

**A REVIEW OF THE TREE, FIG AND FRUIT-INFESTING FLIES
OF THE *AETHIOTHEMARA*, *DIARRHEGMA*, *DIRIOXA* AND
THEMAROIDES GROUPS OF GENERA (DIPTERA: TEPHRITIDAE:
ACANTHONEVRINI)**

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Abstract

Indo-Australian, East Asian and African fruit flies placed in the *Aethiothemara*, *Diarrhegma*, *Dirioxa* and *Themaroides* groups of genera and known or believed to breed in figs, overripe and damaged fruit or beneath the bark of standing trees are reviewed. The 134 recognised species are referred to 39 genera: *Aethiothemara* Hendel, *Afrocneros* Bezzi, *Labeschatia* Munro, *Ocnerioxa* Speiser, *Ptiloniola* Hendel and *Themarictera* Hendel in the *Aethiothemara* group; *Diarrhegma* Bezzi in the *Diarrhegma* group; *Anchiacanthonevra* Hardy, *Dirioxa* Hendel, *Griphomyia* Hardy, *Lumirioxa* Permkam & Hancock, *Micronevrina* Permkam & Hancock, *Mimoeuphranta* Hardy and *Parachlaena* Hering in the *Dirioxa* group; and *Acanthonevroides* Permkam & Hancock, *Alloeomyia* Hardy, *Aridonevra* Permkam & Hancock, *Buloloa* Hardy, *Cheesmanomyia* Malloch, *Clusiosoma* Malloch, *Clusiosomina* Malloch, *Enoplopteron* de Meijere, *Hemichusiosoma* Hardy, *Hexaresta* Hering, *Neothemara* Malloch, *Nothochusiosoma* Hardy, *Paedohexacinia* Hardy, *Pseudacanthoneura* Malloch, *Pseudoneothemara* Hardy, *Quasirhabdochaeta* Hardy, *Rabaulia* Malloch, *Rabauliomorpha* Hardy, *Taeniorioxa* Permkam & Hancock, *Termitorioxa* Hendel, *Themarohystrix* Hendel, *Themaroides* Hendel, *Themaroidopsis* Hering, *Trypanocentra* Hendel and *Walkeraitia* Hardy in the *Themaroides* group. *Lyronotum* Hering, 1941 is placed as a new synonym of *Hexaresta* Hering, 1941 and its type species, *Acanthoneura seriata* de Meijere, 1915, is placed as a new synonym of *Hexaresta multistriga* (Walker, 1859). *Clusiosoma semifuscum* Malloch, 1926 is returned to synonymy with *C. minutum* (de Meijere, 1913). Keys are included to Asian and Australasian genera plus species of *Aethiothemara*, *Diarrhegma*, *Dirioxa*, *Termitorioxa* and *Themaroides* and males of the *Clusiosoma pullatum* group.

Introduction

This is the fifth in a series of papers reviewing and keying Indo-Australian, Oceanian and East Asian fruit flies placed in the tribe Acanthonevrini *sensu* Korneyev (1999) of subfamily Phytalmiinae and deals with species referred to the *Diarrhegma*, *Dirioxa* and *Themaroides* groups of genera, together with the Afrotropical *Aethiothemara* group. *Diarrhegma* occurs from India and China to Indonesia, while the *Dirioxa* and *Themaroides* groups are largely restricted to the Australian and Oceanian Regions. Previous papers dealt with the *Acanthonevra*, *Sophira*, *Rioxa* and *Dacopsis* complexes of the *Acanthonevra* group (Hancock 2011, 2012, 2014a, 2014b).

The Afrotropical *Aethiothemara* group was reviewed and keyed by Hancock (1986) and contains six genera: *Aethiothemara* Hendel, *Afrocneros* Bezzi, *Labeschatia* Munro, *Ocnerioxa* Speiser, *Ptiloniola* Hendel and *Themarictera* Hendel. Keys to the species of *Afrocneros* (3 spp), *Ocnerioxa* (11 spp) and *Ptiloniola* (3 spp) were provided by Munro (1967), while *Labeschatia* and *Themarictera* are monotypic (Hancock 1986). A provisional key to the six species of *Aethiothemara*, based on that of Hendel (1928), is provided below. Larvae of *Afrocneros excellens* (Loew), *A. mundus* (Loew) and *Ocnerioxa sinuata* (Loew) feed on the parenchymatous tissue of standing *Cussonia*

(Araliaceae) trunks (Munro 1967), while *Themarictera flaveolata* (Fabricius) has been bred from fruit of *Maerua cafra* and '*Capparis* sp.' (Capparaceae) (Munro 1925, Hancock 2003).

For the Indo-Australian fauna, the *Dirioxa* group differs from the *Diarrhegma* and *Themaroides* groups in having only a single apical spine on the mid tibia rather than two. The *Diarrhegma* group contains only the genus *Diarrhegma* Bezzi, with two species. *Diarrhegma modestum* (Fabricius) has been reported from decaying wood (Bezzi 1913), including *Moringa pterygosperma* (Moringaceae) (Hancock and Drew 1994b), and at least some genera in the *Dirioxa* and *Themaroides* groups (e.g. *Lumirioxa* Permkam & Hancock and *Termitoriox*a Hendel) are known to breed beneath the decaying bark of standing trees (Permkam and Hancock 1995, Hancock 2002). Adults of *Acanthonevroides* Permkam & Hancock, *Lumirioxa* and *Micronevrina* Permkam & Hancock have been collected in Malaise traps baited with sawn saplings (G.B. Monteith in Hancock 2013).

The *Themaroides* group is currently divided into three – the *Clusiosoma* subgroup with nine genera, *Neothemara* subgroup with six genera and *Themaroides* subgroup with ten genera (Hancock and Drew 2003). In the *Clusiosoma* subgroup, larvae of *Cheesmanomyia nigra* (de Meijere), *Clusiosoma minutum* (de Meijere) [as *C. semifuscum* Malloch], *C. pleurale* Malloch, *C. subpullatum* Hardy, *Clusiosomina puncticeps* Malloch, *Rabaulia fascifacies* Malloch, *R. nigrotibia* Hering and *Trypanocentra nigrithorax* Malloch all feed in the fruit of figs (*Ficus* spp: Moraceae) (Hardy 1986, Permkam and Hancock 1995, Hancock *et al.* 1998, Hancock *et al.* 2000, Hancock and Drew 2003). In the *Themaroides* subgroup, larvae of *Termitoriox*a *termitoxena* (Bezzi) feed beneath damaged bark of trees such as *Terminalia* sp. (Combretaceae) and *Delonix regia* (Fabaceae); an initial record from galleries of *Mastotermes darwiniensis* Froggatt (Bezzi 1919) is believed to indicate feeding on the tree trunk rather than feeding on the termites (Hancock 2002). *Acanthonevroides nigriventris* (Malloch) has been collected on trunks of *Acacia* and *Eucalyptus* and attracted to sawn saplings and all species in the genus are likely to be tree trunk feeders (Permkam and Hancock 1995, Hancock 2013). Larval hosts have not been recorded for any species in the *Neothemara* subgroup.

The New Guinea-Pacific genera *Anchiacanthonevra* Hardy, *Mimoeuphranta* Hardy and *Parachlaena* Hering (Fig. 1) were transferred from the *Acanthonevra* group to the *Dirioxa* group by Hancock (2012), which also includes *Dirioxa* Hendel, *Lumirioxa* and *Micronevrina*. The New Guinea genus *Griphomyia* Hardy was initially placed in tribe Trypetini by Hardy (1987) but the presence of secondary scutellar and intrapostalar setae, together with the setose aculeus, suggest it is better placed in the Acanthonevrini. Its precise relationships remain obscure but the distinct intrapostalar setae, single midtibial spine and shape of the spermathecae

suggest it is best placed in the *Dirioxa* group, at least provisionally. It differs from other acanthonevrine genera in the bare or micropubescent, rather than plumose, arista. Larvae of *Lumirioxa araucariae* (Tryon) feed within a wet rot beneath the bark of *Araucaria cunninghamii* trees (Araucariaceae) (Brimblecombe 1945). Larvae of *Dirioxa pornia* (Walker) attack a wide range of overripe or damaged fruit and even fallen *Araucaria* cones (Permkam and Hancock 1995, Hancock *et al.* 2000), while those of *D. fuscipennis* Hancock & Drew have been bred from the fruit of *Barringtonia edulis* (Lecythidaceae) and *Poutaria guayana* (Sapotaceae) (Hancock and Drew 2003). The hosts of other genera in the group remain unknown, although the attraction of *Micronevrina hyalina* Permkam & Hancock and *M. montana* Permkam & Hancock to sawn saplings (Hancock 2013) suggests they also breed in trees.

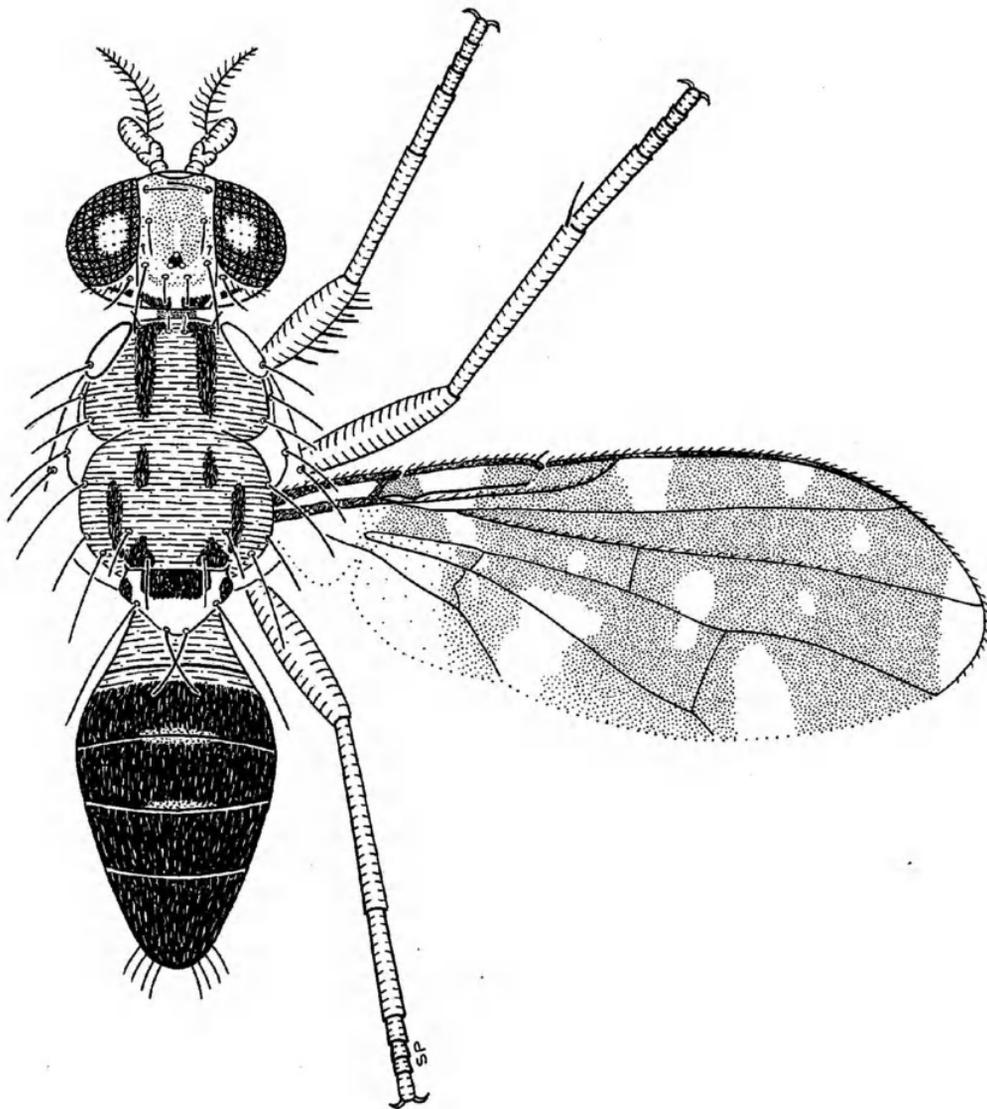


Fig. 1. *Parachlaena greenwoodi* (Bezzi): male from Fiji.

Two further East or Southeast Asian genera sometimes included in the Acanthonevrini, *Hexaptilona* Hering and *Paracanthonevra* Hardy, belong in subfamilies Blepharoneurinae or Trypetinae respectively (Korneyev 1999, Han 1999) and are not included here.

Key to Asian and Australasian genera

- 1 Scutum largely ivory-white posteriorly and with black patches antero- and posterolaterally; scutellum ivory-white and unspotted; wing with pterostigma about half length of cell c; head with 2 pairs each of frontal and orbital setae; mid tibiae with 2 long apical spines [S and SE Asia; 2 species, keyed below] *Diarrhegma* group ... *Diarrhegma* Bezzi, 1913
 - Not as above; scutum and scutellum fulvous to black without ivory-white markings; other characters variable [Australian and Pacific Regions] 2
- 2 Mid tibia with only 1 long apical and no distinct, shorter spines; wing vein Cu₁ and Cu base both bare; cell m with 1 or (rarely) 2 hyaline indentations *Dirioxa* group ... 3
 - Mid tibia with 2 long and subequal or 1 long and 1 or more shorter apical spines; wing vein Cu₁ and/or Cu base often setulose; cell m with 0-3 hyaline indentations *Themaroides* group ... 9
- 3 Arista bare or micropubescent; upper orbital seta weak or absent; 1 pair of frontal setae; R-M crossvein placed near basal third of cell dm and below or before middle of pterostigma; cell bcu extension vestigial [Papua New Guinea (mainland and Bougainville); 5 spp, keyed and illustrated by Hardy 1987] *Griphomyia* Hardy, 1987
 - Arista plumose; upper orbital seta often well developed; 1 or 2 pairs of frontal setae; R-M crossvein placed near or beyond middle of cell dm and usually below or beyond apex of pterostigma; cell bcu extension distinct 4
- 4 Wing cell m with 2 distinct posterior hyaline indentations; apex of cell r₄₊₅ hyaline except for a medial dark band or spot from wing margin [Papua New Guinea (New Britain); 1 sp., illustrated by Hardy 1986] *Anchiacanthonevra* Hardy, 1986
 - Wing cell m largely hyaline to subhyaline or with 1 distinct posterior indentation; apex of cell r₄₊₅ not as above 5
- 5 Upper orbital seta vestigial or absent; 1 pair of frontal setae; wing apex hyaline across posterior half of cell r₂₊₃ and all of cell r₄₊₅ [Fiji; 1 sp, illustrated in Fig. 1] *Parachlaena* Hering, 1944
 - Upper orbital seta normally distinct; 1 or 2 pairs of frontal setae; wing apex not hyaline across posterior half of cell r₂₊₃ and all of cell r₄₊₅ 6

- 6 Upper orbital seta weak, much shorter than lower seta; prescutellar acrostichal setae absent; R-M crossvein placed below middle of pterostigma; wing pattern largely hyaline to subhyaline with a narrow, dark transverse band from costa over DM-Cu crossvein to posterior margin [Papua New Guinea and Solomon Islands; 1 sp., illustrated by Hardy 1986] *Mimoeuphranta* Hardy, 1986
- Upper orbital seta well developed, almost as long as lower seta; prescutellar acrostichal setae present or absent; R-M crossvein placed below or beyond apex of pterostigma; wing pattern dark, usually with numerous hyaline spots and indentations 7
- 7 Anepimeral seta vestigial or absent; usually only 2 pairs of scutellar setae, if 3 then medial pair weak and rudimentary; presutural setae present or absent, if present then wing pattern distinctly sexually dimorphic; aculeus apically dentate and bifid, the preapical setae minute [eastern Australia; 7 spp, keyed and illustrated by Permkam and Hancock 1995]
..... *Micronevrina* Permkam & Hancock, 1995
- Anepimeral seta distinct; 3 pairs of scutellar setae, the medial pair at last half length of apicals; presutural setae present and wing pattern not sexually dimorphic; aculeus apically blunt and non-serrate, the preapical setae well developed 8
- 8 Thorax and scutellum with a black medial stripe; fore femur densely setose ventrally in males; wing cell r_{4+5} with an elongate hyaline indentation posteroapically [eastern Australia (seQld-neNSW); 1 sp., illustrated by Permkam and Hancock 1995 and in Fig. 2]
..... *Lumirioxa* Permkam & Hancock, 1995
- Thorax and scutellum fulvous, without a black medial stripe; fore femur not densely setose ventrally in males; wing cell r_{4+5} entirely dark apically [eastern Indonesia (Papua Province), Australia, New Caledonia and Vanuatu; 3 spp, keyed below] *Dirioxa* Hendel, 1928
- 9 Wing cell m with at most a single posterior hyaline indentation 10
- Wing cell m with 3 posterior hyaline indentations
..... *Neothemara* subgroup ... 11
- 10 Mid tibia with 2 long and subequal apical spines; scutellum bare or densely setulose; scutum often with 2 pairs of supra-alar setae; wings usually with hyaline spots or indentations, if largely brown and scutellum not densely setulose then with an additional 2 pairs of secondary scutellar setae *Themaroides* subgroup ... 16
- Mid tibia normally with 1 long and 1 or more shorter apical spines; scutellum bare or at most weakly setulose marginally; scutum with only 1 pair of supra-alar setae; wings largely brown without hyaline spots or

indentations in at least anterior half; scutellum without additional pairs of secondary setae *Clusiosoma* subgroup ... 25



Fig. 2. *Lumirioxa araucariae* (Tryon): female from SE Queensland. Photograph by Andy Wang (Queensland Museum).

- 11 Vein R_{2+3} curved sharply from level of DM-Cu crossvein to meet costa at an angle of about 60° ; wing pattern with numerous brown rays extending to wing margin in cells r_1 , r_{2+3} and r_{4+5} [Papua New Guinea (New Britain); 1 sp., illustrated by Hardy 1986] *Quasirhabdochaeta* Hardy, 1986
- Not as above; vein R_{2+3} not sharply curved towards costa and pattern without dark marginal rays 12
- 12 Face vertical in profile, the epistome receding 13
- Face concave in profile, the epistome projecting 14
- 13 Ocellar setae distinct and well developed; vein R_{4+5} distinctly curved subapically then straightening to costa [eastern Indonesia (Papua Province), Papua New Guinea and Australia (nQld); 2 spp, illustrated by Hardy 1986 and Permkam and Hancock 1995]
 *Pseudacanthoneura* Malloch, 1939

- Ocellar setae weak and hair-like; vein R_{4+5} curving evenly to costa [eastern Indonesia (West Papua and Papua Provinces), Papua New Guinea and Australia (nQld); 2 spp, keyed by Hardy 1986; *N. trigonifera* Hering, 1951 was placed as a synonym of *N. formosipennis* (Walker, 1861) by Permkam and Hancock 1995; illustrated by Hardy 1986 and Permkam and Hancock 1995] *Neothemara* Malloch, 1939
- 14 Anepimeral seta vestigial; scutum yellow with only a small black spot behind each wing base; mid tibia with apical spine scarcely longer than small secondary spinules [Papua New Guinea; 1 sp., illustrated by Hardy 1986] *Alloeomyia* Hardy, 1986
- Anepimeral seta well developed; scutum with distinct dark markings; mid tibia with 1 long and 1 shorter apical spines 15
- 15 Vein Cu with basal portion along cell bcu setulose; wing with an oblique hyaline band from apex of vein Cu_2+A_1 to vein R_{4+5} above line of DM-Cu crossvein; scutellum with short black setulae at sides [eastern Indonesia (Batjan), Papua New Guinea (New Britain, New Ireland, Bougainville) and Solomon Islands; 2 spp, illustrated by Hardy 1986]
..... *Pseudoneothemara* Hardy, 1986
- Vein Cu bare, including basal portion; wing without an oblique hyaline band from apex of vein Cu_2+A_1 to vein R_{4+5} above line of DM-Cu crossvein; scutellum without marginal black setulae [eastern Indonesia (Sulawesi, Aru, West Papua, Papua), Papua New Guinea and Solomon Islands; 2 spp, illustrated by Hardy 1986; *Lyrnotum* Hering, 1941, **syn. n.** and *Hyponothemara* Hardy, 1986 are both regarded as synonyms; *Acanthoneura seriata* de Meijere, 1915, **syn. n.**, the type species of *Lyrnotum*, is inseparable from *Trypeta multistriga* Walker, 1859, the type species of *Hexaresta*] *Hexaresta* Hering, 1941
- 16 Wing with a row of long costal spines between humeral vein and apex of cell r_1 17
- Wing without a row of long costal spines between humeral vein and apex of cell r_1 18
- 17 Vein Cu base and Cu_1 both setulose; wing pattern not distinctly reticulate [Papua New Guinea; 1 sp., illustrated by Hardy 1986]
..... *Buloloa* Hardy, 1986
- Vein Cu base and Cu_1 both bare; wing pattern distinctly reticulate on disc [eastern Indonesia (Papua Province) and Papua New Guinea (mainland and New Britain); 3 spp, keyed and illustrated by Hardy 1986]
..... *Enoplopteron* de Meijere, 1915
- 18 Wing with a complete hyaline transverse band from middle of costal cell c and enclosing BM-Cu crossvein to posterior margin of cell cu_1 , plus incomplete transverse bands in cells $r_1+r_{2+3}+br$ and $r_{4+5}+dm$; apex of cell

- r_{4+5} and cell m with elongate hyaline indentations; vein R_{4+5} strongly curved anteriorly beyond R-M crossvein; vein M strongly curved posteriorly before R-M crossvein so that cell dm is distinctly petiolate in basal half [eastern Indonesia (West Papua Province); 1 sp., illustrated by Hardy 1986] *Walkeraitia* Hardy, 1986
- Wing pattern not as above, if banding evident then BM-Cu crossvein lies within the dark area; veins R_{4+5} and M not both strongly curved 19
- 19 Wing pattern dark with base largely hyaline and 5 narrow hyaline bands not arising from costa: 2 longitudinal in cells r_1+r_{2+3} and r_{4+5} and 3 obliquely transverse in cells m, br+dm+cu₁ and cu₁; DM-Cu crossvein inwardly oblique and curved towards wing base in anterior half [Australia (seQld); 1 sp., illustrated by Permkam and Hancock 1995]
..... *Taeniorioxa* Permkam & Hancock, 1995
- Wing pattern not as above 20
- 20 Wing pattern with costal cell c hyaline medially and 4 incomplete, obliquely transverse hyaline bands: an indentation in cells r_1+r_{2+3} , a curved band in cells $r_{4+5}+m$, an apical band in cell dm and a narrow basal band along vein Cu_2+A_1 in cell cu₁; DM-Cu crossvein strongly outwardly oblique, its apex situated below the apex of vein R_{2+3} at costa; scutellum black and swollen, with 4 scutellar setae and dense setulae [Australia (swQld); 1 sp., illustrated by Permkam and Hancock 1995]
..... *Aridonevra* Permkam & Hancock, 1995
- Wing pattern not as above; DM-Cu crossvein not strongly outwardly oblique, its apex situated basad of the apex of vein R_{2+3} ; if only 4 scutellar setae then scutellum yellow medially 21
- 21 Vein M setulose along cell dm 22
- Vein M bare 23
- 22 Veins Cu base and Cu₁ setulose; wings normally dark brown with no more than the posterior area hyaline; if base broadly hyaline then hyaline patch from cell dm into cell r_{4+5} not extending into cell r_{2+3} [eastern Indonesia (Misool, West Papua, Papua) and Papua New Guinea; 9 spp, keyed and illustrated by Hardy 1986] *Themarohystrix* Hendel, 1914
- Veins Cu base and Cu₁ bare; wing base broadly hyaline; if hyaline patch from cell dm into cell r_{4+5} present then not extending into cell r_{2+3} [eastern Indonesia (Papua Province) and Papua New Guinea (mainland and Bougainville); 4 spp, keyed and illustrated by Hardy 1986]
..... *Themaroidopsis* Hering, 1941
- 23 Wing with anterior half brown beyond cell sc, if a quadrate hyaline indentation present in cells r_1+r_{2+3} , then cells br and r_{4+5} without medial hyaline spots and scutellum entirely setulose; head with lower orbital

- setae placed below middle of frons [eastern Indonesia (Ambon, West Papua, Papua) and Papua New Guinea (mainland and New Britain); 6 spp, keyed below; *Rioxina* Hering, 1941 is a synonym (Hardy 1986)] ...
 *Themaroides* Hendel, 1914
- Wing with a triangular hyaline indentation from costa in cell r_1 or r_1+r_{2+3} ; cells br and r_{4+5} with medial hyaline spots present, if not then scutellum only laterally setulose; head with lower orbital setae placed above middle of frons, usually in upper quarter 24
- 24 Wing pattern blackish brown; scutellum black with a medial yellow band, swollen and densely setulose [Australia; 5 spp, keyed and illustrated by Permkam and Hancock 1995 and in Fig. 3; the South Australian *A. bicolor* (Macquart, 1855) is a synonym of *A. basalis* (Walker, 1853) (Hancock 1998)] *Acanthonevroides* Permkam & Hancock, 1995
- Wing pattern brown and yellow-brown; scutellum pale with at most basal dark patches, not swollen and setulose only laterally [eastern Indonesia (Timor, Misool and Papua Province), Papua New Guinea and Australia); 11 spp, keyed below; *Kertesziola* Hering, 1941 is a synonym (Permkam and Hancock 1995)] *Termitoriox*a Hendel, 1928



Fig. 3. *Acanthonevroides jarvisi* (Tryon): male from SE Queensland. Photograph by Andy Wang (Queensland Museum).

- 25 Wing veins Cu base and Cu₁ bare; anepisternum with a prominent black seta near lower medial margin [Papua New Guinea and Australia (neQld); 2 spp, keyed and illustrated by Permkam and Hancock 1995 and illustrated by Hardy 1986] *Paedohexacinia* Hardy, 1986
- Wing vein Cu base setulose; vein Cu₁ bare or setulose; anepisternum without a prominent black seta near lower medial margin 26
- 26 Wing vein R₁ extending to beyond level of DM-Cu crossvein, the pterostigma much longer than cell c [eastern Indonesia (Papua Province) and Papua New Guinea; 1 sp., illustrated by Hardy 1986]
..... *Cheesmanomyia* Malloch, 1939
- Wing vein R₁ ending near level of R-M crossvein, the pterostigma no longer than cell c and normally much shorter 27
- 27 Face concave in profile, the epistome protruding; male fore tibia with a densely white-pilose, pad-like posteroapical process [2 subgenera]
..... *Clusiosoma* Malloch, 1926 ... 28
- Face vertical or convex in profile, the epistome not protruding 29
- 28 Scutum black; face black; parafacials yellow; male fore femur with a spinose basoventral tubercle but without ventral spines [Papua New Guinea and Australia (nQld); 1 sp., illustrated by Hardy 1986 and Permkam and Hancock 1995] subgenus *Paraclusiosoma* Hardy, 1986
- Scutum partly fulvous; if face black then parafacials also black; male fore femur with long ventral spines but no tubercle [eastern Indonesia (Ambon, Waigeo, West Papua and Papua), Papua New Guinea (mainland, New Britain, New Ireland), northern Australia and Solomon Islands; 14 spp, keyed and illustrated by Hardy 1986 (non-Australian species) and Permkam and Hancock 1995 (Australian species); *C. minutum* (de Meijere, 1913) appears to have the first and second antennal segments black, not yellow as implied by Hardy (1986) and *C. semifuscum* Malloch, 1926, **syn. rev.**, separated by Permkam and Hancock 1995, is returned to synonymy (as in Hardy 1986); for separation of *pullatum* group males, see key below] subgenus *Clusiosoma* Malloch, 1926
- 29 Face yellow with a pair of brown lateral spots on ventral half; scutum yellow with a pair of submedial brown vittae extending onto scutellum laterally; abdomen yellow with broad brown lateral margins; male fore tibia with 2 preapical setae; male fore basitarsus with an apically spinulose anteroventral process [eastern Australia; 1 sp., illustrated by Permkam and Hancock 1995] *Clusiosomina* Malloch, 1939
- Not as above; if face with dark spots or band then this is placed medially, not in lower half; male fore basitarsus without an apical process 30

- 30 Wing vein R₁ ending beyond line of R-M crossvein, the pterostigma as long as cell c; scutum yellow with 6 black vittae not extending onto scutellum [eastern Indonesia (Papua Province) and Papua New Guinea; 1 sp., illustrated by Hardy 1986] *Nothoclusiosoma* Hardy, 1986
- Wing vein R₁ ending at or before line of R-M crossvein, the pterostigma shorter than cell c; scutum variable, if yellow with 6 black or brown vittae then submedial pair extending over scutellum 31
- 31 Face with a black medial spot; male with fore femur ventrally spinose, fore tibia with a pad-like posteroapical process, fore basitarsus without a ventral comb and surstyli long and slender [Papua New Guinea; 1 sp., illustrated by Hardy 1986] *Hemichlusiosoma* Hardy, 1986
- Face black, yellow or with a pair of usually confluent lateral spots; male with fore femur often not ventrally spinose, fore tibia without a pad-like posteroapical process, fore basitarsus often with a ventral comb and surstyli short and thick *Trypanocentra* ‘complex’ ... 32
- 32 Head with vertex developed into a sharp, thin, posteriorly directed keel; face distinctly convex in profile, highest just below middle and receding to epistome and often with a black, transverse medial band [eastern Indonesia (West Papua), Papua New Guinea (mainland and New Britain), Australia (neQld) and Solomon Islands; 3 spp, keyed and illustrated by Hardy 1986; ‘*R. fascifacies*’ of Permkam and Hancock 1995 is a misidentification of *R. nigrotibia* Hering (Hancock *et al.* 1998)]
 *Rabaulia* Malloch, 1939
- Head with vertex at most weakly keeled, not posteriorly directed; face normally vertical, if convex then all yellow and highest in middle 33
- 33 Face gibbose, the convexity highest in the middle; face yellow and unspotted; scutum with a pair of submedial black vittae; male fore basitarsus with black ventral comb [eastern Indonesia (Papua Province) and Papua New Guinea (mainland and New Britain); 1 sp., illustrated by Hardy 1986] *Rabauliomorpha* Hardy, 1970
- Face vertical in profile or almost so; colour of face and scutum variable; male fore basitarsus with or without a ventral comb [2 subgenera]
 *Trypanocentra* Hendel, 1914 ... 34
- 34 Male fore basitarsus with 1 or 2 ventral combs [eastern Indonesia (Papua Province) and Papua New Guinea (mainland, New Britain, New Ireland); 5 spp, keyed and illustrated by Hardy 1986]
 subgenus *Clusiomorpha* Hering, 1941
- Male fore basitarsus without a ventral comb [eastern Indonesia (Aru), Papua New Guinea and Australia (neQld); 6 spp, keyed and illustrated by Hardy 1986; additional illustrations of *T. nigrithorax* Malloch, 1939 in Permkam and Hancock 1995] subgenus *Trypanocentra* Hendel, 1914

Key to *Aethiothemara* species

- 1 Pterostigma very elongate, the costal section in cell r_1 shorter than that in cell r_{2+3} ; vein M with last section shorter than the second last; hyaline indentation in cell r_1 oval; mid femur with 4 long ventral setae [Equatorial Guinea (Bioko)] *A. transiens* Hendel, 1928
 - Pterostigma less elongate, the costal section in cell r_1 longer than that in cell r_{2+3} ; vein M with last section longer than the second last; hyaline indentation in cell r_1 quadrate; mid femur with 2 long ventral setae 2
- 2 Pterostigma with apex hyaline, included within the hyaline indentation in cell r_1 , which ends at vein R_{2+3} ; hyaline spots in cells br and r_{4+5} narrow and linear [Cameroon, Equatorial Guinea (Bioko), Gabon, Congo, Democratic Republic of Congo and Uganda; var. *trispila* (Bezzi, 1923) has an additional hyaline spot in cell dm below R-M crossvein; illustrated by Enderlein 1911] *A. fallacivena* (Enderlein, 1911)
 - Pterostigma with apex brown or black; hyaline indentation in cell r_1 sometimes extends beyond vein R_{2+3} ; hyaline spots in cells br and r_{4+5} often broad and rounded 3
- 3 Hyaline indentation in cell r_1 ends at vein R_{2+3} ; hyaline spots in cells br and r_{4+5} elongate or broadly oval 4
 - Hyaline indentation in cell r_1 extends beyond vein R_{2+3} ; hyaline spots in cells br and r_{4+5} broadly rounded 5
- 4 Scutum with dorsocentral setae placed just before the supra-alar setae; hyaline spots in cells br and r_{4+5} about 1.5 times as high as broad [Cameroon] *A. trigona* Hendel, 1928
 - Scutum with dorsocentral setae placed just behind the supra-alar setae; hyaline spots in cells br and r_{4+5} broadly oval [Uganda and Tanzania] *A. graueri* Hendel, 1928
- 5 Scutum and scutellum without (?) a pair of dark submedial vittae [‘West Africa’; only partially described in a key] *A. speiseriana* (Bezzi, 1924)
 - Scutum and scutellum with a pair of dark submedial vittae [Uganda; probably synonymous with *A. speiseriana*] *A. striata* Hendel, 1928

Key to *Diarrhagma* species

^ = new records based on examined material in the Natural History Museum, London () or photographs submitted for identification (^).

- 1 Abdomen with dark transverse bands narrower than yellow bands; wing of male with a distinct hyaline spot in cell r_{4+5} (female with 2 spots) and hyaline spots in cells r_{2+3} and dm distinct [India and Sri Lanka*; *Trypeta incisa* Wiedemann, 1824 and *Trypeta viana* Walker, 1849 are synonyms

- (Hardy 1986, Hancock 1998); illustrated by Bezzi 1913 and Hancock and Drew 1994b] *D. modestum* (Fabricius, 1805)
- Abdomen with dark transverse bands broader than yellow bands; wing of male without a hyaline spot in cell r_{4+5} (female with 2 spots) and hyaline spots in cells r_{2+3} and dm vestigial or absent [S China (Yunnan, Guangxi, Guangdong*, Hong Kong*, Macau, Hainan), Vietnam^, Thailand, West Malaysia*, Singapore^, Borneo, Indonesia (Java, Sumba) and southern Philippines (Mindanao, Palawan); the citation of Ambon in the Moluccas as the type locality (Bezzi 1913, Hardy 1986) appears to be an error, since Doleschall (1856) mentioned only Jogjakarta in central Java in his original description (Hancock and Drew 1994b) and the specimen is possibly mislabelled; *Diarrhegma eburata* Zia, 1963 is a synonym (Hancock and Drew 1994b); illustrated by Wang 1998 (both sexes) and Zia 1963 (♀)] *D. paritii* (Doleschall, 1856)

Key to *Dirioxa* species

- 1 Wing largely fuscous, without a hyaline costal indentation in cell r_1 above R-M crossvein or a hyaline band across apex of cell dm; abdomen fulvous to red-brown with or without dark transverse bands on terga I+II, III and IV [Vanuatu; illustrated by Hancock and Drew 2003] *D. fuscipennis* Hancock & Drew, 2003
- Wing with a broad, quadrate hyaline costal indentation in cell r_1 above R-M crossvein and a hyaline band across apex of cell dm; abdomen fulvous on terga I+II, mostly or entirely black on terga III-V 2
- 2 Wing with posterior hyaline indentation in cell cu_1 extending broadly into cell dm medially; hyaline apical band in cell dm distinctly broadened anteriorly and often united posteriorly with medial indentation [Australia and New Caledonia (introduced); *Trypeta musae* Froggatt, 1899 and *Rioxa confusa* Hardy, 1951 are synonyms (Permkam and Hancock 1995); illustrated by Hardy 1951 and Permkam and Hancock 1995] *D. pornia* (Walker, 1849)
- Wing with posterior hyaline indentation in cell cu_1 not extending into cell dm; hyaline apical band in cell dm not broader anteriorly than posteriorly [eastern Indonesia (Papua Province); illustrated by Hardy 1986; placed in *Dirioxa* by Hancock and Drew 2003] *D. incerta* (Hardy, 1986)

Key to *Termitorioxa* species

- 1 Wing cell r_{4+5} with a curved longitudinal hyaline band from spot above DM-Cu crossvein to apex [Australia (Qld); illustrated by Permkam and Hancock 1995] *T. bicalcarata* (Hering, 1944)
- Wing cell r_{4+5} without a curved longitudinal hyaline band at apex 2

- 2 Wing cell dm almost entirely hyaline or with an elongate medial hyaline band along vein Cu₁ 3
- Wing cell dm mostly brown and without an elongate hyaline band along vein Cu₁ 5
- 3 Wing cell dm almost entirely hyaline; large hyaline area in cell dm united with large hyaline spots in cells br and r₄₊₅; a second large hyaline spot in cell r₄₊₅ united with indentation in cell m; postnotum fulvous [Papua New Guinea; illustrated by Hardy 1986] *T. flava* (Hardy, 1986)
- Not as above; cell dm with an elongate medial hyaline band along vein Cu₁; cell r₄₊₅ with second hyaline spot, if present, small and isolated; postnotum largely blackish brown 4
- 4 Cell r₄₊₅ with hyaline spot above DM-Cu crossvein united with indentation in cell m; scutum fulvous [Australia (nQld); illustrated by Permkam and Hancock 1995] *T. testacea* (Hendel, 1928)
- Cell r₄₊₅ with hyaline spot above DM-Cu crossvein not united with indentation in cell m; scutum with a brown to black posterior border [eastern Indonesia (Misool and Papua Province) and Papua New Guinea; *Ptilona lateralis* Kertész, 1901 is a synonym (Hardy 1986); illustrated by Hardy 1986] *T. meritoria* (Walker, 1864)
- 5 Cell cu₁ with a hyaline indentation at apex below DM-Cu crossvein; costal cell c hyaline [northern Australia; illustrated by Permkam and Hancock 1995] *T. exleyae* Permkam & Hancock, 1995
- Cell cu₁ without a hyaline indentation at apex below DM-Cu crossvein; costal cell c hyaline or at least partly yellowish 6
- 6 Head with 1 pair of orbital setae; wing base pale yellowish, including cells bc and c 7
- Head with 2 pairs of orbital setae; wing base hyaline or with pale yellowish markings in cell c or cells c+br 8
- 7 Scutum normally with a pair of brown patches adjacent to scutellum; scutellum normally with a pair of dark basal patches; postnotum blackish brown laterally; wing with hyaline spot in cell r₄₊₅ not united with indentation in cell m and pattern dark brown with distinct yellowish areas in most of cell dm and around R-M crossvein; male with a tuft of fine hairs at apex of arista [northern Australia; illustrated by Permkam and Hancock 1995] *T. termitoxena* (Bezzi, 1919)
- Scutum and scutellum entirely fulvous; postnotum fulvous; wing with hyaline spot in cell r₄₊₅ united with indentation in cell m; male without a tuft of fine hairs at apex of arista [eastern Indonesia (Timor); illustrated by Hardy 1986] *T. timorensis* Hardy, 1986

- 8 Cell r_1 with hyaline indentation small, not crossing into cell r_{2+3} ; cell c hyaline 9
- Cell r_1 with hyaline indentation large, crossing into cell r_{2+3} ; cell c at least partly yellowish 10
- 9 Cells br and r_{4+5} each with a distinct medial hyaline spot; hyaline spot at apex of cell dm anteriorly placed [Australia (NT); illustrated by Permkam and Hancock 1995] *T. inconnexa* Permkam & Hancock, 1995
- Cells br and r_{4+5} without distinct hyaline spots; hyaline spot at apex of cell dm posteriorly placed [eastern Indonesia (Papua Province); illustrated by Hardy 1986] *T. acanthoneurides* (Hering, 1953)
- 10 Postnotum red-brown laterally; cells c+br yellowish, cell c sometimes with only a complete yellow costal band [Australia (NT); illustrated by Hancock 1996] *T. cobourgensis* Hancock, 1996
- Postnotum entirely fulvous; cell c with a yellow costal band over basal two-thirds [northern Australia; illustrated by Permkam and Hancock 1995] *T. laurae* Permkam & Hancock, 1995

Key to *Themaroides* species

- 1 Pleura with a longitudinal black or brown vitta from proepisternum to anatergite; wings largely brown, including costal cells 2
- Pleura pale with at most a dark line along dorsal margin of anepisternum; wings often with large hyaline indentations and base, including costal cells, subhyaline or yellowish 4
- 2 Scutum and scutellum with a complete medial black vitta; face with a medial black vitta on lower half; additional small secondary scutellar setae absent [eastern Indonesia (West Papua and Papua) and Papua New Guinea; *Rioxa debeauforti* de Meijere, 1906 is a synonym (Hardy 1986); illustrated by Hardy 1986] *T. abbreviatus* (Walker, 1865)
- Scutum and scutellum without a complete medial black vitta; face wholly yellow; 2 pairs of additional small secondary scutellar setae present 3
- 3 Scutum and scutellum yellow, without distinct dark vittae; scutellum entirely densely setulose [Papua New Guinea; illustrated by Hardy 1986] *T. robertsi* Hardy, 1986
- Scutum with 5 narrow, dark postsutural vittae; scutellum with dark lateral vittae and only densely setulose laterally, bare medially [Papua New Guinea; illustrated by Hardy 1986] *T. vittatus* Hardy, 1986
- 4 Wings pale brown to subhyaline (possibly teneral) but without distinct large hyaline marginal indentations; vein R_{4+5} straight, not curving posteriorly in apical portion, the wing narrow and elongate [Papua New Guinea; illustrated by Hardy 1986] *T. xanthosoma* Hardy, 1986

- Wings dark brown, subhyaline to yellow basally and with large hyaline marginal indentations in at least cells m and cu_1+dm ; vein R_{4+5} curving posteriorly in apical portion, the wing normal in shape 5
- 5 Wing with a large quadrate hyaline indentation in cells r_1 and r_{2+3} from costa to vein R_{4+5} ; posterior hyaline indentation confined to cells cu_1+dm ; scutellum without an additional pair of small secondary setae [eastern Indonesia (Ambon and West Papua) and Papua New Guinea; *Helomyza optatura* Walker, 1865 is a synonym (Hardy 1986; illustrated by Hardy 1986) *T. quadrifer* (Walker, 1861)
- Wing without an anterior hyaline indentation; posterior hyaline indentation in cells cu_1+dm extending into cell br; scutellum with an additional pair of small secondary subapical setae [Papua New Guinea (New Britain); illustrated by Hancock and Drew 2003]
..... *T. bicolor* Hancock & Drew, 2003

Key to *Clusiosoma pullatum* group males

The *pullatum* group keys to couplet 14 in Hardy (1986). Males of the Australian *C. macalpinei* Permkam & Hancock, 1995 (females unknown) may be separated using the following key.

- 1 Face and genae yellow; occiput yellow posteroventrally; fore femur broadly swollen and with a subbasal clump of ventral spinules in basal third [Papua New Guinea; illustrated by Hardy 1986]
..... *C. subpullatum* Hardy, 1986
- Face and genae black; occiput black posteroventrally; fore femur without a clump of ventral spinules in basal third 2
- 2 Fore femur narrowly swollen and with long spines restricted to middle third, absent from apical third [Papua New Guinea; illustrated by Hardy 1986] *C. pullatum* Hering, 1941
- Fore femur broadly swollen and with long spines continuous over middle and apical thirds [Australia (nQld); illustrated by Permkam and Hancock 1995] *C. macalpinei* Permkam & Hancock, 1995

Discussion

The Afrotropical *Aethiothemara* group of genera have mid tibiae with 1 long and several short apical spines. One of the secondary spines is about half as long as the main spine in *Themarictera* and all are about 1/5 as long in the other genera (A. Freidberg pers. comm.). This is similar to the condition seen in the *Neothemara* and *Clusiosoma* subgroups but cell m has only a single marginal hyaline indentation and the pattern is not almost entirely brown, suggesting a closer relationship with *Diarrhegma* and the *Themaroides* subgroup and a homoplasious reduction in the size of the secondary spine.

It appears likely that the *Aethiothemara*, *Diarrhegma* and *Themaroides* groups represent radiations in Africa, Asia and Australasia respectively, the presence of tree-trunk breeders in all three groups suggesting that decaying tissue beneath the bark is the ancestral larval food source. Fruit-feeding in *Themarictera*, *Dirioxa* and the *Clusiosoma* subgroup, which infest different fruit types, are therefore likely to represent homoplasious apomorphies.

All six African genera lack anepimeral (= pteropleural) setae and the R-M crossvein is placed within the apical third of cell dm, supporting monophyly of the group. *Afrocneros*, *Labeschatia*, *Ocnarioxa* and *Ptiloniola* have only 4 scutellar setae (apomorphy within the group) and appear to form a related series; *Aethiothemara* and *Themarictera* have the usual 6 scutellar setae. In *Themarictera* the pterostigma is shorter and the secondary midtibial spine longer than in the other genera and the male head is expanded, similar in shape to some *Themara* Walker species in the *Acanthonevra* group.

In the Southeast Asian genus *Diarrhegma*, the short, broad epandrium and surstyli in males and long-setose, apically broadly rounded aculeus are typical of the groups treated here. Although host records are few, it is likely to be a non-generalist breeder beneath decaying tree bark.

In the Australasian *Themaroides* group, the *Themaroides* subgroup most resembles the *Diarrhegma* group in having two long, subequal midtibial spines. The male epandrium and surstyli are short and broad, narrowed slightly in *Termitorioxax* and some *Themarohystrix*. The aculeus is apically blunt or broadly rounded except in *Themarohystrix*, where the apex is subtriangular and tapered to a blunt point (apomorphy). In *Buloloa*, *Themarohystrix* and *Themaroidopsis* veins M and/or Cu+Cu₁ are setulose, a character also seen in most *Clusiosoma* subgroup species. *Buloloa* and *Enoplopteron* have a row of long setae on the costa (apomorphy). In the Australian genera *Acanthonevroides*, *Aridonevra* and *Taeniorioxax* the scutellum is distinctly swollen (apomorphy); these three genera, and possibly also *Walkeraitia*, lack the additional supra-alar seta that is present (apomorphy) in all the other genera, although in *Termitorioxax* the additional seta is small and sometimes more than one are present. *Walkeraitia* and *Aridonevra* share an unusually-shaped cell dm, narrowed in basal half and broadly expanded in distal half, together with elements of the wing pattern, that suggest a reasonably close relationship.

The *Neothemara* subgroup is characterised by the numerous hyaline spots or indentations on the wing, including three marginal spots in cell M. Where known, all have a short and broad epandrium and surstyli in males except in *Hexaresta multistriga* (Walker), where the surstyli are distinctly narrowed (apomorphy). The aculeus is apically blunt or broadly rounded except in *Neothemara digressa* Hardy, where it is short and apically triangular (apomorphy); this species is possibly generically distinct.

Within the *Clusiosoma* subgroup, the male epandrium and surstyli are short and broad in *Nothoclusiosoma*, *Paedohexacinia*, *Rabaulia*, *Rabauliomorpha* and *Trypanocentra*, or long and slender (apomorphy) in *Cheesmanomyia*, *Clusiosoma*, *Clusiosomina* and *Hemiclusiosoma*. An apical pad-like process on the fore tibia (apomorphy) links *Nothoclusiosoma* with *Clusiosoma* and *Hemiclusiosoma*; in *Clusiosomina* the pad is absent but the fore basitarsus has a prominent anteroapical process (apomorphy) and in *Cheesmanomyia* both are absent. The face is concave in *Clusiosoma* (apomorphy), convex in *Rabaulia* and *Rabauliomorpha* (homoplasious apomorphies) and vertical or nearly so in the other genera. The female aculeus is tapered and apically acute (apomorphy) in *Paedohexacinia* and broadly blunt apically in all the other genera. *Rabauliomorpha* and *Trypanocentra* (*Clusiomorpha*) both have a ventral comb (apomorphy) on the fore basitarsus; its absence in subgenus *Trypanocentra* suggests that *Clusiomorpha* should be raised to genus level but further study is required. Additionally, *T.* (*Trypanocentra*) *tricuneata* Hardy resembles *Rabaulia* in facial and scutal markings and has a distinct keel on the vertex of the head, also suggesting that *Trypanocentra* is paraphyletic and in need of revision.

The *Dirioxa* group contains both rotting wood (*e.g.* *Lumirioxa*) and rotting fruit infesters (*Dirioxa*) and, with its single midtibial spine, is possibly related to the *Acanthonevra* group (Korneyev 1999). The epandrium and surstyli of males are short and broad. The aculeus is normally long-setose and apically blunt or broadly rounded (including in *Parachlaena*: see Hancock and Drew 1994a) except in *Griphomyia*, where it is short-setose and apically produced to a blunt point (apomorphy) and in *Micronevrina*, where it is microsetose and apically bifurcate (apomorphy). *Griphomyia* and *Mimoeuphranta* have small secondary scutellar setae and similar wing pattern elements, including the R-M crossvein placed below or before the midpoint of the pterostigma; in the other genera it is placed near or beyond its apex. In *Anchiacanthonevra* and *Parachlaena* cell r_1 has two distinct hyaline indentations from costa and the apex of cell r_{4+5} is extensively hyaline. The occasional use of fallen *Araucaria cunninghamii* cones by *Dirioxa pornia* larvae links that genus with *Lumirioxa*, which breeds beneath the bark.

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