figs 38D–F, 94)

*Ronaldia fennahi* Emeljanov, 2000: 261, figs 29–36.

#### Material examined

*Holotype*. ♂, Australia: ACT: Canberra, Black Mt, 3.–10.xii.1990 (A. Kirejtschuk), (ANIC).

*Paratypes*. **Australia: ACT:** 4♂, 10♀ (1♂, 1♀ examined), same data as holotype, (ZIN).

*Other material examined*. **Australia: ACT:** 1♂, Black Mt, Light Trap, 14.xii.1960 (I. F. B. Common) (ANIC); 1♂, 1.xi.1929 (J. Evans) (ANIC). **SA:** 1♂, no other data (MAMU); 1♂, Workanda Creek NP Belair, 13.xii.1947 (R.V. Southcott) (SAM).

#### Description

##### Colour

Forewing hyaline yellow or brown with concolorous veins and tubercles, and pale yellowish area along costa.

##### Morphology

*Body length*. ♂ 3.9–4.6 mm.

*Head*. Median carina of vertex incomplete, 1/2–3/4 as long as vertex. Position of maximum width of frons around centre or distinctly ventrad of centre of frontoclypeal suture; lateral carinae convex (evenly rounded or rectilinear apically).

*Thorax*. Hind margin of pronotum right or obtusely angled. Forewing 3.0–3.5× longer than wide; costa with 15–20 tubercles; fork of Sc+R basad of fork of CuA1+CuA2; position of icu at CuP distad of or at same level as apex of clavus; 10 apical cells. Hind leg: tibia with 0–3 small lateral spines (without large lateral spines); 6–7 apical teeth in row interrupted by narrow gap; 1st tarsomere with seven apical teeth and no platellae; 2nd tarsomere with seven (sometimes 8–10) apical teeth and five (sometimes 6–8) platellae.

*Male genitalia*. Anal tube as in Fig. 94B, C; ventromedian process of pygofer and genital styles as in Fig. 94D, E. Aedeagus (Fig. 94A): phallotheca with a sinuate spine, arising left lateral above midlength and a foliaceous ventral ridge forming long spine-like process with a small base; flagellum with two apical spines.

#### Remarks

Emeljanov's (2000) designation of female paratypes is problematic since females of the genus cannot be identified to species with confidence.

### *Ronaldia emeljanovi* Löcker & Fletcher, sp. nov.

(Figs 39A–C, 95)

#### Material examined

*Holotype*. ♂, Australia: SA: Teatree Gully, by beating *Callitris propinqua*, 7.xii.1958 (R. V. Southcott), (SAM I21677).

*Paratype*. **Australia: ACT:** 1♂, Canberra, 1.xi.1929 (J. Evans) (ANIC).

#### Description

##### Colour

Forewing hyaline yellow, veins and tubercles concolorous with cells.

##### Morphology

*Body length*. ♂ 4.1–4.6 mm.

*Head*. Median carina of vertex incomplete, 1/4–1/2 as long as vertex. Position of maximum width of frons distinctly ventrad of centre of frontoclypeal suture; lateral carinae convex (evenly rounded).

*Thorax*. Hind margin of pronotum rectangular. Forewing 3.5–4.0× longer than wide; costa with 14–16 tubercles; fork of Sc+R basad, distad of or at same level as fork of CuA1+CuA2; position of icu at CuP distad of apex of clavus; 10–11 apical cells. Hind leg: tibia with 0–1 small lateral spine (without large lateral spines); seven apical teeth in a row interrupted by a narrow gap; 1st tarsomere with 7(–8) apical teeth and no platellae; 2nd tarsomere with 7–8 apical teeth and 5–6 platellae.

*Male genitalia*. Anal tube as in Fig. 95B, C; ventromedian process of pygofer and genital styles as in Fig. 95D, E. Aedeagus (Fig. 95A): phallotheca with a straight spine, turned 90° in apical third, arising left laterally above midlength and a foliaceous ventral ridge forming long spine-like process with a large base; flagellum lacking spines.

#### Etymology

Named in honour of the authors' colleague Alexandre Emeljanov.

Genus *Schuerrera* Löcker & Fletcher, gen. nov.

Type species *Schuerrera ecarinata* Löcker & Fletcher, sp. nov.

*Description*

*Morphology*

*Body length.* ♂ 4.0–5.3 mm, ♀ 4.8–6.8 mm.

*Head.* Vertex 0.6–0.9× as long as wide, produced before eyes by 1/4–1/2 of an eye length; caudal border u-shaped. Frons 1.1–1.5× longer than wide; lateral carinae

slightly elevated, lateral margins foliaceous, concealing base of antennae; median carina complete. Postclypeus with well developed lateral carinae; anteclypeus lacking carinae.

*Thorax.* Concavity at costal border of forewing absent; Sc+R+M forming common stem; r-m1 distad of fork MA–MP. Hind tibia with six apical teeth in a row; 2nd tarsomere with nine apical teeth and seven platellae.

*Male genitalia.* Genital styles broadly spoon-shaped as in Figs 96–97F, 98E. Aedeagus with spines (a) and (b), occasionally with an additional spine (c).

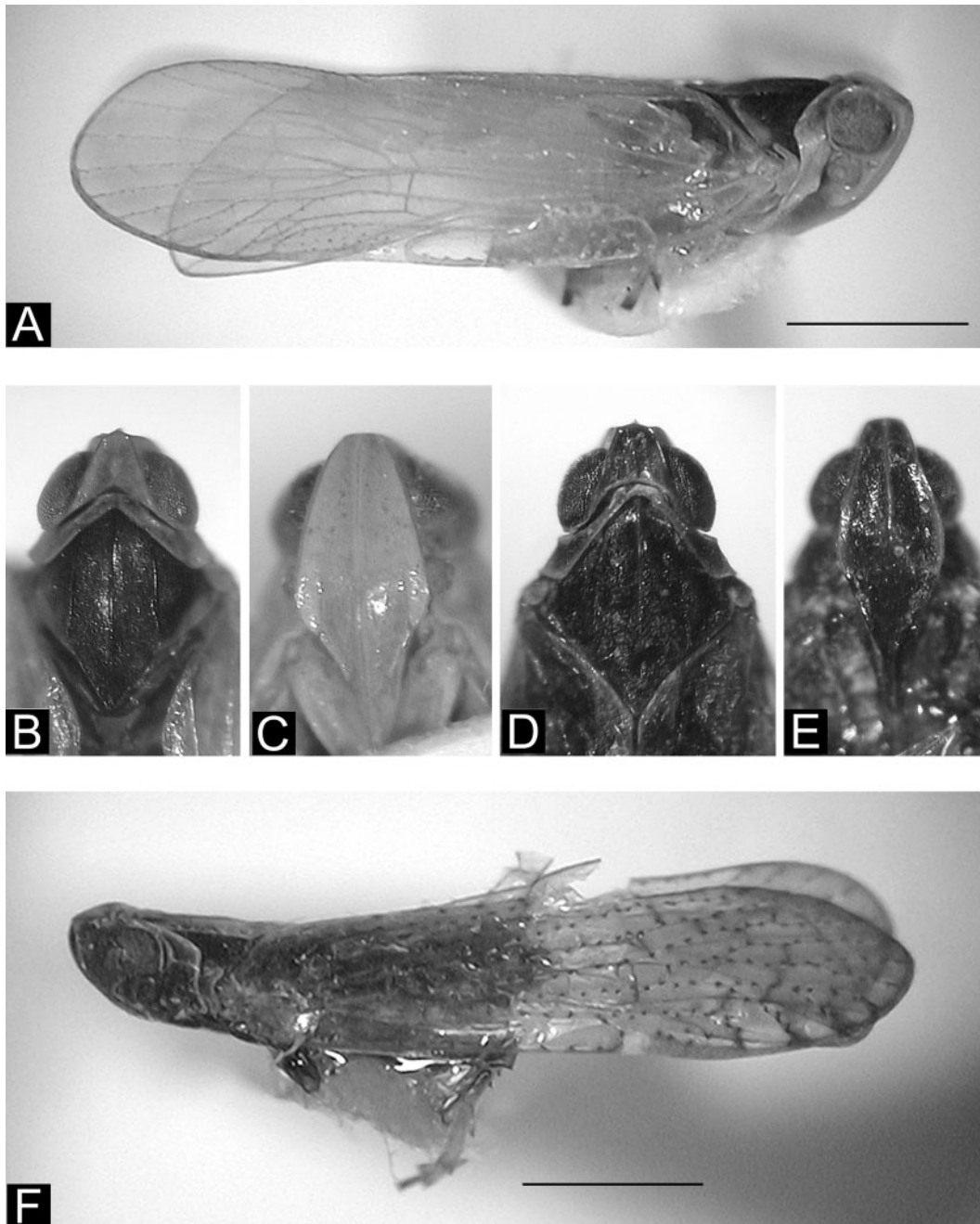


Fig. 39. *Ronaldia emeljanovi*: A, habitus; B, C, head. *Schuerrera ecarinata*: D, E, head; F, habitus.

*Distribution*

NSW, Qld.

*Remarks*

This clade is well supported by all weighting regimes, despite the fact, that the external morphology varies considerably within this genus. For example *S. ecarinata* and *S. merula* are characterised by the absence of a median carina on most of the clypeus, whereas *S. clypeocarinata* shows a well developed median carina on post- and anteclypeus. The shape of the forewing, more than 4× longer than wide in *S. ecarinata*, 3.5–4.0× longer than wide in *S. merula* and less than 3× longer than wide in *S. clypeocarinata* is another feature that varies within the genus. All three species, however, share the following characters: broadly spoon-shaped genital styles in ventral view (Figs 96–97F, 98E), triangularly shaped genital styles in lateral view, and the same configuration of spines on the aedeagus. If the additional spine (*c*) in *S. merula* is an autapomorphy, or if the other two species lost this spine is contradictory in different analyses. The following combination of characters is diagnostic for the genus *Schuerrera*: broadly spoon-shaped genital styles, not bearing a tooth on the inner side of the basal arms, and the arrangement of 2–3 aedeagal spines as in Figs 96–97A, B; 98A.

*Etymology*

Derived from the name of the first author's parents Irtraut and Ferdinand Schürer. Gender: feminine.

**Key to species of *Schuerrera***

- Median carina well developed on post- and anteclypeus; mesonotum orange brown . . . . . *S. clypeocarinata*, sp. nov.  
Median carina of postclypeus absent or only developed over a short length, anteclypeus always lacking median carina; mesonotum dark brown to black . . . . . 2
- Aedeagus with two spines (Fig. 96A, B); body length of males at least 4.7 mm, of females at least 6.1 mm . . . . .  
. . . . . *S. ecarinata*, sp. nov.  
Aedeagus with three spines (Fig. 98A); body length of males less than 4.3 mm, of females less than 5.0 mm . . . . .  
. . . . . *S. merula* (Distant), comb. nov.

***Schuerrera ecarinata* Löcker & Fletcher, sp. nov.**

(Figs 39D–F, 96)

*Material examined*

*Holotype*. ♂, Australia: NSW: Cabramatta, 28.xii.1965, by sweeping in orchard (M. I. Nikitin) (ASCU ASCTHE026677).

*Paratypes*. **Australia: Qld:** 1♂, Bowen, 18.viii.1970 (F. McDonald) (ASCU); 1♂, Rockhampton, 29.viii–28.ix.1980, Malaise trap (R. J. Elder) (QDPI); 1♀, Samford, 30.xi.1960 (M. F. Day & N. E. Grylls) (ANIC); 2♀, Pine Creek, c. 19 km S of Bundaberg, 27.ix.1975 (H. Frauca) (ANIC). **NSW:** 1♀, Cabramatta, at light, 28.xii.1965 (M. I. Nikitin) (ASCU).

*Description**Colour*

Head mid to dark brown, carinae paler; pronotum mid brown, carinae light brown; mesonotum dark brown, central parts and carinae paler; legs straw coloured to light brown; forewing hyaline light brown with brown marks along crossveins and apical parts of veins, the latter concolorous with cells, tubercles mid brown; abdominal sternites brown, intersegmental membranes pale yellowish.

*Morphology*

*Body length*. ♂ 4.7–5.3 mm; ♀ 6.1–7.1 mm.

*Head*. Apex of vertex broadly truncate; median carina incomplete, ~3/4 as long as vertex; lateral carinae moderately elevated. Frons with its maximum width distinctly ventrad of centre of frontoclypeal suture; lateral carinae convex (evenly rounded) or slightly s-shaped. Frontoclypeal suture semicircular, median part reaching at least lower margin of antennal scape; median carina on postclypeus well developed close to frontoclypeal suture, otherwise evanescent; anteclypeus lacking median carina

*Thorax*. Pronotum with sinuate carinae; hind margin right or acutely angled. Forewing more than 4× longer than wide; costa with 9–15 tubercles; fork of Sc+R distad of or at same level as fork of CuA1+CuA2; position of icu at CuP distad of apex of clavus; 10 (rarely nine) apical cells. Hind leg: tibia with 2–3 small lateral spines (without large lateral spines); six apical teeth in a row interrupted by a wide gap; 1st tarsomere with 10–11 apical teeth and five platellae.

*Male genitalia*. Anal tube as in Fig. 96C, D; ventro-median process of pygofer and genital styles as in Fig. 96E, F. Aedeagus (Fig. 96A, B): phallosome with a very long, curved spine (*a*) arising ventrolaterally near apex and a shorter moderately curved spine (*b*) arising ventrally above midlength; flagellum unarmed.

*Remarks*

The male genitalia of this species looks very similar to those of *S. clypeocarinata* the two species being differentiated most easily by the absence of a median carina on most of the clypeus and the longer forewing.

*Etymology*

This species lacks a median carina in most parts of the clypeus.

***Schuerrera clypeocarinata* Löcker & Fletcher, sp. nov.**

(Figs 40A–C, 97)

*Material examined*

*Holotype*. ♂, Australia: Qld: 32 km W of Mareeba, N Qld, 31.i.1982 (J. F. Donaldson) (QM T123597, originally from QDPI).

*Paratype*. **Australia: Qld:** 1♂, same data as holotype (QDPI).

*Description**Colour*

Head light to mid brown, carinae paler; pronotum light brown; mesonotum orange brown, central parts and carinae paler; legs light brown; forewing hyaline straw coloured basally, mid brown apically, veins concolorous with cells, tubercles mid brown; abdominal sternites brown, intersegmental membranes yellow to orange.

*Morphology*

*Body length.* ♂ 4.7–4.8 mm.

*Head.* Apex of vertex broadly truncate; median carina incomplete, ~3/4 as long as vertex; lateral carinae slightly elevated. Frons with its maximum width around centre of frontoclypeal suture; lateral carinae slightly s-shaped. Frontoclypeal suture semicircular, median part reaching at least lower margin of antennal scape; postclypeus and anteclypeus with well developed median carina.

*Thorax.* Pronotum with sinuate carinae; hind margin obtusely angled. Forewing less than 3× longer than wide; costa with 20–21 tubercles; fork of Sc+R basad of fork of CuA1+CuA2; position of icu at CuP distad of apex of clavus; 11 or 13 apical cells. Hind leg: tibia with 1–2 small lateral spines (without large lateral spines); six apical teeth in a row interrupted by a wide gap; 1st tarsomere with 10(–12) apical teeth and 4–6 platellae.

*Male genitalia.* Anal tube as in Fig. 97C, D; ventro-median process of pygofer and genital styles as in Fig. 97E, F. Aedeagus (Fig. 97A, B): phallosome with a very long, curved spine (a) arising ventrolaterally near apex and a shorter slightly curved spine (b) with broad base, arising ventrally above midlength; flagellum unarmed.

*Remarks*

The male genitalia of this species looks very similar to that of *S. ecarinata* from which this species can be distinguished by the presence of a well developed median carina on post- and anteclypeus and by shorter forewing.

*Etymology*

This species shows a well developed median carina on the clypeus.

***Schuerrera merula*** (Distant), comb. nov.

(Figs 40D–F, 98)

*Cixius merula* Distant, 1907: 284.

*Material examined*

*Syntypes.* Australia: Qld: 4♀, Peak Downs (BMNH).

*Other material examined.* **Australia:** Qld: 1♂, 50 km along Dalby-Moonie road, 21.xi.1985, sweeping (QDPI); 1♂, 2♀, same data (QDPI).

*Description**Colour*

Head dark brown, median carinae orange brown, lateral carinae yellow (except dark brown on postclypeus); pronotum dark brown, carinae and hind border of yellow; mesonotum dark brown to black; legs straw coloured to brown; forewing hyaline white with a few brown marks along crossveins and apical veins, the latter white to pale yellow, tubercles mid brown; abdominal sternites dark brown, intersegmental membranes yellow.

*Morphology*

*Body length.* ♂ 4.0–4.2 mm; ♀ 4.8–4.9 mm.

*Head.* Apex of vertex broadly truncate or pointed; median carina incomplete, 1/2–3/4 as long as vertex; lateral carinae slightly to moderately elevated. Frons with its maximum width distinctly ventrad of centre of frontoclypeal suture; lateral carinae slightly convex (although rectilinear apically). Frontoclypeal suture semicircular, median part not reaching lower margin of antennal scape; post- and anteclypeus lacking median carina.

*Thorax.* Pronotum with arched carinae; hind margin rectangular. Forewing 3.5–4.0× longer than wide; costa with 15–18 tubercles; fork of Sc+R distad of or at same level as fork of CuA1+CuA2; position of icu at CuP distad of or at same level as apex of clavus; nine (rarely 10) apical cells. Hind leg: tibia with 2–3 small lateral spines (without large lateral spines); six apical teeth in row interrupted by a narrow gap; 1st tarsomere with 10 apical teeth and four platellae.

*Male genitalia.* Anal tube as in Fig. 98B, C; ventro-median process of pygofer and genital styles as in Fig. 98D, E. Aedeagus (Fig. 98A): phallosome with a long, moderately curved spine (a) arising ventrolaterally near apex, a strongly curved spine (b) and a moderately curved spine (c), both arising ventrolaterally above midlength; flagellum unarmed.

*Remarks*

The type series consists of two groups mounted on card. One group comprises four female syntypes (examined) and the other card has evidence of two specimens, both of which are now missing (M. Webb, personal communication). No lectotype has been designated because of the absence of male specimens.

*Etymology*

Named after the three spines on the phallosome.



Genus *Wernindia* Löcker & Fletcher, gen. nov.

Type species *Wernindia rhomboidea* Löcker & Fletcher, sp. nov.

*Description*

*Morphology*

*Body length.* ♂ 3.6–4.4 mm, ♀ 3.9–4.6 mm.

*Head.* Tip of head obtusely angled in lateral view. Apex of vertex broadly truncate; caudal border v- or u-shaped. Frons 1.1–1.5× longer than wide. Frontoclypeal suture slightly semicircular, median part not reaching lower margin of antennal scape.

*Thorax.* Forewing with Sc+R+M forming common stem; nine apical cells. Hind tibia with six apical teeth in row; 2nd tarsomere with nine apical teeth and seven platellae.

*Distribution*

NSW, Qld, Vic.

*Remarks*

Most of the analyses performed show a monophyletic group including all three species of *Wernindia*. Some analyses, such as the modified scaled weighting of dataset *A* and the

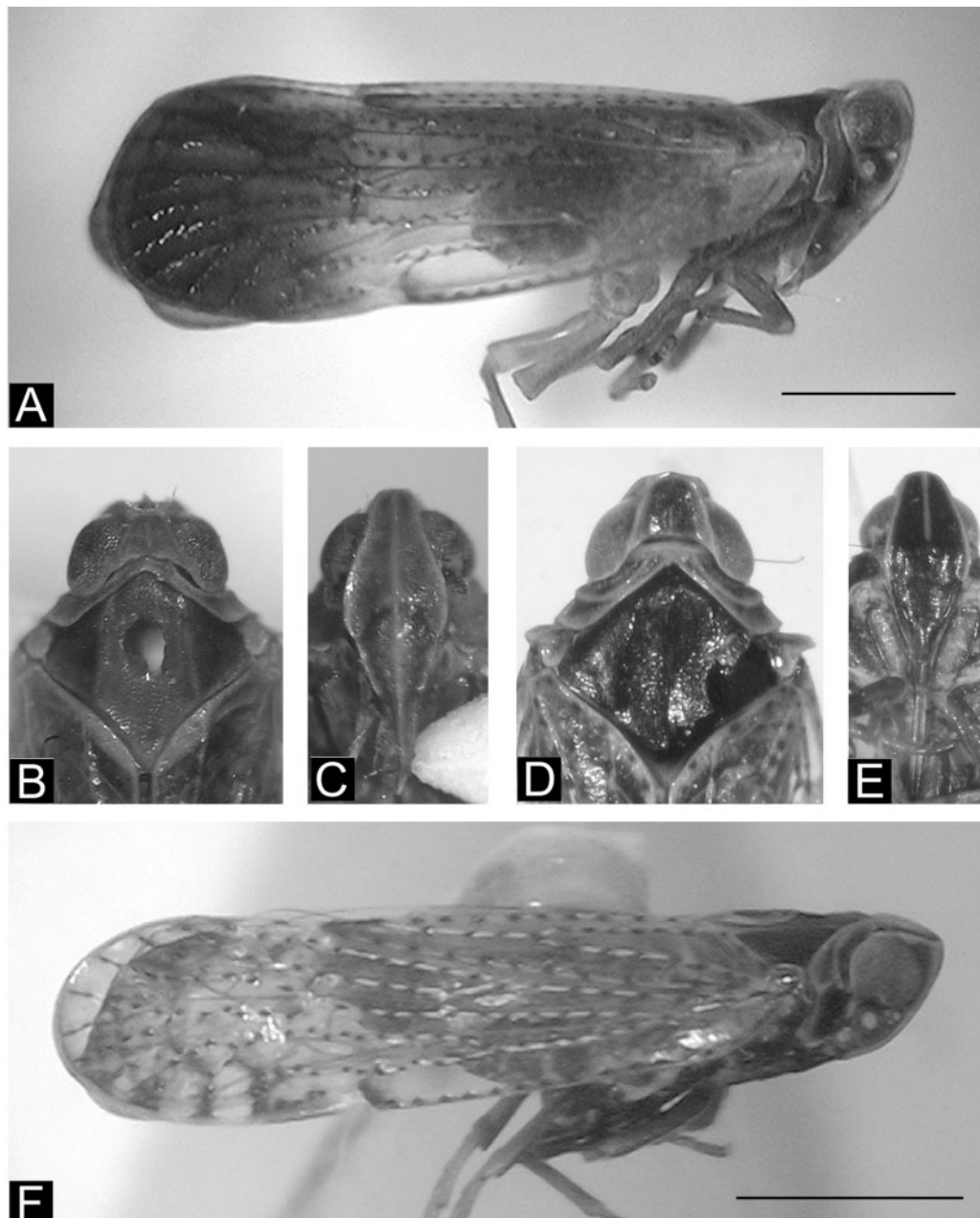


Fig. 40. *Schuerrera clypeocarinata*: A, habitus; B, C, head. *Schuerrera merula*: D, E, head; F, habitus.

successive approximations weighting of dataset *B*, place *W. lorda*, sp. nov. apart from the others. This is due to differences in characters such as the angle of the hind border of pronotum, the position of the icu at CuP and the shape of the frontoclypeal suture.

However, *W. lorda*, sp. nov. and *W. rhomboidea*, sp. nov. share the same chaetotaxy on the hind tarsomeres and the same shape of genital styles in ventral and lateral view (Figs 99D, E; 101E, F).

In general there is a lot of variation in character states, such as presence or absence of platellae on the 1st tarsomere, within this genus. *Wernindia bubalis*, sp. nov. differs considerably from *W. lorda*, sp. nov. and *W. rhomboidea*, sp. nov. in the shape of the genital styles in ventral view and in the chaetotaxy of the 1st hind tarsomere (five platellae in *W. bubalis*, sp. nov., no platellae in *W. lorda*, sp. nov. and *W. rhomboidea*, sp. nov.), but based on characters such as the obtusely angled tip of head in lateral view (Figs 41F; 42A, F), the slightly semicircular frontoclypeal suture (median part not reaching to the level of antennal scapes), the chaetotaxy of the second tarsomere (nine apical teeth, seven platellae) and similarities in the lateral view of the genital styles (Figs 99–100D, 101E), all three species are preliminarily put into one genus, additional information is needed to verify this placement.

#### Etymology

Derived from the names of the authors' friends and colleagues Ingrid and Werner Holzinger. Gender: feminine.

#### Key to species of *Wernindia*

- 1st hind tarsomere with five platellae; genital styles as in Fig. 100D, E . . . . . *W. bubalis*, sp. nov.  
First hind tarsomere lacking platellae; genital styles as in Figs 99D, E; 101E, F . . . . . 2
- Face in lateral view in two planes meeting at postclypeus (Fig. 42A); frons long and narrow (Fig. 42C); median carina on frons absent; aedeagus with one long spine on each side (right and left lateral) of the phallosome (Fig. 101A, B) . . . . . *W. lorda*, sp. nov.  
Face in lateral view more or less evenly convex (Fig. 41A); frons distinctly widening at the level of the frontoclypeal suture; median carina on frons present, but incomplete (only 1/4–1/3 as long as frons); aedeagus with one long spine (*a*) left lateral and a short spine (*c*) arising ventrally (Fig. 99A) . . . . . *W. rhomboidea*, sp. nov.

*Wernindia rhomboidea* Löcker & Fletcher, sp. nov.

(Figs 41A–C, 99)

#### Material examined

*Holotype*. ♂, Australia: Qld: Lake Broadwater, nr. Dadly, site A, 27°21'S 151°06'E, 1.v.1987 (G. and A. Daniels) (QM T123588, originally from UQIC).

#### Description

##### Colour

Vertex mid brown except for whitish mark on each side, lateral carinae yellow to brown; face and lateral carinae of postclypeus mid brown, other carinae yellow; pronotum mostly yellow with some brown; mesonotum dark brown with light brown carinae; legs yellow to brown; forewing hyaline white with numerous brown marks, veins whitish yellow, tubercles dark brown; abdominal sternites mid brown, intersegmental membranes yellowish orange.

##### Morphology

*Body length*. ♂ 4.4 mm.

*Head*. Vertex 0.8× as long as wide, produced before eyes by less than 1/4 of an eye length; lateral carinae strongly elevated; median carina incomplete, less than 1/4 as long as vertex. Frons distinctly widening at the level of the frontoclypeal suture (maximum width around centre of frontoclypeal suture); lateral carinae slightly sinuate, slightly elevated; median carina incomplete, 1/4–1/3 as long as frons. Postclypeus with well developed lateral carinae and evanescent median carina; anteclypeus with evanescent median carina.

*Thorax*. Pronotum with sinuate carinae; hind margin obtusely angled. Forewing more than 4× longer than wide; costa with 12–15 tubercles; concavity at costal border present; Sc+R+M forming a short common stem; fork of Sc+R basad of fork of CuA1+CuA2; r-m1 distad of fork MA–MP; position of icu at CuP at same level as apex of clavus; nine apical cells. Hind leg: tibia with one small lateral spine (without large lateral spines); six apical teeth in a row interrupted by a very narrow gap; 1st tarsomere with 8–9 apical teeth and no platellae.

*Male genitalia*. Anal tube as in Fig. 99B, C; ventro-median process of pygofer and genital styles as in Fig. 99D, E. Aedeagus (Fig. 99A): phallosome with a long rather thick, strongly curved, apically sinuate spine (*a*) arising left lateral near apex and a rather thick, short, slightly curved spine (*c*) ventrally about midlength; flagellum unarmed.

#### Etymology

Named after the face, that is the shape of a rhombus.

*Wernindia bubalis* Löcker & Fletcher, sp. nov.

(Figs 41D–F, 100)

#### Material examined

*Holotype*. ♂, Australia: Qld: Cunnamulla, x.1933 (N. Geary) (AM).

*Paratypes*. **Australia: Qld:** 1♂, same data as holotype (AM K113776). **NSW:** 1♂, Lightning Ridge, 14.x.1989 (R. O. Buddle) (AM).

*Description**Colour*

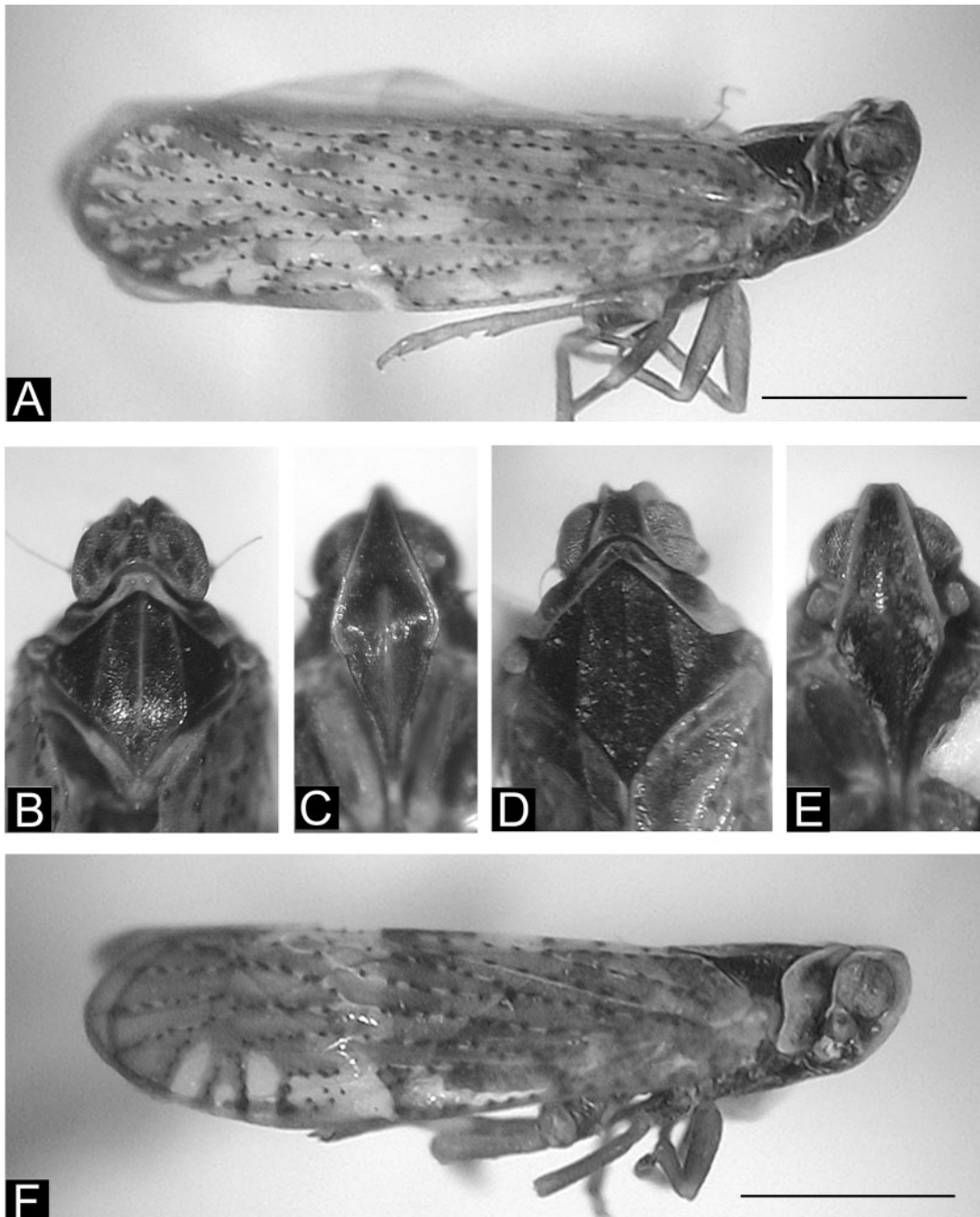
Vertex mid brown, lateral carinae yellow; face mid brown, median carina paler, lateral carinae on frons yellow; pronotum mid to dark brown, carinae yellow to brown, hind border of pronotum as well as lateral parts behind carinae yellow; mesonotum dark brownish black; legs straw coloured to brown; forewing hyaline white with scattered brown marks, a brown transverse band basad of pterostigma,

and a large brown area apically, veins white to brown, tubercles dark brown; abdominal sternites mid brown, intersegmental membranes yellow.

*Morphology*

*Body length.* ♂ 3.7–4.1 mm.

*Head.* Vertex 0.7–0.8× as long as wide, produced before eyes by 1/4–1/2 of an eye length; lateral carinae slightly to moderately elevated; median carina incomplete,



**Fig. 41.** *Wernindia rhomboidea*: A, habitus; B, C, head. *Wernindia bubalis*: D, E, head; F, habitus.

~1/2 as long as vertex. Frons with its maximum width distinctly ventrad of centre of frontoclypeal suture; lateral carinae convex (although rectilinear apically), slightly to moderately elevated; median carina absent. Postclypeus lacking lateral carinae, median carina evanescent; anteclypeus lacking carinae.

*Thorax.* Pronotum with sinuate carinae; hind margin right or obtusely angled. Forewing 3.0–3.5× longer than wide; costa with 14–17 tubercles; concavity at costal border present; Sc+R+M forming long common stem; fork of Sc+R

basad, at same level or distad of fork of CuA1+CuA2; r-m1 distad of or at same level as fork MA–MP; position of icu at CuP basad of or at same level as apex of clavus; nine (rarely 10) apical cells. Hind leg: tibia with 2–3 small lateral spines (without large lateral spines); six apical teeth in a row interrupted by a narrow gap; 1st tarsomere with nine apical teeth and five platellae.

*Male genitalia.* Anal tube as in Fig. 100B, C; ventro-median process of pygofer and genital styles as in Fig. 100D, E. Aedeagus (Fig. 100A): phallosheca with a long, strongly

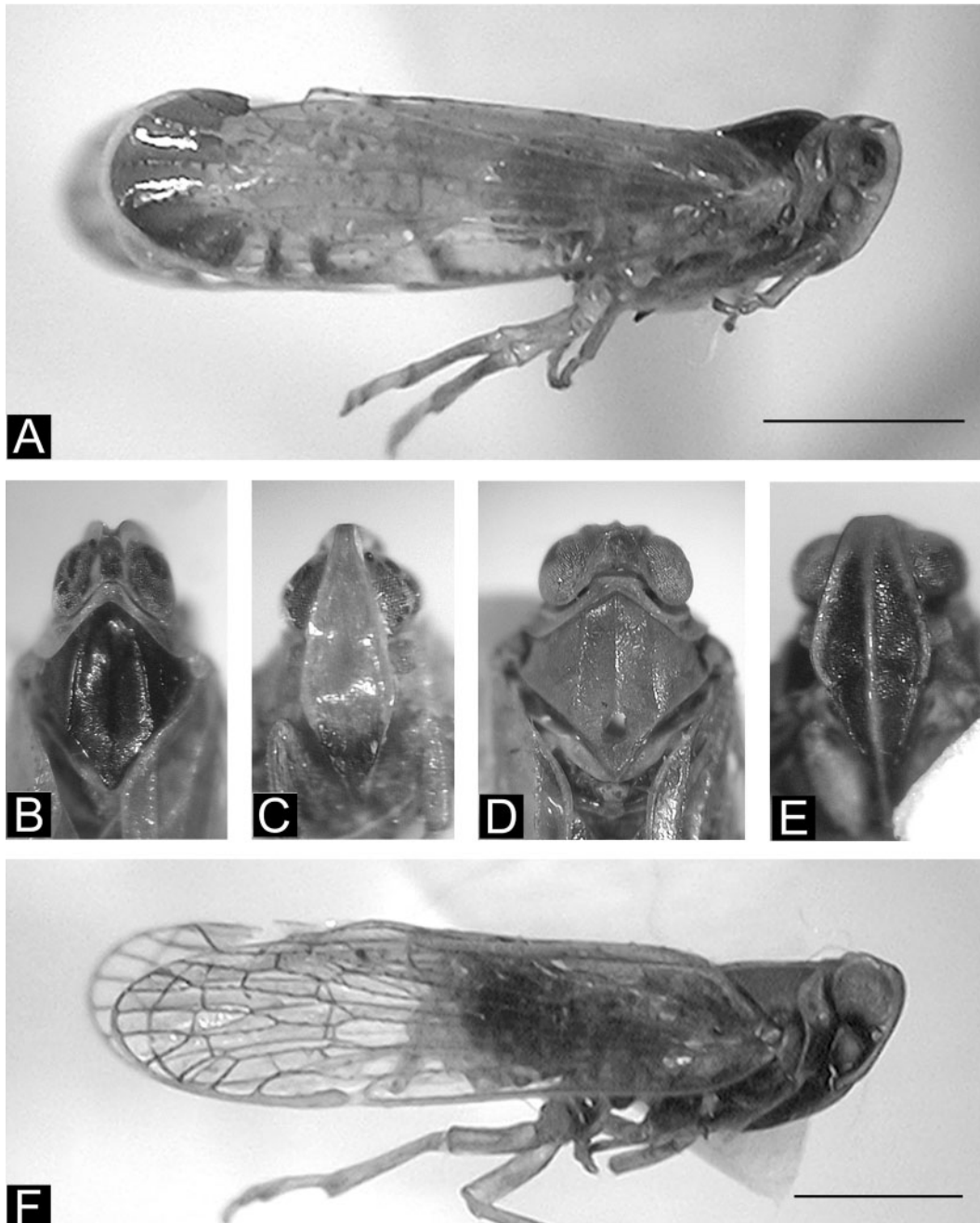
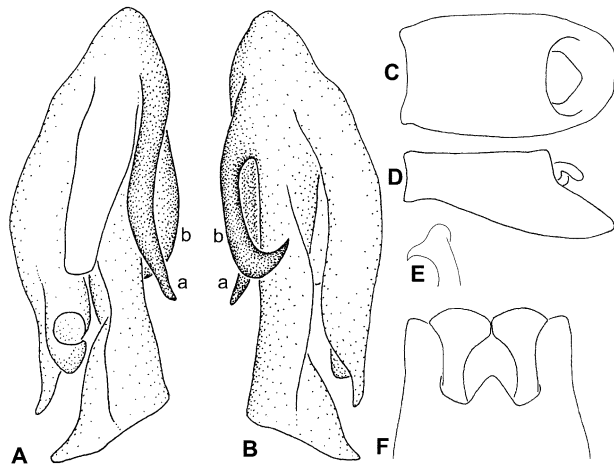


Fig. 42. *Wernindia lorda*: A, habitus; B, C, head. *Yarnikada ulliae*: D, E, head; F, habitus.



**Fig. 43.** *Dysoliarus unicornis*: A, aedeagus left lateral; B, aedeagus right lateral; C, D, anal tube; E, F, genital styles.

curved, upwardly pointing spine (*a*) arising ventrolaterally above midlength and a shorter slightly curved spine (*c*) arising ventrolaterally about midlength; flagellum unarmed.

#### Etymology

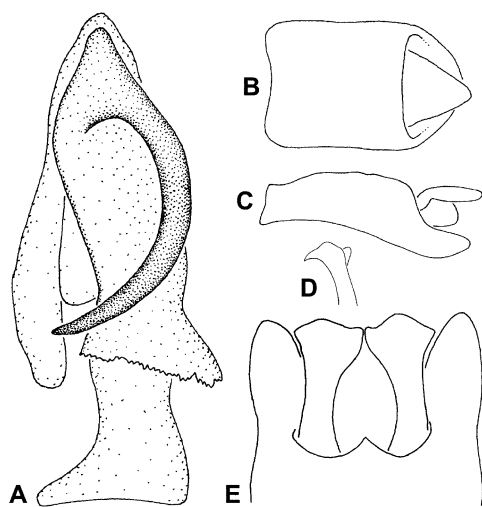
Named after one spine of the phallosome that is shaped like the horns of a water buffalo (*Bubalus bubalis*)

#### *Wernindia lorda* Löcker & Fletcher, sp. nov.

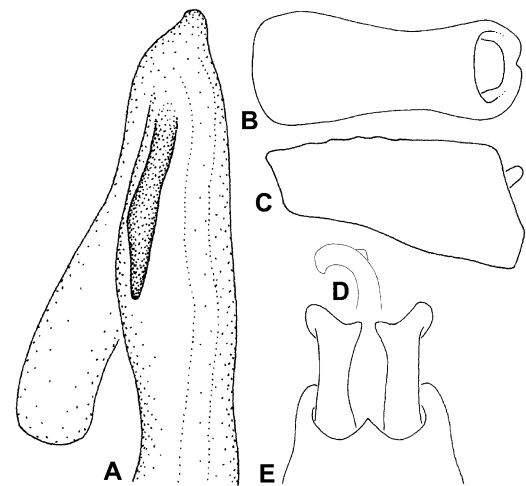
(Figs 42A–C, 101)

#### Material examined

**Holotype.** ♂, Australia: NSW: Blue Mtns NP, Pisgah Ridge, nr Glenbrook, 33°50'S 150°33'E, 210 m, ex malaise trap, 5.ii–25.iii.1988 (G. R. Brown) (ASCU ASCTHE009112).

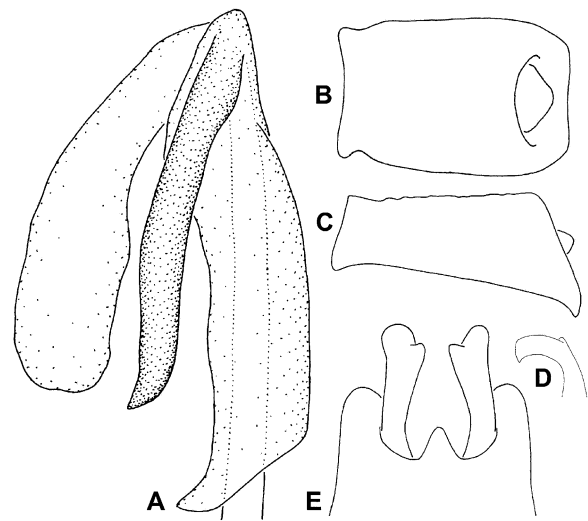


**Fig. 44.** *Orphninus mouldsi*: A, aedeagus left lateral; B, C, anal tube; D, E, genital styles.

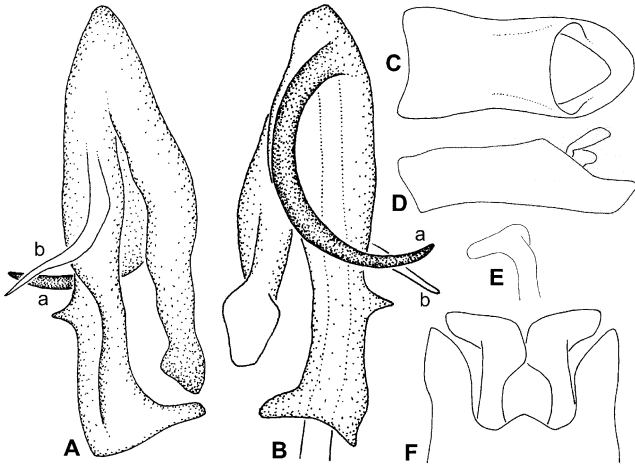


**Fig. 45.** *Rhigedanus fomibundus*: A, aedeagus left lateral; B, C, anal tube; D, E, genital styles.

**Paratypes.** **Australia:** **NSW:** 3♂, 2♀, same data as holotype (ASCU); 3♂, 1♀, same locality as holotype, 25.iii–10.v.1988 (G. R. Brown & S. G. Hunter) (ASCU); 4♂, Blue Mts, King's Tableland, nr Wentworth Fall[s], 19.ii.1997 (L. B. O'Brien) (LOB); 2♂, 3♀, New England NP, Wrights Lookout, 5000 ft, iii.1966 (J. W. Evans) (ASCU); 1♂, New England NP, 4500 ft, iii.1966 (ASCU); 1♂, Katoomba, 4.v.1966 (J. W. & F. E[vans]) (ASCU); 1♂ no other data (MAMU); 1♂, 20 km S Grafton, 19.iii.1981 (B. J. Loudon) (ASCU); 1♂ 1♀, Hornsby, 18.iv.1964 (M. I. Nikitin) (BMNH); 1♀, Broughton's Pass, 17.v.1954 (M. I. Nikitin) (AM); 1♀, 35 km W–SW of Coramba, 26.vi.1976 (Z. Liepa) (ANIC); 1♀, Mt Kosciusko, Wilsons Valley (J. W. & F. Evans) (ASCU); 1♀, Dharug Nat. Pk, 19.v.1985 (G. R. Brown & H. M. Holmes) (ASCU). **Qld:** 3♂, 2♀, Illaweena St, Drewvale, 27°38.6'S 153°03.8'E, 40 m, scribbly gum/heath, sweeping, 51185, 29.iv.2003 (E. Volschenk) (QM); 2♂, Illaweena St, Drewvale, 27°38.6'S 153°03.8'E, 40 m, scribbly gum/heath, sweeping, 51843, 17.ii.2004 (QM Party) (QM); 3♂, Illaweena St, Drewvale, 27°38.6'S



**Fig. 46.** *Rhigedanus maculipennis*: A, aedeagus left lateral; B, C, anal tube; D, E, genital styles.



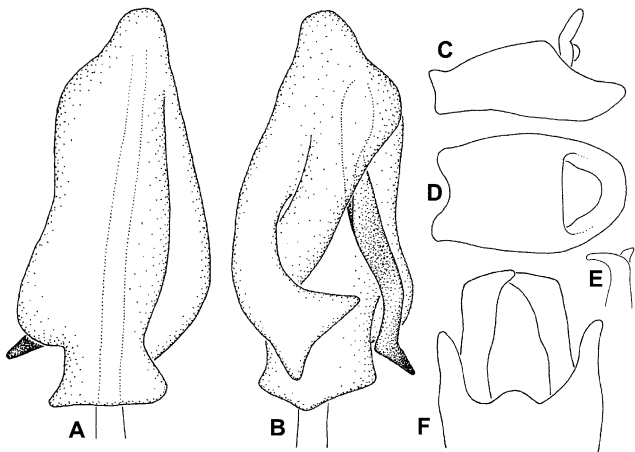
**Fig. 47.** *Aubirestus semicirculatus*: A, aedeagus right lateral; B, aedeagus left lateral; C, D, anal tube; E, F, genital styles.

153°03.8'E, 40 m, scribbly gum/heath, pyrethrum, 51183, 17.iv.2003 (C. J. Burwell) (QM); 4 ♀, Gold Ck Reservoir, site 1, 27°27.9'S 152°52.5'E, 140 m, sweeping spotted gum open forest, 29.iv.2003 (E. Volschenk), 51150; 1 ♂, Binna Burra, Lamington NP, 30.v.1966 (Z. Liepa) (ANIC); 1 ♂, 1 ♀, Bulimba Ck, Carindale, 27°30.2'S 153°06.6'E, 15 m, forest red gum woodland, sweeping, 51193, 22.iv.2003 (E. Volschenk) (QM); 1 ♂, Ransome Reserve, 27°29.6'S 153°11.1'E, 10 m, sweeping *Casuarina* woodland, 51155, 23.iv.2003 (E. Volschenk) (QM); 1 ♀, 5 km E Elimbah, SE Qld, 22.ii.1978 (J. F. Donaldson) (QDPI); 1 ♀, Cooloola Forestry Area, E Gympie, open forest, iv.1978 (I. D. Galloway) (QDPI); 1 ♀, SE Qld, Cooloola Nat. Pk via Camp Milo, sweeping dry sclerophyll, 6.iii.1984 (I. D. Galloway) (QDPI). **Vic:** 6 ♀, Ready Creek, 5 km E of Cann River, 1.vi.1989 (G. Cassis) (AM).

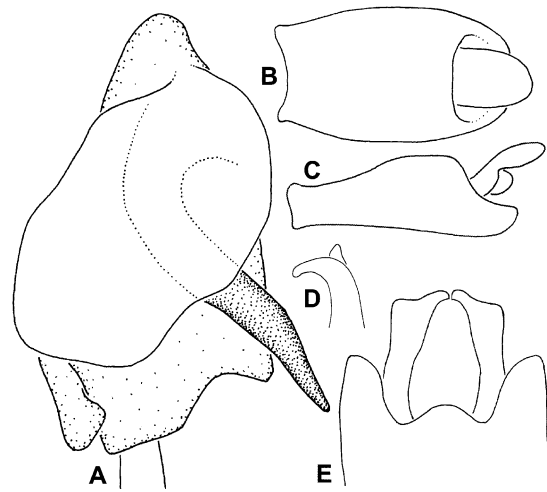
**Description**

**Colour**

Vertex mid brown, yellow stripe between lateral carinae and caudal border; frons light to mid brown; clypeus dark brown except for mid brown area close to frontoclypeal



**Fig. 48.** *Balyadimetopia frederi*: A, aedeagus right lateral; B, aedeagus left lateral; C, D, anal tube; E, F, genital styles.



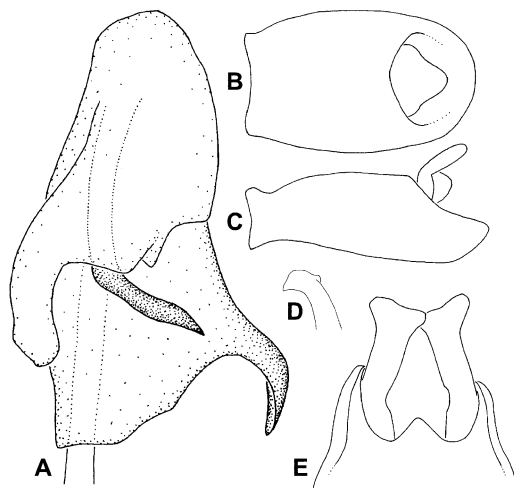
**Fig. 49.** *Balyadimetopia krahalla*: A, aedeagus left lateral; B, C, anal tube; D, E, genital styles.

suture, median carina mid brown; pronotum yellow; mesonotum black; legs light to mid brown; forewing hyaline white, with large yellow areas, some dark brown marks apically on veins, sometimes apex of wings fumous, brown stripe starting basad of pterostigma running at most half way towards apex of clavus, veins concolorous with cells, tubercles dark brown; abdominal sternites dark brown, intersegmental membranes yellow.

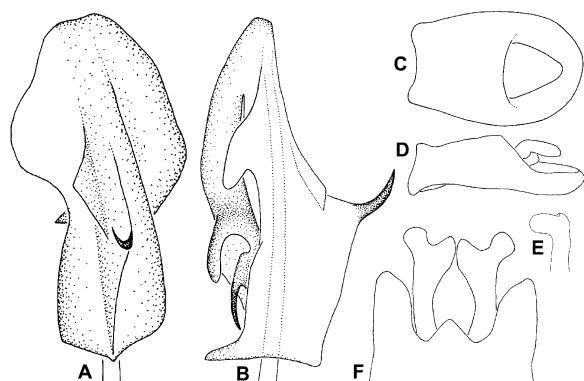
**Morphology**

**Body length.** ♂ 3.6–4.1 mm; ♀ 3.9–4.6 mm.

**Head.** Vertex 0.9–1.6× as long as wide, produced before eyes by 1/2–3/4 of an eye length; lateral carinae strongly elevated; median carina incomplete, less than 1/4 as long as vertex. Face distinctly bent caudally at level of post-clypeus. Frons long and narrow, with its maximum width



**Fig. 50.** *Balyadimetopia marci*: A, aedeagus left lateral; B, C, anal tube; D, E, genital styles.

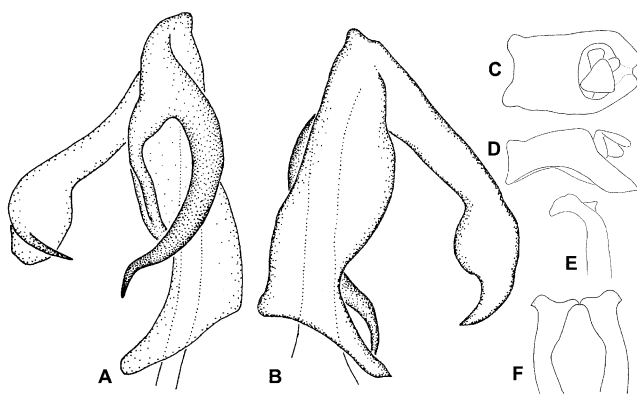


**Fig. 51.** *Barbonia spectabilis*: A, aedeagus ventral; B, aedeagus left lateral; C, D, anal tube; E, F, genital styles.

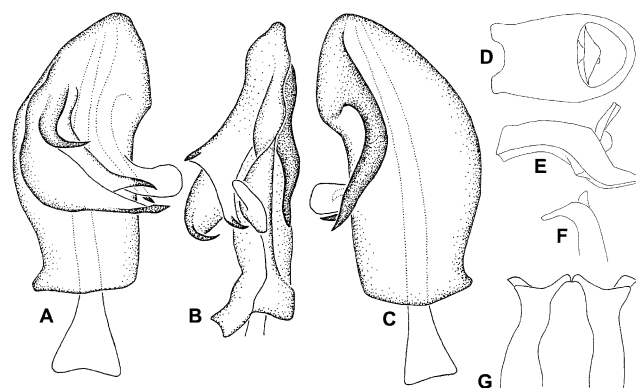
around centre of frontoclypeal suture; lateral carinae convex (although rectilinear apically), slightly elevated; median carina absent. Postclypeus with well developed lateral carinae and median carina; anteclypeus with well developed median carina.

**Thorax.** Pronotum with arched or sinuate carinae; hind margin right or acutely angled. Forewing 3.0–3.5× longer than wide; costa with 19–20 tubercles; concavity at costal border absent or present; Sc+R+M forming short common stem; fork of Sc+R basad of fork of CuA1+CuA2; r-m1 basad, distad of or at same level as fork MA–MP; position of icu at CuP distad of or at same level as apex of clavus; nine (rarely eight) apical cells. Hind leg: tibia with 0–4 small lateral spines (without large lateral spines); six apical teeth in a row interrupted by a small or wide gap; 1st tarsomere with (8–)9 apical teeth and no platellae.

**Male genitalia.** Anal tube as in Fig. 101C, D; ventro-median process of pygofer and genital styles as in Fig. 101E, F. Aedeagus (Fig. 101A, B): phallosome with a long strongly curved spine (a) arising left laterally above midlength and a long strongly curved spine (b) arising right laterally near apex; flagellum unarmed.



**Fig. 52.** *Candicarina pulchra*: A, aedeagus left lateral; B, aedeagus right lateral; C, D, anal tube; E, F, genital styles.



**Fig. 53.** *Candicarina geroldi*: A, aedeagus dorsal; B, aedeagus left lateral; C, aedeagus ventral; D, E, anal tube; F, G, genital styles.

#### Remarks

Some specimens in the material examined are paler or darker than described. The extreme curvature of the clypeus (postclypeus in lateral view strongly convex over a very short distance), that results in the anteclypeus and the lower half of postclypeus being at least parallel to the pronotum, is diagnostic.

#### Etymology

‘Lordos’ is the Greek term for ‘bent backward’. Named after the extreme curvature of the clypeus in lateral view.

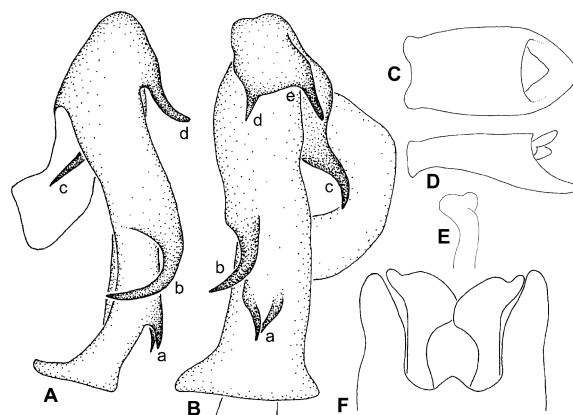
#### Genus *Yarnikada* Löcker & Fletcher, gen. nov.

Type species *Yarnikada ulliae* Löcker & Fletcher, sp. nov.

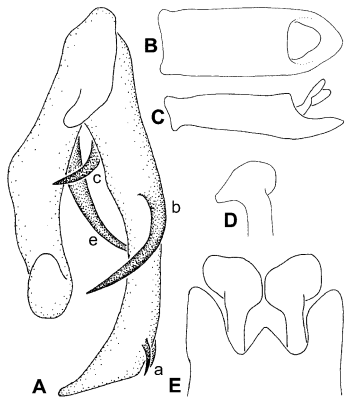
#### Description

##### Morphology

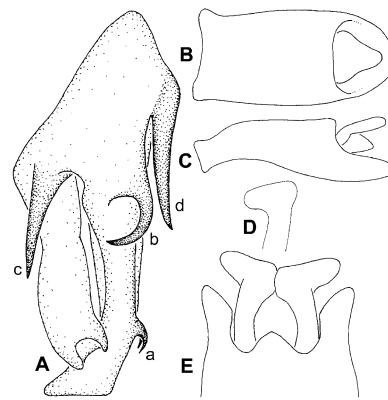
**Head.** Vertex 0.6× as long as wide; produced before eyes by less than 1/4 of an eye length; apex broadly pointed;



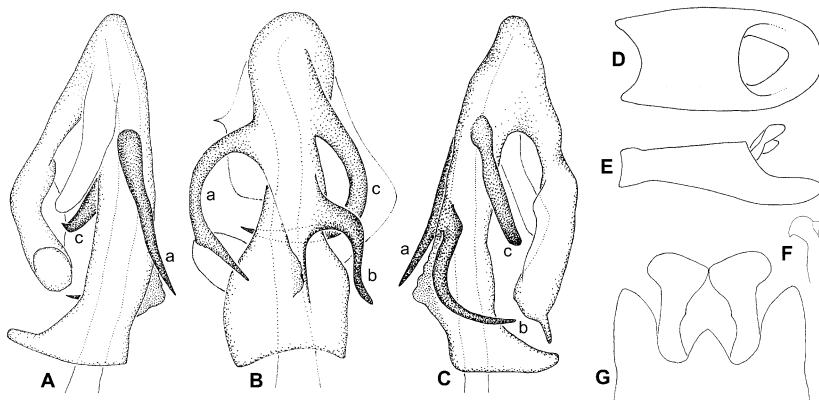
**Fig. 54.** *Carolus crispus*: A, aedeagus left lateral; B, aedeagus ventral; C, D, anal tube; E, F, genital styles.



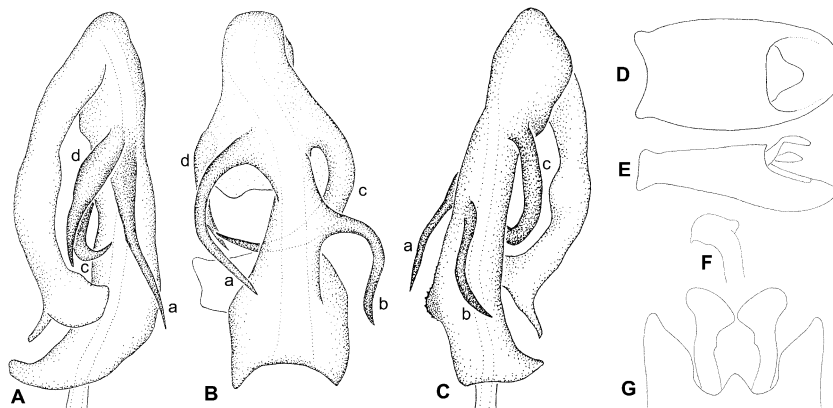
**Fig. 55.** *Carolus carinatus*: A, aedeagus left lateral; B, C, anal tube; D, E, genital styles.



**Fig. 56.** *Carolus stiriae*: A, aedeagus left lateral; B, C, anal tube; D, E, genital styles.

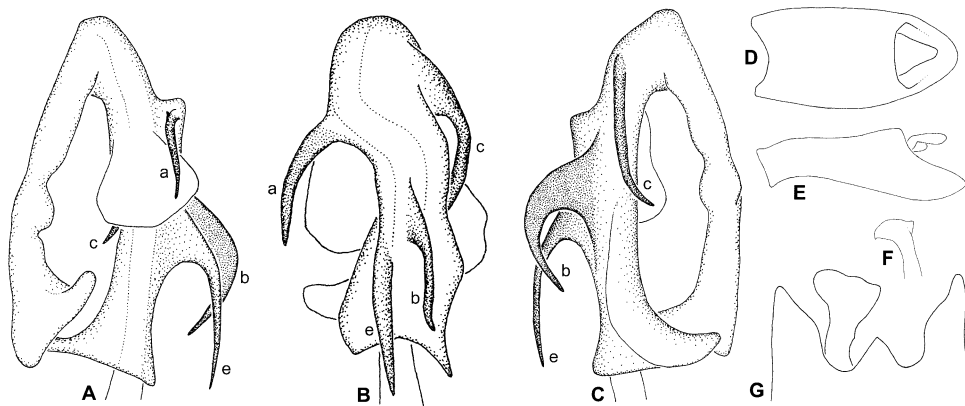


**Fig. 57.** *Corylonga loisae*: A, aedeagus, (a) aedeagus left lateral; B, aedeagus ventral; C, aedeagus right lateral; D, E, anal tube; F, G, genital styles.

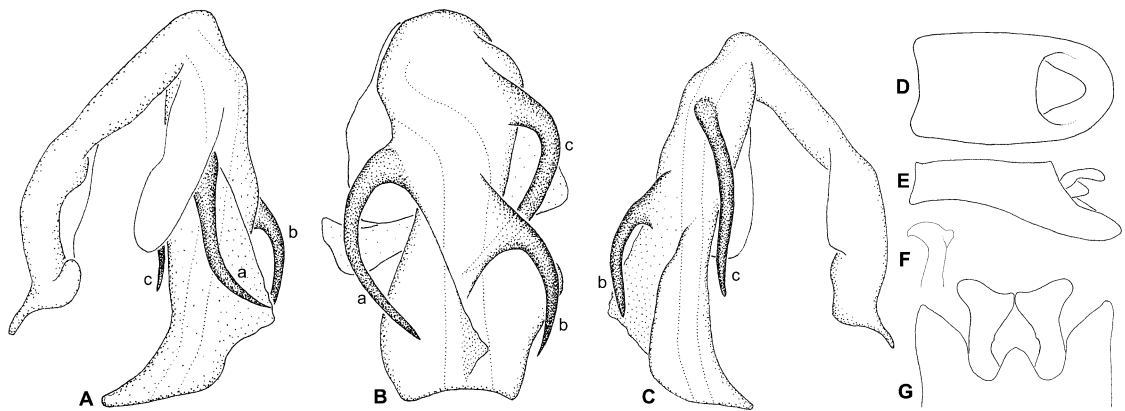


**Fig. 58.** *Corylonga aaroni*: A, aedeagus left lateral; B, aedeagus ventral; C, aedeagus right lateral; D, E, anal tube; F, G, genital styles.

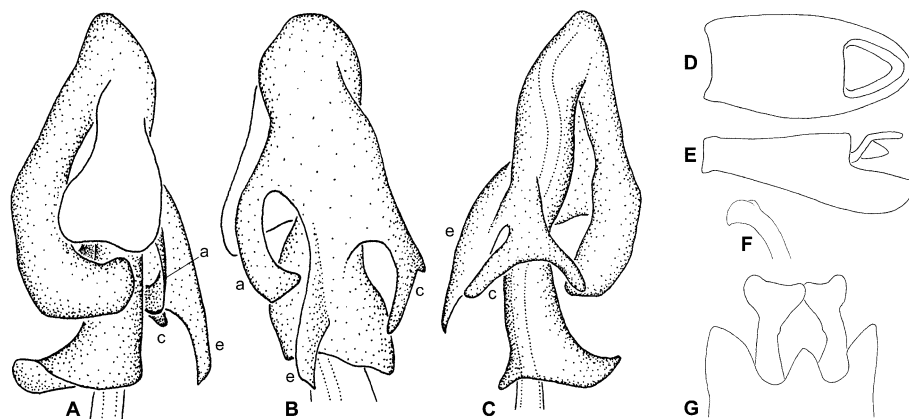




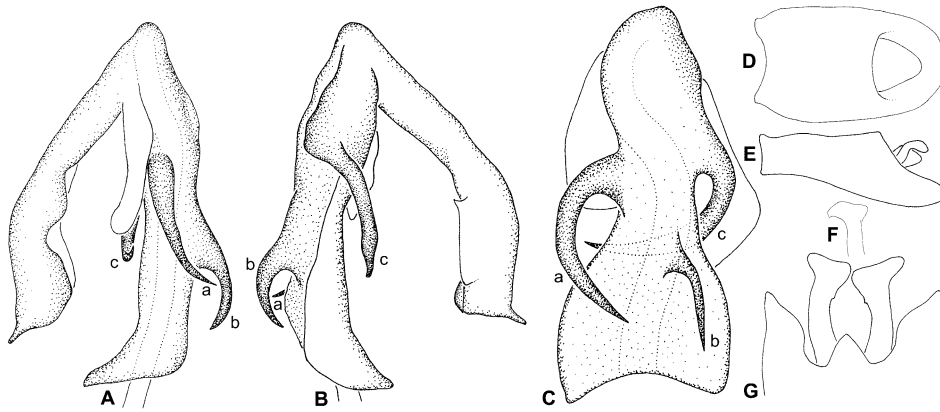
**Fig. 59.** *Corylonga krottendorfi*: A, aedeagus left lateral; B, aedeagus ventral; C, aedeagus right lateral; D, E, anal tube; F, G, genital styles.



**Fig. 60.** *Corylonga leighi*: A, aedeagus left lateral; B, aedeagus ventral; C, aedeagus right lateral; D, E, anal tube; F, G, genital styles.



**Fig. 61.** *Corylonga lobata*: A, aedeagus left lateral; B, aedeagus ventral; C, aedeagus right lateral; D, E, anal tube; F, G, genital styles.



**Fig. 62.** *Corylonga mahmudae*: A, aedeagus left lateral; B, aedeagus right lateral; C, aedeagus ventral; D, E, anal tube; F, G, genital styles.

caudal border broadly u-shaped; lateral carinae strongly elevated; median carina incomplete, 1/2–3/4 as long as vertex. Frons 1.1–1.5× longer than wide; maximum width distinctly dorsad of centre of frontoclypeal suture; lateral carinae convex (although rectilinear apically); slightly elevated, lateral margins foliaceous, concealing base of antennae; median carina complete. Frontoclypeal suture semicircular, median part not reaching lower margin of antennal scape; postclypeus with well developed lateral carinae and median carina; anteclypeus with well developed median carina.

**Thorax.** Pronotum with arched carinae; hind margin obtusely angled. Forewing 3.5–4.0× longer than wide; costa with ~8 tubercles; concavity at costal border present; no Sc+R+M stem, Sc+R forming common stem, M emerging separately from basal cell; fork of Sc+R basad of fork of CuA1+CuA2; r-m1 distad of fork MA–MP; position of icu at CuP distinctly distad of apex of clavus; 9–10 apical cells. Hind leg: tibia with three small lateral spines (without large lateral spines); six apical teeth in row interrupted by a wide gap; 1st tarsomere with seven apical teeth and no platellae; 2nd tarsomere with eight apical teeth and six platellae.

#### *Distribution*

Qld.

#### *Etymology*

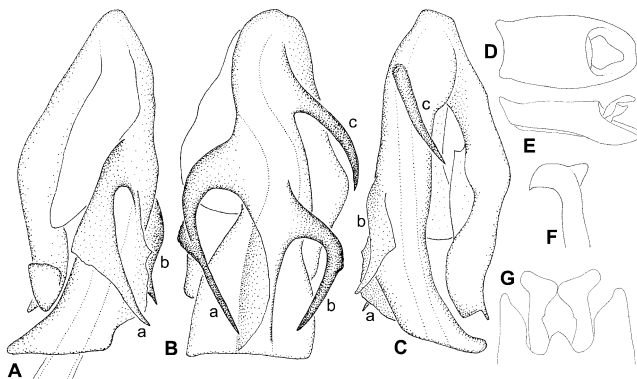
‘Yarni’ means ‘short’ in Paakantyi, a language spoken by Aboriginal people living along the Darling River (Thieberger and McGregor 1994). ‘Kada’ means ‘head’ in Nyungar, a language spoken by Aboriginal people living in Western Australia. The genus is named after the short vertex. Gender: feminine.

#### *Yarnikada ulliae* Löcker & Fletcher, sp. nov.

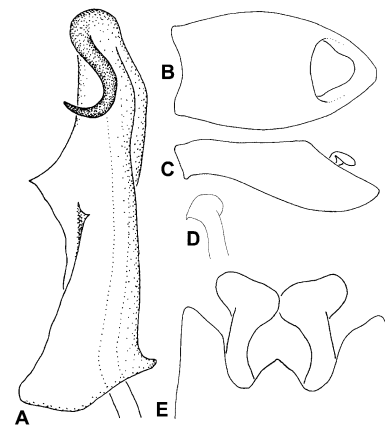
(Figs 42D–F, 102)

#### *Material examined*

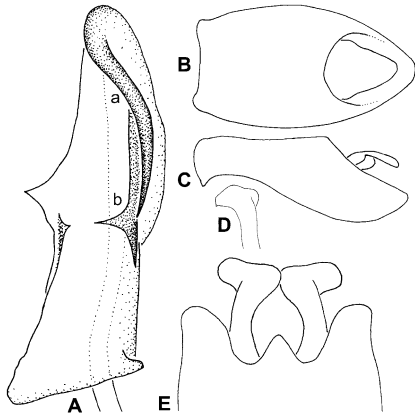
**Holotype.** ♂, Australia: Qld: 6 km N Taroom, 25°36′S 149°46′E, 200 m, 1.x.1991 (G. Daniels) (QM T123585, originally from UQIC).



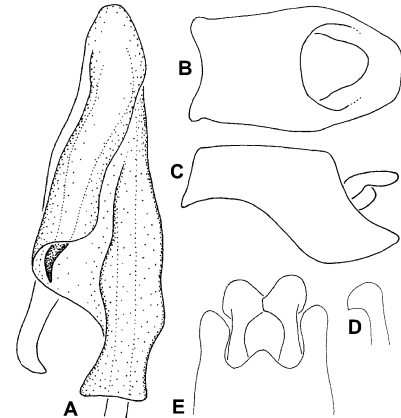
**Fig. 63.** *Corylonga triangula*: A, aedeagus left lateral; B, aedeagus ventral; C, aedeagus right lateral; D, E, anal tube; F, G, genital styles.



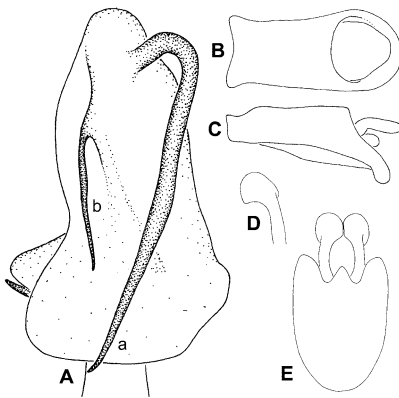
**Fig. 64.** *Fletcherolus monospinosus*: A, aedeagus right lateral; B, C, anal tube; D, E, genital styles.



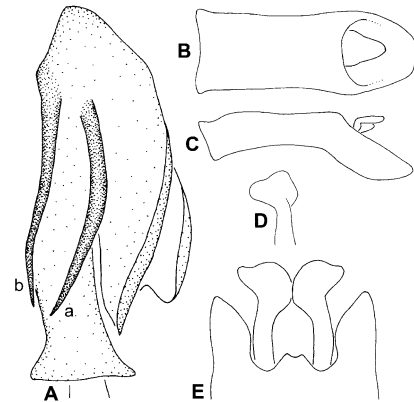
**Fig. 65.** *Fletcherolus lanceolatus*: A, aedeagus right lateral; B, C, anal tube; D, E, genital styles.



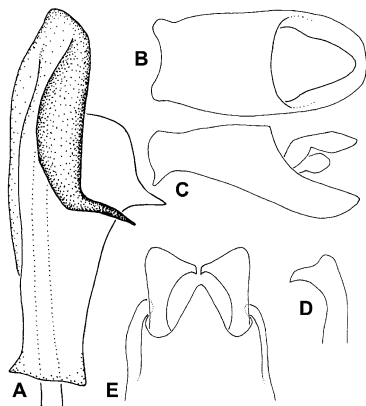
**Fig. 68.** *Gelastocephalus velifer*: A, aedeagus left lateral; B, C, anal tube; D, E, genital styles.



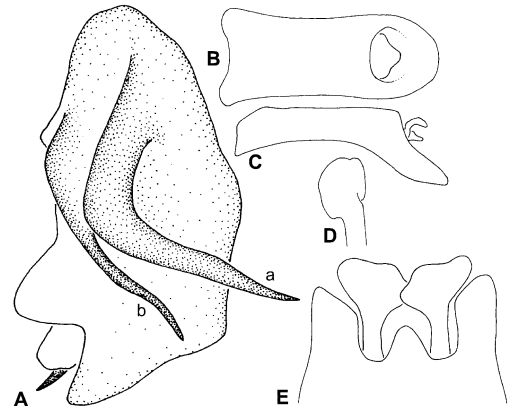
**Fig. 66.** *Gelastocaledonia monteithi*: A, aedeagus ventral; B, C, anal tube; D, E, genital styles.



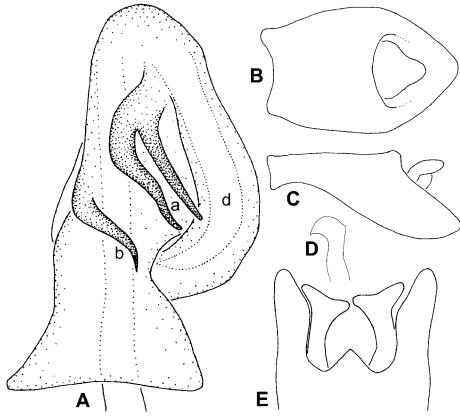
**Fig. 69.** *Gurrundus fuscomarginatus*: A, aedeagus right lateral; B, C, anal tube; D, E, genital styles.



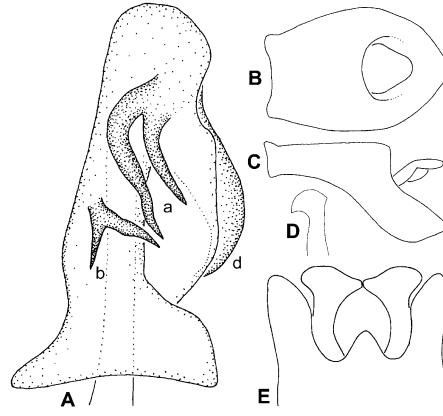
**Fig. 67.** *Gelastocephalus ornithoides*: A, aedeagus left lateral; B, C, anal tube; D, E, genital styles.



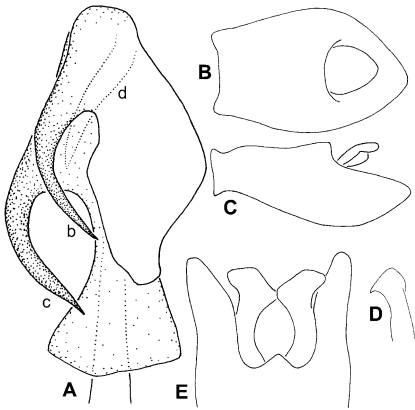
**Fig. 70.** *Gurrundus nectostylus*: A, aedeagus ventral; B, C, anal tube; D, E, genital styles.



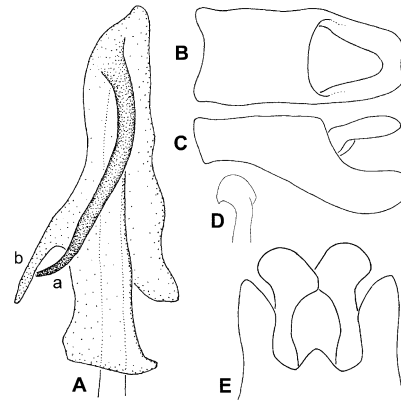
**Fig. 71.** *Guttala mona*: A, aedeagus ventral; B, C, anal tube; D, E, genital styles.



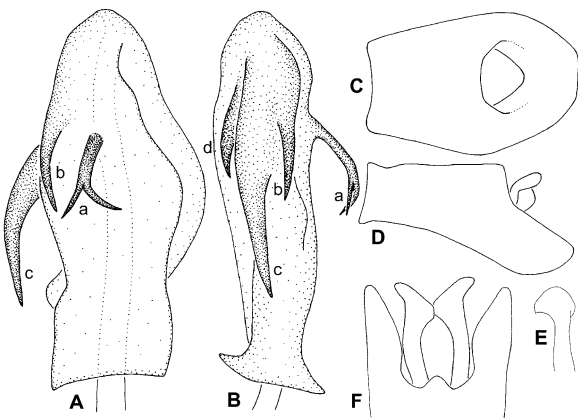
**Fig. 74.** *Guttala robierae*: A, aedeagus ventral; B, C, anal tube; D, E, genital styles.



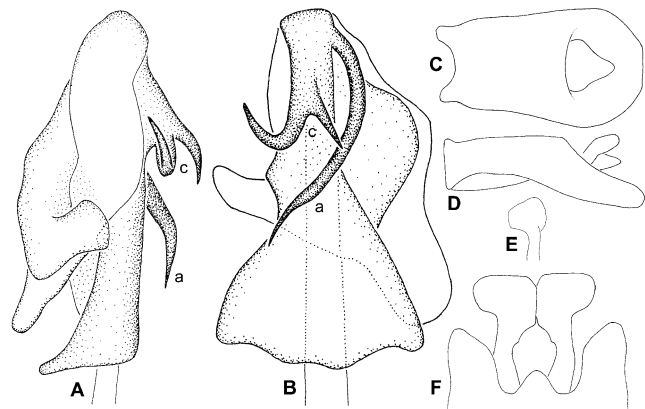
**Fig. 72.** *Guttala bernhardtae*: A, aedeagus ventral; B, C, anal tube; D, E, genital styles.



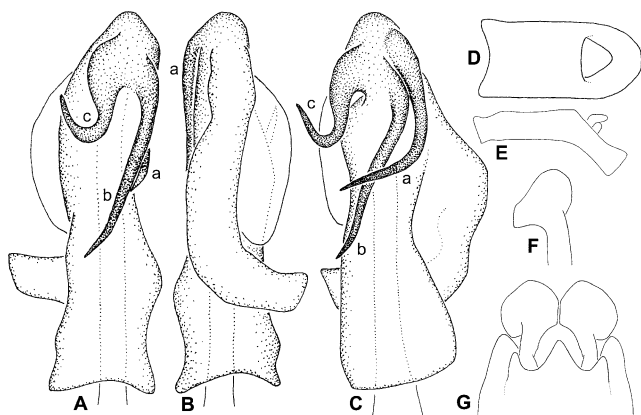
**Fig. 75.** *Hartliebia towinna*: A, aedeagus right lateral; B, C, anal tube; D, E, genital styles.



**Fig. 73.** *Guttala nickeli*: A, aedeagus ventral; B, aedeagus left lateral; C, D, anal tube; E, F, genital styles.



**Fig. 76.** *Holgus liafredis*: A, aedeagus left lateral; B, aedeagus ventral; C, D, anal tube; E, F, genital styles.



**Fig. 77.** *Holgus ancistrus*: A, aedeagus left lateral; B, aedeagus right lateral; C, aedeagus ventral; D, E, anal tube; F, G, genital styles.

### Description

#### Colour

Vertex yellow; face dark brown, carinae yellow except for dark brown lateral carinae on postclypeus; pronotum yellow; mesonotum yellow to orange; legs yellow; forewing hyaline grey, veins and tubercles yellow to light brown; abdominal sternites dark brown, intersegmental membranes yellow.

### Morphology

*Body length.* ♂ 4.7 mm.

*Male genitalia.* Anal tube as in Fig. 102B, C; ventro-medial process of pygofer and genital styles as in Fig. 102D, E. Aedeagus (Fig. 102A): phallosome with a single long, slightly curved spine left laterally near apex and a triangular ventral ridge; flagellum unarmed.

### Etymology

Named in honour of the first author's friend Ulli Fellner.

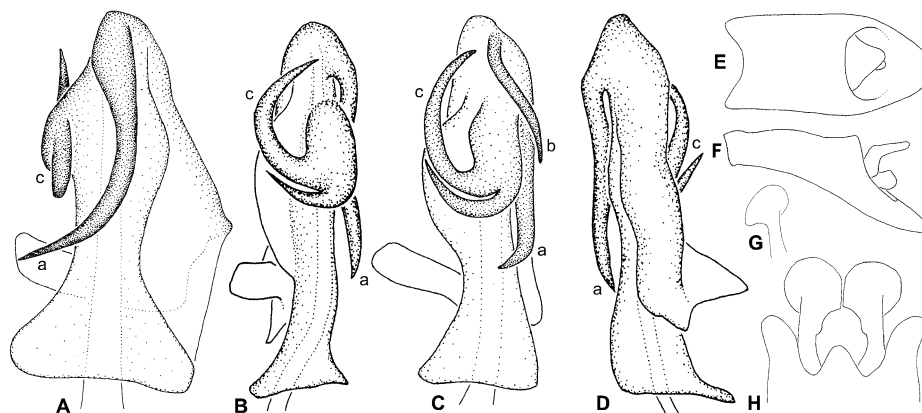
## Discussion

### *Homoplasy and reversals within the family Cixiidae*

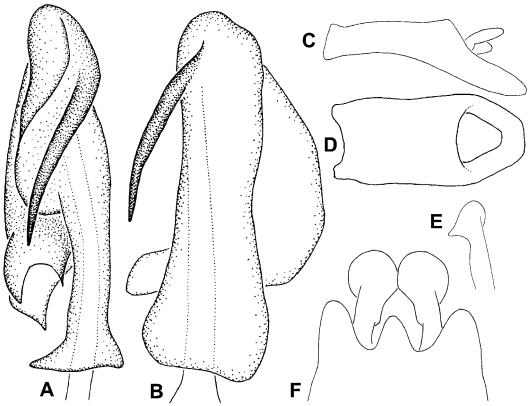
The phylogenetic hypothesis derived from our analysis reflected a high degree of homoplasy and reversals in the original data. This was further supported by the fact that changes in outgroups or elimination of characters had considerable impact on tree topology. Some characters that we first thought could be phylogenetically informative showed very low consistency indices in the analyses, e.g. characters 4, 7–9, 11–13, 18–19, 24, 29–30, 39, 44, 47, 48. Emeljanov (2002: 104), in his attempt to compile a preliminary phylogeny for the Cixiidae, also encountered high amounts of homoplasy. He stated, 'It is unclear which cixiids are the most basal ones, this situation exists because the majority of elementary characters are subjected to great homologous variability and, consequently, to reversals; on this reason they can not be interpreted as sound synapomorphies'. This comment applies particularly to the Gelastocephalini and some other groups, since Emeljanov (2002) was not able to place the Gelastocephalini, Bennarellini Emeljanov 1989 and Borystheninae Emeljanov 1989 on his preliminary cladogram of Cixiidae.

We have recognised ten genera that are monotypic. One possible explanation for the number of monotypic genera is that vast areas of Australia have not yet been comprehensively sampled. Therefore, numerous new species undoubtedly await discovery. The New Guinean fauna may also have additional species in these genera, but New Guinean material is poorly represented in the collections examined in this study.

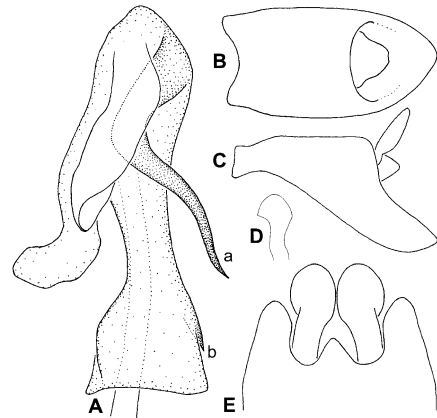
The relationships between genera remain mostly unresolved, but some generic groupings were consistent in most or all of the analyses. Based on the narrowly rounded or truncate apex of vertex and the low number (7–8) of apical teeth on the 2nd tarsomere, *Candicarina*, *Gelastocephalus* and *Melanoclypeus* were grouped together in most of the analyses although clear synapomorphies to prove derivation from a common ancestor have not yet been found.



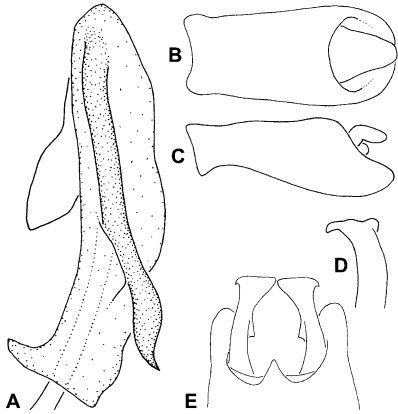
**Fig. 78.** *Holgus spiralis*: A, aedeagus ventral; B, aedeagus left lateral, main form; C, aedeagus left lateral, variant form; D, aedeagus right lateral; E, F, anal tube; G, H, genital styles.



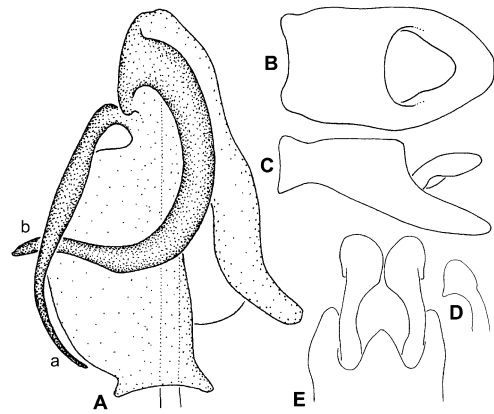
**Fig. 79.** *Holgus unispinosus*: A, aedeagus left lateral; B, aedeagus ventral; C, D, anal tube; E, F, genital styles.



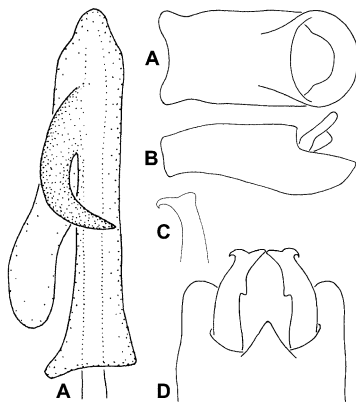
**Fig. 82.** *Lipsia mystrostylus*: A, aedeagus left lateral; B, C, anal tube; D, E, genital styles.



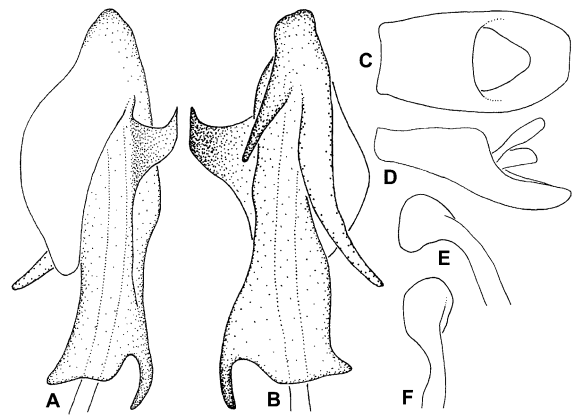
**Fig. 80.** *Lariviera yalthei*: A, aedeagus left lateral; B, C, anal tube; D, E, genital styles.



**Fig. 83.** *Melanoclypeus cristatus*: A, aedeagus right lateral; B, C, anal tube; D, E, genital styles.



**Fig. 81.** *Lariviera yokunna*: A, aedeagus left lateral; B, C, anal tube; D, E, genital styles.



**Fig. 84.** *Melanoclypeus uncinatus*: A, aedeagus left lateral; B, aedeagus right lateral; C, D, anal tube; E, F, genital styles.

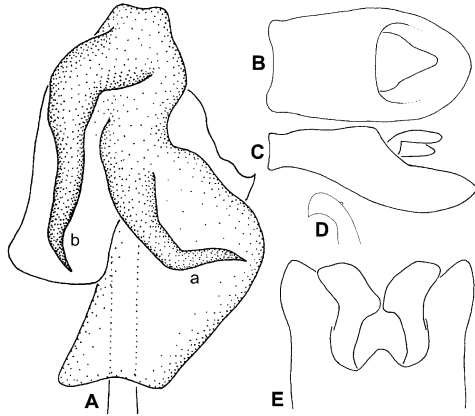


Fig. 85. *Metaplacha tobiasi*: A, aedeagus ventral; B, C, anal tube; D, E, genital styles.

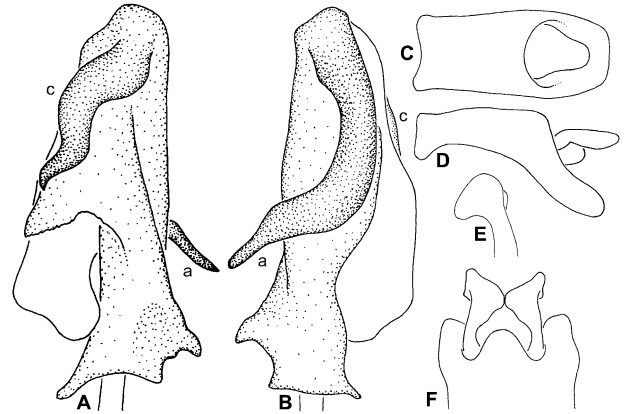


Fig. 88. *Novotarberus pseudorphninus*: A, aedeagus left lateral; B, aedeagus right lateral; C, D, anal tube; E, F, genital styles.

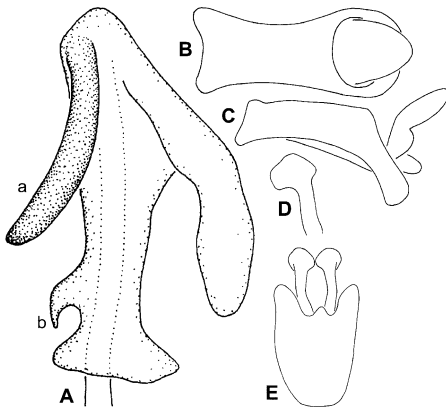


Fig. 86. *Novotarberus jacobii*: A, aedeagus right lateral; B, C, anal tube; D, E, genital styles.

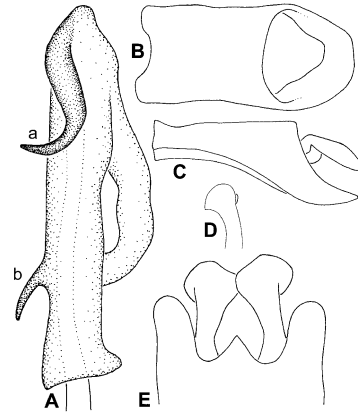


Fig. 89. *Novotarberus remanei*: A, aedeagus right lateral; B, C, anal tube; D, E, genital styles.

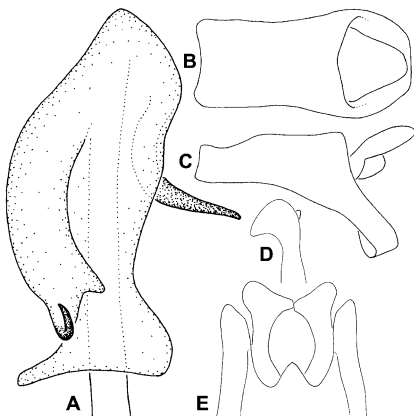


Fig. 87. *Novotarberus flagellospinosus*: A, aedeagus left lateral; B, C, anal tube; D, E, genital styles.

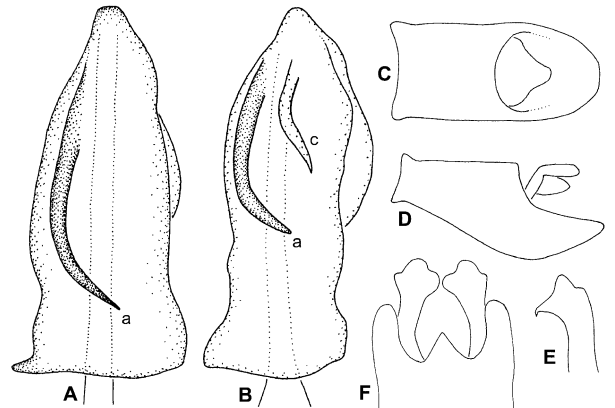
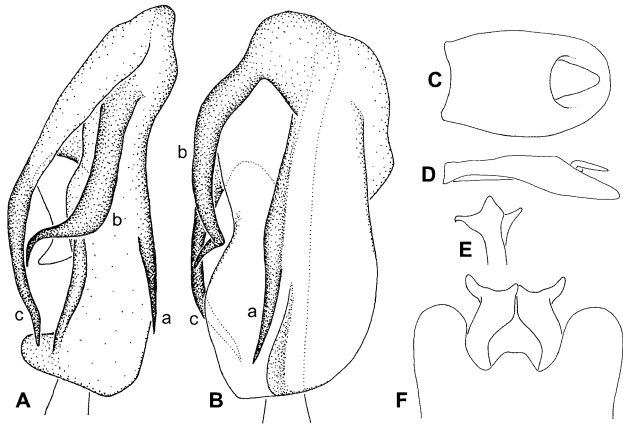
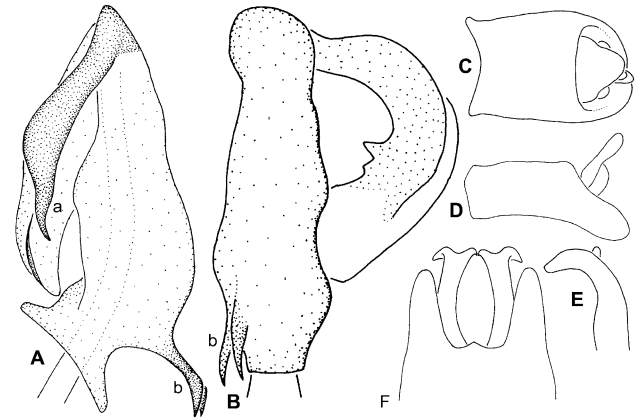


Fig. 90. *Payastylus gekiae*: A, aedeagus ventral – form without membranous spine; B, aedeagus ventral – form with membranous spine; C, D, anal tube; E, F, genital styles.



**Fig. 91.** *Payastylus brichrius*: A, aedeagus left lateral; B, aedeagus ventral; C, D, anal tube; E, F, genital styles.



**Fig. 93.** *Rokebia australis*: A, aedeagus left lateral; B, aedeagus ventral; C, D, anal tube; E, F, genital styles.

*Use of continuous data in the phylogenetic analysis*

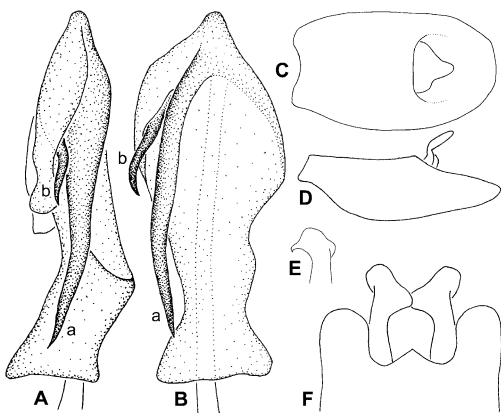
Dataset *A* contains several characters based on continuous data such as ratios of length of pronotum to body length, length of hind tibia to body length, width of forewings to length of forewings and width of frons to length of frons. Statistical examination of the data using showed significant differences, but most of the ranges overlapped which meant not all of the states could be sorted into clearly defined groups. Therefore, we divided the data into approximately equal ranges acknowledging any obvious gaps in the data. To minimise the impact of the arbitrary limits of the character states and also because we assume that in order to evolve from one extreme to the other (e.g. from a short vertex to a long vertex) a taxon would most likely go through intermediate stages we treated these characters as ordered.

However, we acknowledge that some of the character state designations were arbitrary. Therefore to examine if our *a priori* assumptions biased the analysis in any significant

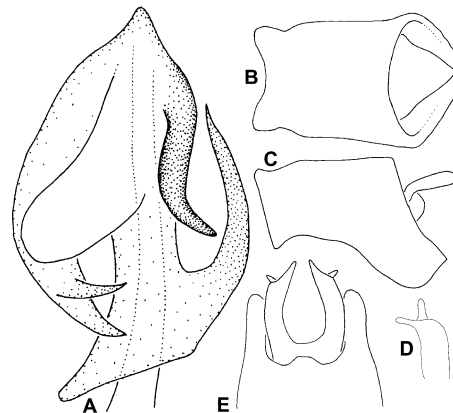
way, we conducted another set of analyses based on dataset *B*, which treated all characters as unordered and excluded characters based on continuous data.

Overall the cladograms obtained through analyses of both datasets were very similar.

Comparison of the equal weighting and scaled weighting regimes of the two datasets showed some differences, e.g. the topology of *Cixius sidnicus* and *Cajeta singularis*. The *a priori* assumptions applied in dataset *A* may be the reasons why these two outgroup genera appear on the tree as part of the ingroup. Some analyses of dataset *B*, using different sets of outgroups, however, also showed *Cajeta* and *Cixius* as part of the ingroup. Other differences noticed were that some of the genera such as *Holgus*, *Candicarina*, *Balyadimetopia*, *Gurrundus*, *Novotarberus* and the subtribe Rhigedanina proved to be monophyletic in the analysis of one dataset but not in the other one. The analyses using dataset *B* are regarded as being potentially less robust because the omission of several characters reduced the ratio of number of characters to number of taxa.

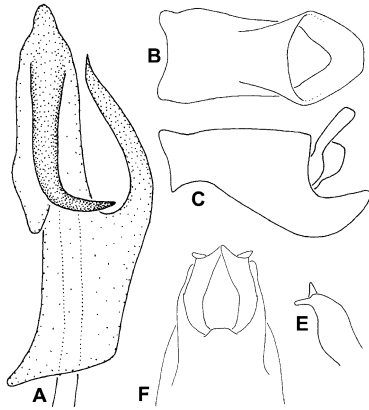


**Fig. 92.** *Payastylus kernaes*: A, aedeagus left lateral; B, aedeagus ventral; C, D, anal tube; E, F, genital styles.



**Fig. 94.** *Ronaldia fennahi*: A, aedeagus left lateral; B, C, anal tube; D, E, F, genital styles.



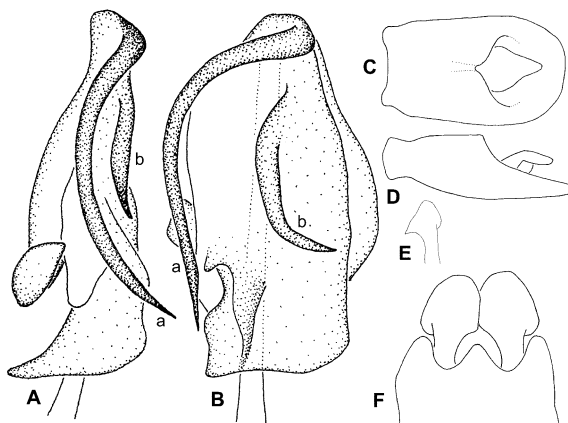


**Fig. 95.** *Ronaldia emeljanovi*: A, aedeagus left lateral; B, C, anal tube; D, E, genital styles.

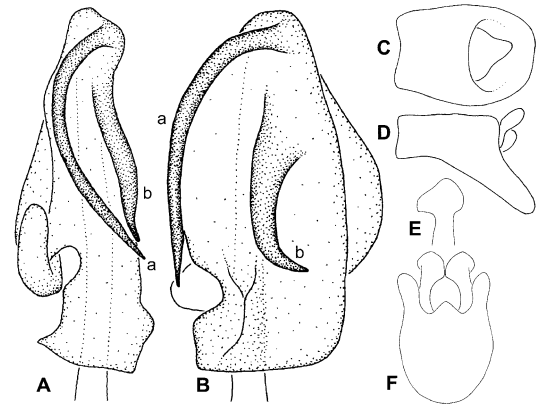
#### Testing the monophyly of Gelastocephalini

*Cajeta singularis* and ‘*Cixius*’ *sidnicus* were chosen as outgroups, based on characters of the legs and anal tube, they were expected to form a sister group to Gelastocephalini. Some analyses (e.g. equal weighting and scaled weighting regimes of dataset A), however, placed these two taxa as part of the ingroup. These results raise some doubts about the monophyly of the tribe Gelastocephalini, though many analyses support the monophyly of the tribe.

When Emeljanov (2000: 257) introduced the tribe, he neither defined it as a monophyletic tribe nor gave any synapomorphies, but he stated, ‘The tribe is characterised by the swollen clypeus; absence of the median ocellus; lack of wax plate in ovipositor; diastema in a row of apical teeth on the hind tibia; ScMR [Sc+R+M] stalk on the forewing; vein icu running at some distance from the apex of clavus; and originally divided male abdominal sternite VIII (in some advanced representatives of the tribe, e.g. *Ronaldia fennahi* and *Rhigedanus fomibundus*, sternite VIII is secondarily entire)’. This contains an error in translation from the origi-



**Fig. 96.** *Schuerrera ecarinata*: A, aedeagus left lateral; B, aedeagus ventral; C, D, anal tube; E, F, genital styles.

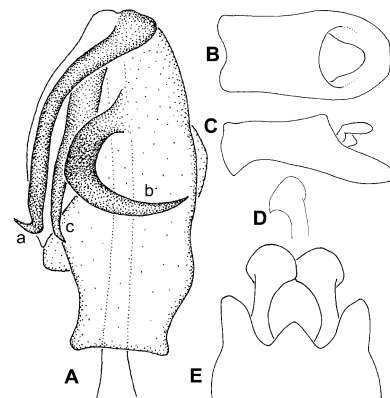


**Fig. 97.** *Schuerrera clypeocarinata*: A, aedeagus left lateral; B, aedeagus ventral; C, D, anal tube; E, F, genital styles.

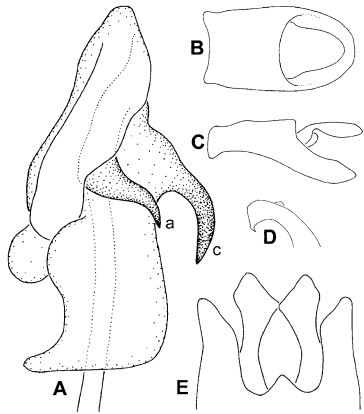
nal Russian version (Emeljanov 2000). The correct wording should be: ‘originally entire and secondary divided abdominal sternite VIII’ (A. F. Emeljanov, personal communication, 2003). Some of the characters mentioned here, such as swollen clypeus and icu distad of apex of clavus, when examined on a larger number of specimens, proved to be prone to intraspecific variation, the latter sometimes even between the two wings on one specimen.

The character state ‘swollen clypeus’, where the clypeus protrudes deeply into the frons at least to the level of the lower margins of the antennae, did not apply to *Carolus crispus*, *Gelastocephalus ornithoides* and to several new species within the tribe Gelastocephalini. Here the post-clypeus protruded into the frons but not as far as the antennae. In *Rhigedanus maculipennis* both states were observed. Looking at species of other tribes within Cixiidae both states were found plus an additional state, where the clypeus did not protrude at all into the frons. This state was found in the tribe Oecleini in genera such as *Volcanalia* Distant.

The lack of the median ocellus was shared amongst all Gelastocephalini but also with other taxa such as members of



**Fig. 98.** *Schuerrera merula*: A, aedeagus ventral; B, C, anal tube; D, E, genital styles.



**Fig. 99.** *Wernindia rhomboidea*: A, aedeagus left lateral; B, C, anal tube; D, E, genital styles.

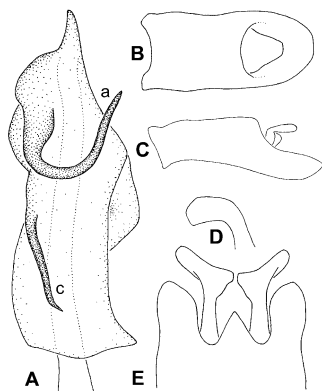
the tribes Cajetini, Eucarpiini and Duiliini as well as ‘*Cixius*’ *sidnicus* and outgroups 1–4.

Although females were not studied in detail, it was noted that all Gelastocephalini females lack wax plates.

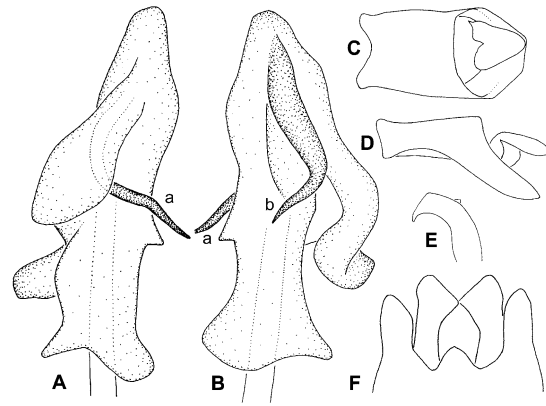
A gap (diastema) in the row of apical teeth on the hind tibia was observed in all Gelastocephalini. This feature was shared with Oecleini, Bothriocerinae and some other taxa such as ‘*Cixius*’ *sidnicus*, *Volcanalia* sp. and outgroup 2. Emeljanov (2002) showed that this state corresponds to the intermediate ontogenetic stage of all Fulgoromorpha, transforming into an uninterrupted row of spines in adults.

An Sc+R+M stalk was found in most Gelastocephalini, but some representatives of *Corylonga*, *Fletcherolus*, *Payastylus* and *Yarnikada* had a common Sc+R stem, with M emerging separately from the basal cell. This feature was also found in several taxa outside Gelastocephalini, such as *Volcanalia* sp (Oecleini), *Cajeta singularis* (Cajetini), ‘*Cixius*’ *sidnicus* (Cixiini), *Apartus michalki* (Cixiini) and *Oliarus* sp (Pentastirini).

The position of the icu at CuP showed extensive intraspecific variation. Three states were observed within



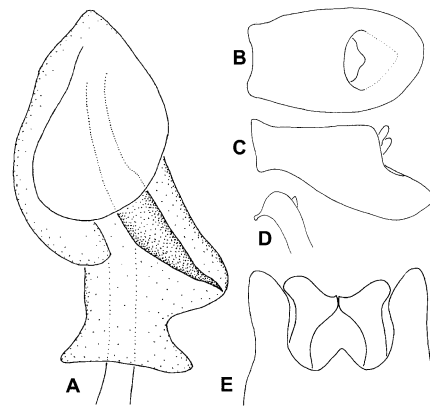
**Fig. 100.** *Wernindia bubalis*: A, aedeagus ventral; B, C, anal tube; D, E, genital styles.



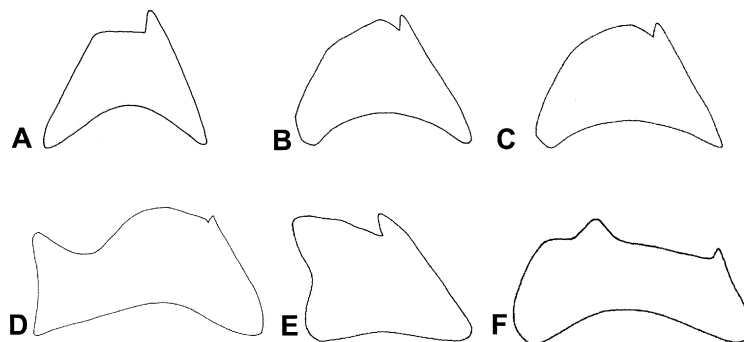
**Fig. 101.** *Wernindia lorda*: A, aedeagus left lateral; B, aedeagus right lateral; C, D, anal tube; E, F, genital styles.

Gelastocephalini: icu distad of apex of clavus (not running into the CuP), icu joining CuP where it connects to the hind border of the wing and icu basad of apex of clavus (joining CuP some distance before it connects to the hind border of the wing). The latter was only found in *Aubirestus semicirculatus* and in some specimens of *Wernindia bubalis*. In *Carolus crispus* and numerous other taxa icu joined CuP at the apex of the clavus. The state where icu is distad of the apex of the clavus was present in *Novotarberus jacobii*, *Dysoliarus unicornis* and in the genus *Rhigedanus*. *Gelastocephalus ornithoides*, *Ronaldia fennahi*, *Metaplacha tobiasi* and *Orphninus mouldsi* showed intraspecific variation, displaying two states: position of icu at CuP distad of or at the same level as the apex of the clavus.

The 8th sternite formed by a single uninterrupted sclerotised plate, as is present in *Ronaldia*, *Orphninus*, *Dysoliarus* and *Rhigedanus fomibundus*, was considered to be the plesiomorphic state (Emeljanov 2002, personal communication). A divided 8th sternite was found in *Gelastocephalus ornithoides* and *Metaplacha tobiasi*. Both states were found in *Rhigedanus maculipennis*.



**Fig. 102.** *Yarnikada ulliae*: A, aedeagus left lateral; B, C, anal tube; D, E, genital styles.



**Fig. 103.** Shape of pygofer, left lateral. *A*, *Holgus ancistrus*; *B*, *Balyadimetopia krahalla*; *C*, *B. frederi*; *D*, outgroup 2; *E*, *Oliarus* sp.; *F*, *Vocanalia* sp.

In his key to differentiate Oecleini and Gelastocephalini Emeljanov (2000) lists another character: male anal style short, entirely concealed by edge of the 11th segment. This character state was found in all Gelastocephalini but also in some representatives of the following genera: *Andes* Stål 1866 (Emeljanov 2002), *Benna* Walker 1857 (Bennini Metcalf 1938), *Cubana* Uhler 1895 (Pintaliini Metcalf 1938) and *Cubanella* Fennah 1948 (Pintaliini). The plesiomorphic state of the anal tube seemed to comprise a very long anal style and a short segment XI, as this situation was found in most genera of Cixiidae, and in species of Delphacidae and Achilidae. The presence of a very short anal style in genera outside of Gelastocephalini indicated that this state, that represents a synapomorphy for Gelastocephalini, had originated more than once.

Interestingly, '*Cixius*' *sidnicus* and *Cajeta singularis* showed an intermediate state between these two extremes. The anal style found in these species was about the same length as the segment XI. This suggested that these two taxa may share a common ancestor with Gelastocephalini. '*Cixius*' *sidnicus* and *Cajeta singularis* remained on the intermediate stage, whereas in Gelastocephalini the anal style became further reduced, while the segment XI increased. The following character states that were shared by '*Cixius*' *sidnicus*, *Cajeta singularis* and all Gelastocephalini, also supported a common ancestry: absence of the median ocellus; 2nd hind tarsomere triangularly shaped, apical teeth (except for the external ones) reduced, bearing platellae.

Some of the trees, however, favoured a hypothesis where '*Cixius*' *sidnicus* and *Cajeta singularis* were derived from

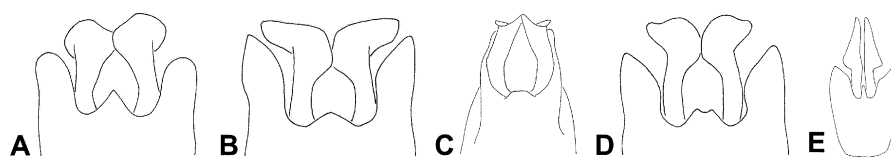
the Gelastocephalini that would indicate that the anal style character is somewhat of a reversal. Analyses on the world cixiid fauna including all genera/tribes, are needed to clarify this issue.

With our current knowledge, Gelastocephalini are characterised by the following combination of characters: absence of a median ocellus; a single distinct transverse carina between vertex and clypeus; hind tibia with six (rarely five or seven) apical teeth separated into two groups by a gap (diastema); the outermost spine of the outer group being larger than the second and third spine; spines of the inner group short, not levelled basally with outer group, but still extending as far as the first spine of the outer group (Fig. 1F); 2nd hind tarsomere triangularly shaped, apical teeth (except for the external ones) reduced, bearing platellae; absence of wax plates in ovipositor; male pygofer with triangularly shaped (angle  $>60^\circ$ ) ventromedian process, sometimes truncated apically. The short male anal style, entirely concealed by the edge of the 11th segment is seen as a synapomorphy for the tribe Gelastocephalini.

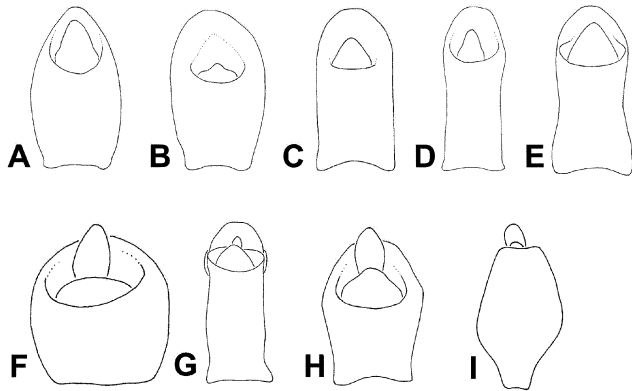
All these characters have yet to be included and this new definition of the tribe tested in a forthcoming phylogenetic analysis of the world genera and tribes of Cixiidae.

#### *Monophyly and paraphyly of the subtribes*

*Orphninus*, *Dysoliarus* and *Rhigedanus* formed a clade in every analyses performed, except for the equal weighting analysis of dataset B. A synapomorphy, the presence of ear-shaped lobes on the pronotum, confirmed the monophyly of the genera representing the subtribe Rhigedanina. The presence of large lateral spines on the hind tibia was another

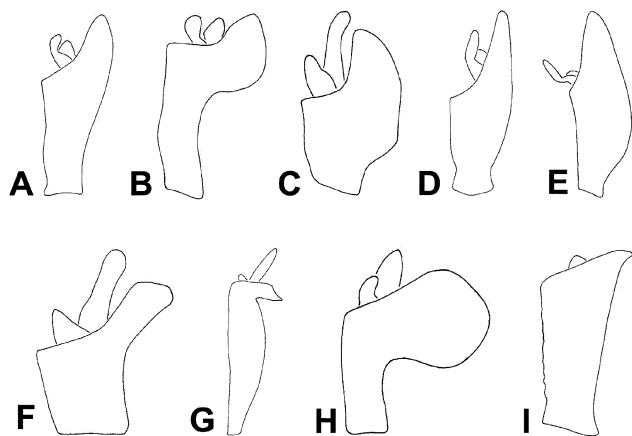


**Fig. 104.** Shape of ventromedian process, ventral. *A*, *Novotarberus remanei*; *B*, *Aubirestus semicirculatus*; *C*, *Ronaldia emeljanovi*; *D*, *Gurrundus fuscomarginatus*; *E*, *Oliarus* sp.



**Fig. 105.** Shape of anal tube, dorsal. *A*, *Fletcherolus lanceolatus*; *B*, *Yarnikada ulliae*; *C*, *Holgus ancistrus*; *D*, *Gurrundus fusco-marginatus*; *E*, *Aubirestus semicirculatus*; *F*, *Volcanalia* sp.; *G*, *Cixius sidnicus*; *H*, outgroup 1; *I*, *Oliarus* sp.

synapomorphy for this subtribe, however, this feature has also been observed in *Payastylus brichrius*, where it has to be interpreted as convergence. The fact that *Rhigedanina* is a derivative of other *Gelastocephalini* was shown through *Orphninus*. In many characters *Orphninus* showed intermediate stages between ‘*Gelastocephalina*’ and *Rhigedanina*. For example in contrast to all other *Gelastocephalini*, the pronotal carinae in *Rhigedanus* and *Dysoliarus* were raised to form ear-shaped lobes. In *Orphninus*, however, the pronotal carinae were only slightly raised forming very indistinct ear-shaped lobes. In *Rhigedanus* and *Dysoliarus*, a polymerisation of apical teeth and platellae on the 2nd hind tarsomere was taking place, displaying numbers of apical teeth ranging from 14 to up to 40. Only 11–15 apical teeth were counted on the hind tarsus of *Orphninus*, whereas all other *Gelastocephalini* (except for *Guttala nickeli* with 13) bear 11 or fewer apical teeth. A feature shared only by



**Fig. 106.** Shape of anal tube, left lateral. *A*, *Corylonga mahmudae*; *B*, *Cajeta singularis*; *C*, outgroup 1; *D*, *Schuerriera ecarinata*; *E*, *Payastylus kernaes*; *F*, outgroup 2; *G*, *Oliarus* sp.; *H*, *Volcanalia* sp.; *I*, *Rhigedanus maculipennis*.

*Rhigedanus* and *Dysoliarus* was the distinctly lowered head in lateral view. A similar configuration of a lowered head and declined pronotum was found in *Cajeta*, included in the analyses as one of the outgroups. For the phylogenetic analysis, the character states present in these three genera have been coded as being homologous, but they may be analogies.

The subtribe ‘*Gelastocephalina*’ is paraphyletic. Further studies are needed to determine whether a subtribal classification is useful in *Gelastocephalini*. The current subtribal concept of *Gelastocephalina*, established by Emeljanov (2000) was retained for convenience despite being paraphyletic pending a more comprehensive reassessment of the higher classification of the Cixiidae. New genera described herein were placed within this subtribe, since they did not show the synapomorphies of *Rhigedanina*.

#### *Biogeography of the genera represented in New Caledonia*

Currently *Gelastocephalini* are known only from Australia (58 species) and New Caledonia (two species). *Gelastocephalini* are unlikely to occur in New Zealand, since a comprehensive revision of the NZ Cixiidae (Larivière, 1999) has been undertaken. However, the tribe may be present in New Guinea (no material from New Guinea was available for this study).

Assuming that the tribe is monophyletic this distributional pattern (Australia and New Caledonia) raises interesting questions about the evolutionary history of the tribe or ability of the included species to disperse.

The monotypic genus *Gelastocaledonia* is endemic to New Caledonia, whereas *Novotarberus* has one representative in New Caledonia (*N. jacobii*) and three in Australia. According to the analyses performed, these two genera did not seem to be closely related, except for the successive approximations weighting regime, where *Gelastocaledonia* formed a clade with *Novotarberus jacobii*. This leads to the following alternative hypotheses:

1) *Gelastocephalini* are an ancient lineage dating from at least 80 million years ago when New Caledonia broke away from west Antarctica (that was connected to Australia) and moved north-west (Sanmartín and Ronquist 2004).

*Gelastocaledonia monteithi* and all four species of the genus *Novotarberus* were widely distributed in those parts of Gondwana that later became Australia and New Caledonia. After the separation of New Caledonia from Gondwana, several extinction-events occurred, so that only the species currently present in these land masses remained.

2) *Gelastocephalini* mainly occurred in those regions of Gondwana, that later became Australia. However, the two species, *G. monteithi*, and *N. jacobii*, managed to colonise the eastern parts of New Caledonia, or evolved there based on vicariance. From the time when New Caledonia broke away from Australia: it showed the current situation, with *G. monteithi* and *N. jacobii* present only in New Caledonia

and the other three species occurring only in Australia (still retaining the possibility that the New Caledonian species also occur in Australia).

This hypothesis is favoured by the authors, as it minimises (or does not require) any extinction events and also reflects the current distribution of *Novotarberus* with *N. flagello-spinosus* and *N. pseudorphninus* inhabiting WA and *N. remanei* occurring in ACT, NSW and Vic.

One might also wonder, why Gelastocephalini are absent from New Zealand, as the latter was connected to New Caledonia when it separated from Gondwana. Similar distributional patterns (taxa endemic to Australia and New Caledonia) are found in other insect groups, such as Archostemata (Hörschemeyer, 2004) and Dolichopodidae. Two genera of Dolichopodidae displayed a classical 'Bassian' distribution pattern (Australia: Tasmania, eastern Australia to SE Qld and south-western Australia; New Caledonia: in altitudes above 500 m), that is typically associated with Gondwanan taxa (Bickel 2004). The 'Bassian' distribution pattern is also found in *Novotarberus* and *Gelastocaledonia*. With the exception of a few specimens found in north-western Australia (Pilbara district) the former occurs in south-western (Gingin, Waroona, Augusta and Albany) and south-eastern Australia (Newmerella, Mt Kosciuszko and Mt Gingera). Unfortunately no information was available on the altitude at which the single specimen from Tontouta (New Caledonia) was collected although this region is mainly below 500 m (that does not comply with the typical 'Bassian' distribution). However, the genus *Gelastocaledonia*, fits into the described pattern, since it was found at altitudes ranging from 1300–1350 m.

One potential reason for the absence of taxa from New Zealand is explained in Bickel (2004: 27), '... during the Tertiary, New Zealand underwent major climatic and tectonically induced extinction events, losing much of its ancestral flora, and probably associated insects as well'. This might explain the lack of representatives of the tribe Gelastocephalini in New Zealand.

3) The presence of Gelastocephalini in New Caledonia is due to long-distance dispersal, which means Gelastocephalini are not necessarily an ancient group.

This hypothesis is not likely because of the great geographic distance between New Caledonia and Australia but there are some examples of Fulgoromorpha moving over large distances, such as the planthopper *Nilaparvata lugens* (Stål) performing a trans-oceanic migration of 600–1000 km each spring and early summer, travelling from China to Korea and Japan, in order to colonise newly transplanted rice crops (Della Giustina 2002). Moreover, in order to support this hypothesis, two separate incursions of Gelastocephalini must have taken place, since the two genera do not seem to have a common lineage. However, this would imply that the two New Caledonian species must also occur in Australia and there is no evidence of this.

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