

## **Revision of the Genus *Apterodromia* (Diptera: Empidoidea), With a Redefinition of the Tribe Ocydromiini**

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**ABSTRACT.** The Australian endemic genus *Apterodromia* Oldroyd (Diptera: Empidoidea) is revised and includes four apterous species (*A. evansi* Oldroyd, *A. minuta* n.sp., *A. setosa* n.sp., and *A. tasmanica* n.sp.) and eight fully winged species (*A. aurea* n.sp., *A. bickeli* n.sp., *A. irrorata* n.sp., *A. monticola* n.sp., *A. pala* n.sp., *A. spilota* n.sp., *A. tonnoiri* n.sp., and *A. vespertina* n.sp.). The male of *A. evansi* is described and zoogeographic patterns of the genus are discussed. On the basis of wing venation and male terminalia *Apterodromia* is transferred from the Tachydromiinae to the tribe Ocydromiini (subfamily Ocydromiinae). The Ocydromiini is redefined, two new genera (*Neotrichina* n.gen. and *Leptodromia* n.gen.) are described, and all included genera are listed. Keys to major lineages of Australian Empidoidea and Southern Hemisphere genera of Ocydromiini are provided. The following new combinations are listed: *Hoplopeza tachydromiaeformis* (Bezzi), *Leptodromia bimaculata* (Bezzi), *Neotrichina abdominalis* (Collin), *N. digna* (Collin), *N. digressa* (Collin), *N. distincta* (Collin), *N. elegans* (Bigot), *N. fida* (Collin), *N. indiga* (Collin), *N. insignis* (Collin), *N. insons* (Collin), *N. laeta* (Collin), *N. media* (Collin), and *N. obscurata* (Collin).

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The genus *Apterodromia* Oldroyd (Diptera: Empidoidea) was originally described on the basis of a single apterous female from Tasmania (Oldroyd, 1949, fig. 1). Although superficially resembling hemerodromiines, it has been considered to belong to the Tachydromiinae, possibly related to *Tachydromia* Meigen (= *Tachista* Loew) (Oldroyd, 1949; Smith, 1989). Oldroyd (1949) was initially hesitant to describe a new genus on the basis of an apterous specimen,

but it has proven to be a unique taxon, distinct from all other Australian empidoids. With greater emphasis on various mass-trapping collecting methods, further species and specimens of this genus have recently been collected for a total of 12 included species. In addition, this new material, including discovery of both males and fully winged species, now allows for a reevaluation of the phylogenetic placement of *Apterodromia* within the Empidoidea.

### Materials and methods

This study is based on more than 200 adult specimens of *Apterodromia* housed in the following institutions: American Museum of Natural History, New York (AMNH); Australian National Insect Collection, Canberra (ANIC); Australian Museum, Sydney (AMS); The Natural History Museum, London (BMNH); Canadian National Collection of Insects, Ottawa (CNC); Museum Victoria, Melbourne (MVM); University of Queensland Insect Collection, Brisbane (UQIC); Western Australian Museum, Perth (WAM).

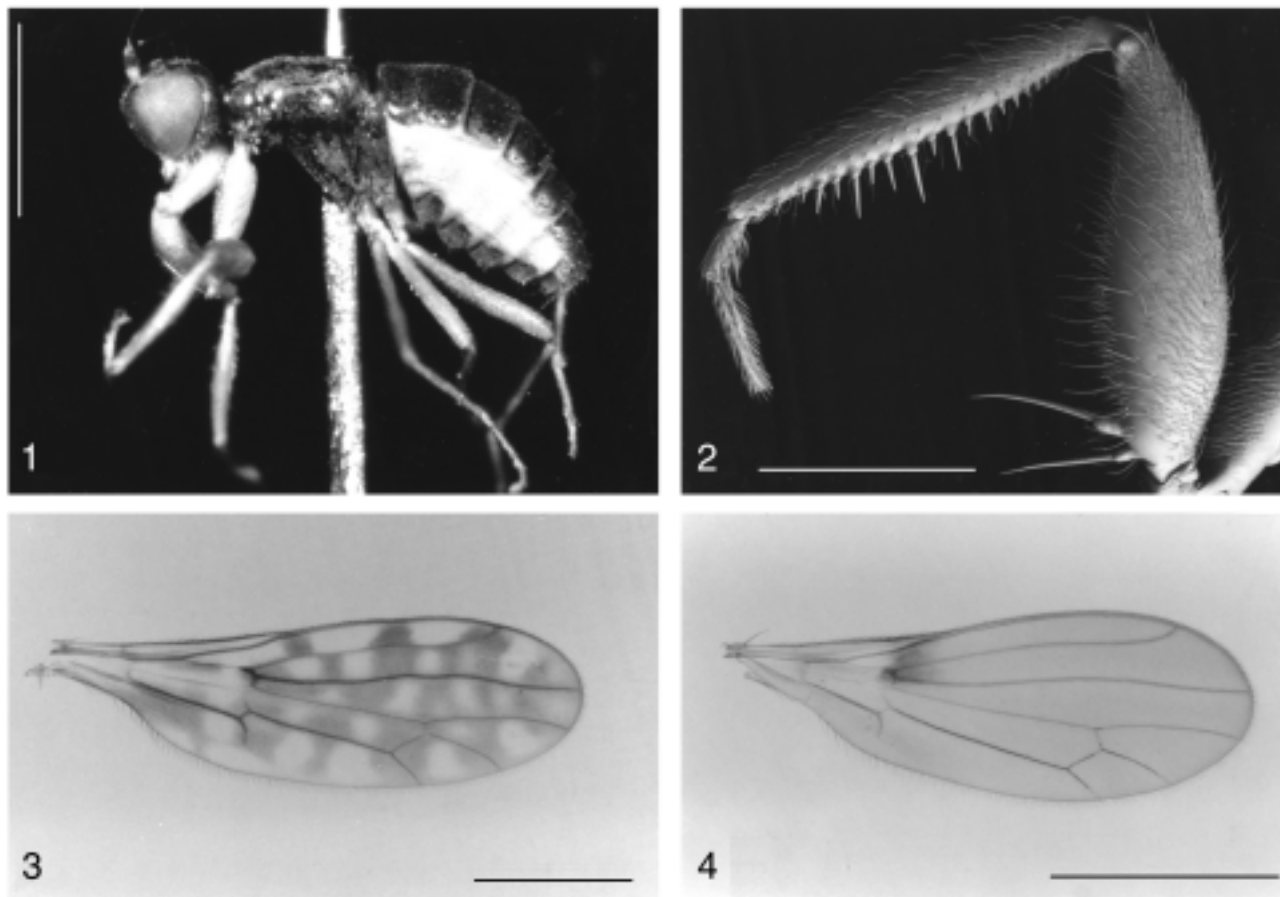
Terms used for adult structures primarily follow those of J.F. McAlpine (1981). Homologies of the male terminalia follow those of Cumming *et al.* (1995) and Sinclair (1996). To facilitate observation, terminalia were macerated in hot 85% lactic acid and immersed in glycerin. Label data of holotypes are cited in full, with original spelling, punctuation and date; lines are delimited by a slash (/), and a semicolon separates data quoted from different labels. In descriptions and key, right and left side of the male terminalia are based on the unrotated position viewed posteriorly, such that in the illustrations the right surstylus appears on the readers left side and vice versa. All male terminalia are figured in their unrotated position, except Fig. 14.

A number of specimens were collected through the use of shallow yellow plastic pans. The use of coloured pans has proven to be an effective and simple method for sampling Dolichopodidae and other empidoids (Pollet & Grootaert, 1987; Bickel, 1994). Pans containing a mixture of water, salt and several drops of detergent were distributed on the forest litter, usually near wet depressions, streams and marshy regions. Specimens of this genus are rarely collected with sweep nets and have only recently been obtained in numbers through the use of mass-trapping methods such as coloured pans and malaise traps. Many apterous species were extracted from wet leaf litter using berlese funnels.

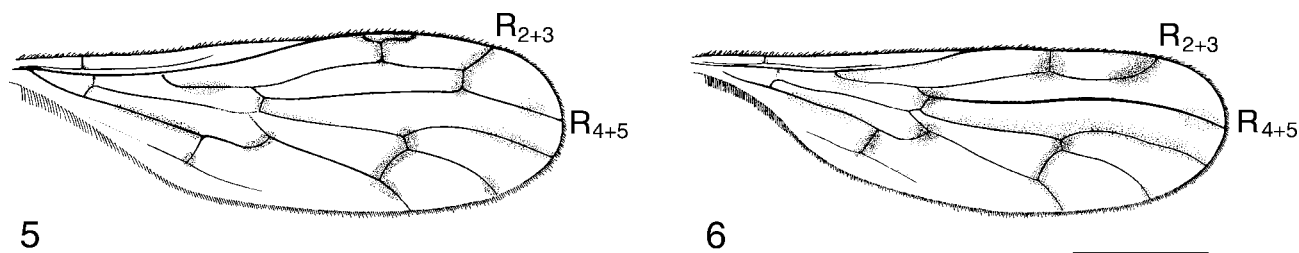
### *Apterodromia* Oldroyd

*Apterodromia* Oldroyd, 1949: 278. Type-species *A. evansi* Oldroyd (original designation).

**Diagnosis.** Distinguished from other empidoids by the following combination of characters: eyes meet below antennae, with dense ommatrichia; face flattened and angled posteriorly; base of fore femur armed with pair of long spine-like setae, mounted on short tubercles; fore tibia and



**Figures 1–4.** 1, Female of *Apterodromia evansi*. 2, Scanning Electron Micrograph, left foreleg of *A. irrorata*, posterior view. 3–4, Wing: 3, *A. irrorata*; 4, *A. bickeli*. Scale bars = 1.0 mm, except Fig. 2 where scale bar = 0.5 mm.



Figures 5–6. Wings of *Apterodromia*. 5, *A. spilota*; 6, *A. tonnoiri*. Scale bars = 1.0 mm.

first tarsomere with row of stout ventral setae; fore tibial gland present; proepisternum with 1–2 spine-like seta(e) above fore coxa; three veins emitted from cell dm,  $A_1$  faint below cell cup.

**Description.** Body length 1.5–4.5 mm.

**Male.** *Head* black. Eye contiguous on strongly flattened face; facets enlarged below antennae; ommatrichia present, longer on lower facets. Gena not extended below eye; ventral surface of head, posterior to mouth opening clothed in long, pale setulae. Frons broadly linear with sides nearly parallel in winged forms; broadly divergent in apterous forms; entirely clothed in pruinescence. Two pairs of fine ocellar setulae, directed forward. One pair of vertical and 1–2 pairs of upper occipital setae. Antennae inserted above middle of head; scape small, devoid of setulae; pedicel globose; first flagellomere pointed ovate to conical, with long, two-articled apical arista. Palpus tapered to point, two-thirds length of proboscis; palpifer bearing pair of setae; labrum and hypopharynx strongly arched posteriorly; 4 pairs of pseudotracheae present (Fig. 7).

*Thorax* yellow to entirely black. Thoracic macrotrichia mostly slender and short; acrostichal setulae biserial; dorsocentral setulae uniserial, increasing in length posteriorly; supra-alar setulae biserial; 1 notopleural seta, with scattered setulae; 1 pair of long, apical scutellar setae. Mesonotum entirely pruinescent. Postpronotal lobe differentiated. Prosternum fused to proepisternum forming precoxal bridge; anteppronotum well developed, forming wide “neck”-like extension; proepisternum with 1–2 spine-like setae above fore coxa. Meso- and metapleuron clothed entirely in dense whitish pruinescence.

*Wings* present or absent (reduced to traces of tegula); narrow and blunt-tipped; microtrichia of equal length; costal setae short; basal costal seta short or absent; C ending at  $M_1$ ; Sc evanescent, fading away beyond Rs; stigma lacking; Rs long arising near base of cell bm;  $A_1$  along lower margin of cell cup faded. Halter (if present) with white knob.

*Legs* yellow to brown. Fore coxa long, nearly 3 times as long as other coxae; clothed in long, white pile. Fore femur strongly swollen; base armed with pair of long spine-like setae, mounted on short tubercles (Fig. 2); long white pile beneath. Fore tibia somewhat dilated, with posteroventral row of 9–20 spine-like setae, alternating long and short; conspicuous tubular gland near base. First tarsomere of foreleg shorter than second, with posteroventral row of 4 spine-like setae, ending in long projecting spine (Fig. 2);

remaining tarsomeres slender, unarmed; mid and hindlegs slender, simple; hind femur thickened apically and bow-legged (apterous species) or straight (winged species).

*Abdomen.* Sclerites heavily sclerotized in wingless species (except sternites 1 and 2), more thinly sclerotized and usually reduced in size in winged species. Sclerites of segment 8 fused to form wide ring. Hypopygium asymmetrical, rotated approximately  $90^\circ$  to right (Fig. 14). Hypandrium narrow, posterior apex bluntly rounded; dorsal bridge heavily sclerotized; postgonites and ventral apodeme lacking. Epandrium deeply cleft; left surstylus elongate, cylindrical, bearing stout, inner dorsal setae; right surstylus shorter than left, bent nearly perpendicularly to epandrium. Right bacilliform sclerite elongate, bearing stout setae. Cercus usually short, thinly sclerotized, unmodified. Phallus with flexible, lateral cap lined with membrane; ejaculatory apodeme fused to base of phallus.

**Female.** Similar to male except as follows: winged species with abdomen lightly pigmented, sclerites thinly sclerotized except eighth segment; tergite 8 fused anteroventrally with sternite 8 (Figs. 8–10). Wingless species with all sclerites concolorous with thorax, heavily sclerotized. Cercus long, cylindrical, bearing long, fine setulae. Tergite 10 membranous, sternite 10 triangular. Spermatheca unpigmented, in form of long, slender, trachea-like tube, tightly coiled apically (Fig. 10).

**Distribution.** This genus is endemic to Australia, where it is widely disjunct, known from northern Queensland (above 700m), Western Australia, and Tasmania (Fig. 32). Despite extensive efforts using various collecting methods (e.g., malaise and yellow pan traps, sweeping) no specimens of *Apterodromia* have been found in New South Wales, Victoria, or ACT (Australian Capital Territory), which are probably the most extensively surveyed regions of Australia. This genus is most diverse in Tasmania, where all four apterous species and two winged species occur.

**Biology.** The genus has been collected in various humid habitats, including southern temperate and tropical rainforests, wet sclerophyll forests, and alpine herb fields. The adults are presumably predacious on small arthropods inhabiting leaf litter.

Several pairs of species (e.g., *A. aurea* and *A. bickeli*; *A. monticola* and *A. bickeli*; *A. monticola* and *A. pala*) are completely sympatric in Northern Queensland, collected on the same day in a series of malaise or yellow pan traps.

**Key to the species of *Apterodromia***

- 1 Wings and halteres absent ..... 2
- Wings and halteres present ..... 5
- 2 Fore femur yellow to yellowish-brown and concolorous with fore coxa, not distinctly darker on basal half; first flagellomere and arista brown, only slightly darker than scape and pedicel ..... *A. tasmanica*
- Fore femur brown to reddish-brown and darker than fore coxa, distinctly darker on basal half; first flagellomere and arista brownish-black, distinctly darker than scape and pedicel ..... 3
- 3 Male hypopygium with right surstylus short and blunt, subequal in length to right cercus (Fig. 17); scape and pedicel bright yellow ..... *A. evansi*
- Male hypopygium with right surstylus longer, at least twice length of right cercus (Figs. 22, 25); scape and pedicel yellowish-brown ..... 4
- 4 Male hypopygium with right bacilliform sclerite and each surstylus bearing long slender setae (Fig. 25), right surstylus with blunt conical tip; fore tibia reddish-brown, concolorous with basal half of fore femur ..... *A. setosa*
- Male hypopygium with right bacilliform sclerite and each surstylus bearing short stouter setae (Fig. 22), right surstylus abruptly constricted with narrow tip; fore tibia yellowish-brown, distinctly paler than basal half of fore femur ..... *A. minuta*
- 5 Wing with clouding along crossveins (Figs. 5, 6) or with irrorations (pale spots) (Fig. 3) ..... 6
- Wing lacking clouding along crossveins or irrorations (Fig. 4) ..... 9
- 6 Wing with irrorations (numerous pale spots) (Fig. 3); fore femur lacking row of ventral spine-like setae (as in Fig. 2) ..... 7
- Wing with clouding along crossveins, lacking irrorations (Figs. 5,6); fore femur with row of ventral spine-like setae ..... 8
- 7 Proepisternum with one spine-like seta above each fore coxa ..... *A. irrorata*
- Proepisternum with two spine-like setae above each fore coxa ..... *A. vespertina*
- 8 Wing with auxiliary crossvein between  $R_{2+3}$  and  $R_{4+5}$  (Fig. 5); fore coxa with inner row of short stout setae ..... *A. spilota*
- Wing lacking auxiliary crossvein between  $R_{2+3}$  and  $R_{4+5}$  (Fig. 6); fore coxa without inner row of short stout setae ..... *A. tonnoiri*
- 9 Scutum pale, mostly yellow or orange ..... 10
- Scutum dark, mostly brown or black ..... 11
- 10 Mesopleuron, metapleuron and mediotergite yellow or yellowish-orange ..... *A. pala*
- At least lower half of mesopleuron, most of metapleuron and mediotergite black or dark brown ..... *A. aurea*

- 11 Right bacilliform sclerite of male hypopygium with blunt spine-like setae on basal half (Fig. 23); tergite 8 of female weakly sclerotized on lateral margin subapically, with Y-shaped, dorsoapical sclerite; scutum brownish-orange to brown laterally, paler than anteromedial portion ..... *A. monticola*
- Right bacilliform sclerite of male hypopygium with blunt spine-like setae along entire length (Fig. 14); tergite 8 of female weakly sclerotized apically, with pair of rectangular dorsomedian sclerites; scutum brown to black laterally, concolorous with anteromedial portion ..... *A. bickeli*

***Apterodromia aurea* n.sp.**

Figs. 7–8, 11–13, 33

**Material examined.** HOLOTYPE ♂, “AUSTRALIA: N[orthern]. Q[ueens]L[and]: 11km/ up Mt. Lewis Rd. 900m/ 15–16.iv.1994; rainfor./ D.J. Bickel; ex. yellow/ pans nr. creek; Stop 1/ 16°36′[S] 145°17′E”; “HOLOTYPE/ *Apterodromia/ aurea/ Sinclair & Cumming* [red label]” (AMS). ALLOTYPE ♀, same data as holotype (AMS). PARATYPES: QUEENSLAND: ♀, Devil’s Thumb, 12km NW Mossman, 1000 m, 5.ix.1992, I.D. Naumann (ANIC); 8♀ ♀ 3♂ ♂, same data as holotype (ANIC, CNC); 4♂ ♂, 12km up Mt. Lewis Rd., 860 m, 16°30′S 145°17′E, 15–16.iv.1994, D.J. Bickel (AMS); ♂, 25 km up Mt. Lewis Rd., 1000 m, 16°32′S 145°17′E, 16.iv.1994, B.J. Sinclair (CNC); ♀, 25km up Mt. Lewis Rd., 1000 m, 16°32′S 145°17′E, 21.iv.1994, M. Moulds (AMS); ♀, Mt. Lewis at For. Hut, 1020 m, 16°36′S 145°16′E, 16.iv.1994, D.J. Bickel (ANIC); ♀, Mt. Spurgeon, wet scler. for., tree trunks, 16°26′S 145°12′E, 19.iv.1994, D.J. Bickel (AMS); 2♂ ♂, ♀, Windsor Tableland, montane for., 1260 m, 16°14′01″S 145°00′14″E, 17–18.iv.1994, D.J. Bickel (AMS).

**Diagnosis.** Distinguished from other winged species of *Apterodromia* by the scutum and upper half of the pleura coloured golden or orange-yellow, and lower half black. The male terminalia are characterized by blunt, spine-like setae on the basal half of the left surstylus and entire length of the right bacilliform sclerite.

**Description.** Body length 2.5–3.0 mm.

**Male. Head.** Scape, pedicel and first flagellomere brown; first flagellomere conical.

*Thorax* with dorsum orange except anteprototum and posterior third of notopleuron black; postpronotal lobe outlined in black. Proepisternum with 1 spine-like seta above fore coxa; notopleural seta stout. Lower half of mesopleuron black, upper half orange, extending to base of halter; laterotergite orange. Metapleuron and mediotergite black.

*Wing* infusate, with dark band from tip of R<sub>1</sub> to tip of cell br; basal costal seta short; cell dm elongate, narrow, nearly twice length of basal cells; M<sub>2</sub> and CuA<sub>1</sub> faded prior to wing margin; cell cup longer than cell bm; CuA<sub>2</sub> convex.

*Legs* yellowish-brown, except mid and hind coxae tinged with black. Fore coxa slender, parallel-sided, lacking inner setae. Anterior basal spine-like seta of fore femur twice length of posterior spine-like seta; lacking ventral row of spine-like setae. Fore tibia with 12 spine-like posteroventral setae.

*Abdomen.* Sclerites thinly sclerotized and reduced in size.

Hyandrium with crown of blunt, apical, spine-like setae (Fig. 13). Posterior margin of epandrium irregular. Left surstylus elongate, cylindrical, bearing blunt, inner dorsal spine-like setae on basal half; right surstylus short, pointed, strongly held inwards (Fig. 11). Right bacilliform sclerite elongate, bearing blunt, spine-like setae along entire length. Cerci thinly sclerotized, unmodified and symmetrical (Fig. 11). Phallus with broad lateral, flexible cap (Fig. 12).

**Female.** Similar to male except setae of foreleg more pronounced; fore tibia with 12–15 spine-like, posteroventral setae. Tergite 8 weakly sclerotized on lateral margin subapically, with Y-shaped, dorsoapical sclerite bearing several pairs of lateral setae (Fig. 8).

**Distribution.** Confined to high tablelands in the wet tropics region of northern Queensland near Cairns (Fig. 33).

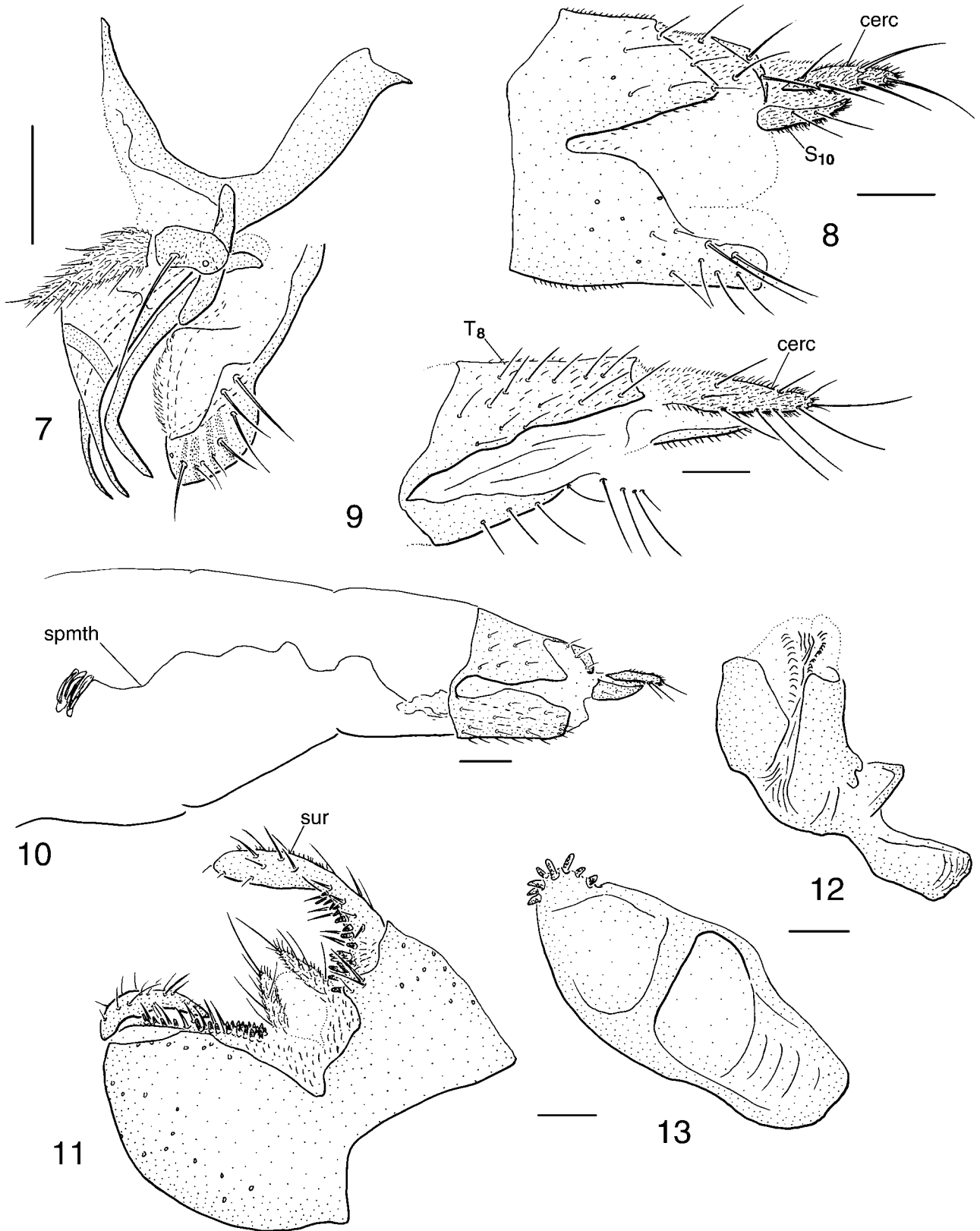
**Biology.** Collected in cool, submontane rainforests (above 700 m). The vegetation of these forests can be classified into several groupings, including simple microphyll vine-fern forest (MFT). See Adam (1992) for summary of the major rainforest types of northeastern Queensland.

**Etymology.** The specific name is derived from the Latin *aureus* (golden), referring to the golden or orange coloured thorax of this species.

***Apterodromia bickeli* n.sp.**

Figs. 4, 14–16, 34

**Material examined.** HOLOTYPE ♂, “AUSTRALIA: N[orthern]. Q[ueens]L[and]: 11km/ up Mt. Lewis Rd. 900m/ 15–16.iv.1994; rainfor./ D.J. Bickel; ex. yellow/ pans nr. creek; Stop 1/ 16°36′[S] 145°17′E”; “HOLOTYPE/ *Apterodromia/ bickeli/ Sinclair & Cumming* [red label]” (AMS). ALLOTYPE ♀, same data as holotype (AMS). PARATYPES: QUEENSLAND: 2♂ ♂, ♀, Bellenden Ker Range, Summit T.V. Sta., 1560 m, rainfor., malaise tp., 17.x–5.xi.1981, Earthwatch/ QLD Museum (ANIC); ♂, Devil’s Thumb, 12km NW Mossman, 1000 m, 5.ix.1992, I.D. Naumann (ANIC); 2♂ ♂, 2♀ ♀, Hugh Nelson Range, 1150 m, 17°27′S 145°29′E, 1.xii.1994–3.i.1995, 6.iii–4.iv., 1.viii–1.ix.1995, L. Umback, P. Zborowski (ANIC); 10♂ ♂, 5♀ ♀, Longlands Gap, 17°28′S 145°29′E, 1150 m, 4.iv–2.v.1995, 1.vi–3.vii., 1.viii–1.xi.1995, 30.xi.1995–3.i.1996, L. Umback, P. Zborowski (ANIC); 3♂ ♂, 8♀ ♀, Massey Ck., 17°37′S 145°34′E, 1000 m, 1.xii.1994–6.iii.1995, 5.iv–3.v.1995, P. Zborowski (ANIC); 5♂ ♂, 17♀ ♀, Mt. Edith, 17°06′S 145°37′E, 1050 m, 4.ii–6.iv.1995, 4–31.v.,



**Figures 7–13.** 7, Mouthparts of *Apterodromia aurea*, lateral view. 8–10, Female terminalia, lateral view: 8, *A. aurea*; 9, *A. irrorata*; 10, *A. pala*. 11–13, Male terminalia of *A. aurea*: 11, epandrium and cerci, dorsal view; 12, phallus; 13, hypandrium, dorsal view. Scale bars = 0.1 mm. Abbreviations: cerc, cercus; S<sub>10</sub>, sternite 10; spmth, spermatheca; sur, surstylus; T<sub>8</sub>, tergite 8.

30.v–31.viii.1995, L. Umback, P. Zborowski (ANIC); ♂, 4km up Mt. Edith Rd., Danbulla S.F., 800 m, 22–27.iv.1994, B.J. Sinclair (CNC); ♂, Mt. Edith For., 1.5m off Danbulla Rd. 6.v.1967, D.H. Colless (ANIC); 5 ♂♂, 2 ♀♀, Mt. Fisher, 17°33'S 145°32'E, 1150 m, 4.ii–21.iii.1995, 26.iii–2.v., 1–30.viii.1996, malaise tp., P. Zborowski (ANIC); 8 ♂♂, 16 ♀♀, Mt. Haig, 17°06'S 145°36'E, 1150 m, 1.xii.1994–3.i.1995, 6.iv–4.v.1995, 4–31.v., 30.vi–29.ix.1995, L. Umback, P. Zborowski (ANIC); ♂, Mt. Hypipamee N.P., 960 m, rainfor., 17°26'S 145°29'E, 13–27.iv.1994, D.J. Bickel (AMS); 2 ♂♂, 2 ♀♀, same data as holotype (AMS); ♂, Mt. Lewis Rd. at For. Hut, 1020 m, pans, 16°36'S 145°16'E, rainfor., 16.iv.1994, D.J. Bickel (AMS); ♀, 12km up Mt. Lewis Rd., 860 m, 16°30'S 145°17'E, 15–16.iv.1994, D.J. Bickel (AMS); ♀, 5–8 m Mt. Lewis Rd. off Mossman–Mt. Mulloy Rd., 22.iv.1967, D.H. Colless (ANIC); 2 ♂♂, ♀, Mt. Windsor Tableland, For. Hut, 1060 m, 16°15'42"S 145°02'25"E, 16–27.iv.1994, D.J. Bickel (AMS); 2 ♂♂, Windsor Tableland, montane for., 1260 m, 16°14'01"S 145°00'14"E, 17–18.iv.1994, D.J. Bickel (AMS). Several duplicates have been deposited in UQIC, CNC and AMNH.

**Diagnosis.** Distinguished from other winged species of *Apterodromia* by the mostly black thorax with only small posterior areas brownish. The male terminalia are characterized by blunt, spine-like setae distributed for nearly the length of the left surstylus and entire length of the right bacilliform sclerite. See *A. monticola* for additional distinguishing features.

**Description.** Body length 2.0–2.8 mm.

**Male. Head.** Scape, pedicel and first flagellomere brown; first flagellomere conical.

*Thorax* entirely black, except for golden iridescence on margin of scutum at base of wing. Proepisternum with 1 spine-like seta above fore coxa; notopleural seta stout. Mesopleuron, metapleuron and mediotergite black.

*Wing* (Fig. 4) infusate, with dark band from tip of  $R_1$  to tip of cell br; basal costal seta short; cell dm elongate, narrow, nearly twice length of basal cells;  $M_2$  and  $CuA_1$  faded prior to wing margin; cell cup longer than cell bm;  $CuA_2$  convex.

*Legs* yellowish-brown, except mid and hind coxae tinged with black. Fore coxa slender, parallel-sided, lacking inner setae. Anterior basal spine-like seta of fore femur less than twice length of posterior spine-like seta; lacking ventral row of spine-like setae. Fore tibia with 14–15 spine-like posteroventral setae.

*Abdomen.* Sclerites thinly sclerotized and reduced in size. Hypandrium with crown of blunt, apical, spine-like setae (Fig. 15). Posterior margin of epandrium with pair of deep U-shaped clefts. Left surstylus elongate, cylindrical, bearing blunt, spine-like setae along most of inner dorsal margin; right surstylus short, pointed, strongly arched. Right bacilliform sclerite elongate, bearing blunt, spine-like setae along entire length. Cerci thinly sclerotized, unmodified and symmetrical (Fig. 14). Phallus with broad lateral, flexible cap (Fig. 16).

**Female.** Similar to male except setae of foreleg more pronounced. Tergite 8 weakly sclerotized apically, with pair of rectangular dorsomedian sclerites, bearing transverse row of 3 subapical setae.

**Distribution.** Widespread in the high tablelands (above 700 m), in the wet tropics region of northern Queensland near Cairns (Fig. 34).

**Biology.** Adults appear to be present year-round, found in the cooler wet rainforests of the tablelands west of Cairns and montane forests of the Bellenden Ker Range. Some of the first specimens collected of this species were from the summit region of Mt. Bellenden Ker (1560 m), one of the highest points in northern Australia. The vegetation type on the summit is simple microphyll vine-fern thicket which represents a true tropical upper montane rainforest (Adam, 1992).

**Etymology.** The name *bickeli* is proposed in thanks to Dr Daniel J. Bickel (AMS) whose collecting efforts in northern Queensland have markedly increased our knowledge of this rare empidid genus.

### *Apterodromia evansi* Oldroyd

Figs. 1, 17–19, 35

*Apterodromia evansi* Oldroyd, 1949: 279.

**Material examined.** HOLOTYPE ♀, “Type [red bordered circle]”; “TASMANIA/J.W. EVANS”; “*Apterodromia/ evansi* n.sp ♀/ det. H. Oldroyd 1948/ HOLOTYPE” (BMNH).

**Additional material.** TASMANIA: ♂, ♀, Waldheim, Cradle Mt., 12–14.ii.1967 (UQIC); ♀, Hartz Mtns N.P., Hartz Rd., 740 m, eucalyp. scrub, 8–10.ii.1980 (ANIC).

**Diagnosis.** Distinguished from other apterous species by the darkly coloured basal half of the fore femur (including tubercles of spine-like setae), bright yellow basal antennal segments and blunt, short right surstylus.

**Description.** Body length 2.0–2.5 mm.

**Male. Head.** Scape and pedicel bright yellow; first flagellomere and arista dark brown; first flagellomere pointed ovate.

*Thorax* entirely black (Fig. 1). Proepisternum with 1 spine-like seta above fore coxa; notopleural seta stout. Mesopleuron, metapleuron and mediotergite black.

*Wings.* Absent. Halter absent.

*Legs.* Fore coxa pale yellow; lacking inner setae. Fore femur strongly attenuated apically; basal half of posterior surface reddish-brown, including tubercles of basal setae; anterior basal spine-like seta less than twice length of posterior spine-like seta; lacking ventral row of spine-like setae. Fore tibia with 9 spine-like posteroventral setae. Fore tibia, first and second tarsomeres reddish-brown, remaining tarsal segments brown. Mid and hind coxae black, except yellowish at apex. Mid and hind femora, tibiae, first tarsomere and basal half of second tarsomere reddish-brown, remaining tarsal segments brown.

*Abdomen.* Sclerites heavily sclerotized (except sternites 1 and 2 which are weakly sclerotized); tergites 1 and 2 immovably fused together with intersegmental suture still obvious at lateral margin. Hypandrium with scattered, pointed, stout setae near apex (Fig. 19). Posterior margin

of epandrium deeply cleft, rectangular. Left surstylus elongate, cylindrical, bearing long, tapering setae on inner dorsal margin near base; right surstylus short, blunt, geniculate near base, bearing long, stout setae along outer margin. Right bacilliform sclerite elongate, bearing stout setae along entire length. Cerci thinly sclerotized, unmodified and symmetrical (Fig. 17). Phallus with small oval flexible cap, with narrow extension (Fig. 18).

**Female.** Similar to male except setae of foreleg more pronounced; fore tibia with row of 11 spine-like posteroventral setae. Tergite 8 sclerotized along entire margin, not subdivided apically.

**Distribution.** Confined to wet forests of western Tasmania (Fig. 35). Oldroyd (1964: 95) erroneously listed this species from New Zealand.

**Biology.** This species was collected at an altitude of approximately 900 m at Cradle Mtn N.P.

*Apterodromia irrorata* n.sp.

Figs. 2–3, 9, 20–21, 32

**Material examined.** HOLOTYPE ♂, “AUST[ralia]:WA [Western Australia] Pemberton/Crowea St. For./Nov.–Dec. 1979/S.J. Curry”; “HOLOTYPE/ *Apterodromia/ irrorata/ Sinclair & Cumming* [red label]” (ANIC). ALLOTYPE ♀, same data as holotype. PARATYPES: WESTERN AUSTRALIA: ♂, Pemberton, 3.xii.1936, K.R. Norris (ANIC); 21 ♂♂, 14 ♀♀, same locality as holotype, xi–xii.1976, 1977, 1979, S.J. Curry (ANIC); 2 ♀♀, Pemberton, karri for., 30.xi–2.xii.1998, B.J. Sinclair (AMS); ♂, 10km SE Pemberton, karri for., yellow pans, 1–2.xii.1998, B.J. Sinclair (CNC). Several duplicates have been deposited in AMS, CNC, and WAM.

**Diagnosis.** Distinguished from all other winged species of *Apterodromia* by irrorated pattern on the wings and 1 spine-like proepisternal seta. The male terminalia are characterized by short, pointed setae on basal two-thirds of the left surstylus and entire length of the right bacilliform sclerite.

**Description.** Body length 2.5–3.0 mm.

**Male. Head.** Scape, pedicel, first flagellomere and arista dark brown; first flagellomere conical to subtriangular.

**Thorax** dark brown to black. Proepisternum with 1 spine-like seta above fore coxa; notopleural seta slender. Mesopleuron, metapleuron and mediotergite brown to black.

**Wing** (Fig. 3) infuscate; basal costal seta short, slender; veins weakly undulating; numerous pale spots or irrorations: cell  $r_1$  with 3 broad spots, cell  $r_{2+3}$  with 4–5 round spots, cell  $r_{4+5}$  with 5 spots, 2–3 spots in cell dm, 2 spots in cell  $m_1$ , cell  $m_2$  with 1 large spot, cell  $cua_1$  with 2 spots, cell  $cup$  with 1 apical spot. Auxiliary crossveins lacking; cell dm narrow, ca. one-third longer than cell bm;  $M_2$  and  $CuA_1$  faded prior to wing margin; cell  $cup$  longer than cell bm;  $CuA_2$  convex.

**Legs.** Fore coxa usually yellow, sometimes dark brown; lacking inner setae. Fore femur brown on posterior face, tubercles of basal setae yellow; femur not strongly

attenuated apically; anterior basal spine-like seta ca. equal in length to posterior spine-like seta; lacking ventral row of spine-like setae. Fore tibia with 14–16 spine-like posteroventral setae (Fig. 2), sometimes with 14–20 spine-like setae. Fore tibia and first tarsomere yellow, remaining tarsal segments dull brown. Mid and hind coxae brown, becoming black basally. Mid and hind femora with basal fourth pale yellow, remaining femora brown, darker towards apex; remaining leg segments yellowish-brown gradually darkening on tarsal segments.

**Abdomen.** Sclerites lightly sclerotized. Hypandrium with scattered, pointed, stout setae near apex. Posterior margin of epandrium deeply cleft, U-shaped. Left surstylus elongate, cylindrical, outer margin with long setae and pile of setulae; inner dorsal margin near base with dense stout setae. Right surstylus less than half length of left surstylus, geniculate near base, bearing long, stout basal setae; tapered to narrow apex. Right bacilliform sclerite elongate, bearing short, stout setae along entire length. Cerci thinly sclerotized, unmodified and symmetrical (Fig. 20). Phallus with oval flexible cap (Fig. 21).

**Female.** Similar to male, except spine-like setae more pronounced. Tergite 8 sclerotized along entire margin, not subdivided apically (Fig. 9).

**Distribution.** This species is confined to the extreme southwestern corner of Australia (Western Australia) (Fig. 32).

**Biology.** All known specimens of this species were collected in wet sclerophyll forests dominated by giant Karri trees (*Eucalyptus diversicolor*). These forests grow in deep red clay loams and receive more than 750 mm of annual rainfall.

Two female specimens were collected by sweep net while walking a hiking trail. They appeared slow moving in the net, with their forelegs held outstretched in front.

**Etymology.** The specific name is derived from the Latin *irroratus*, meaning bedewed, in reference to the pale punctations or clear areas on the wings.

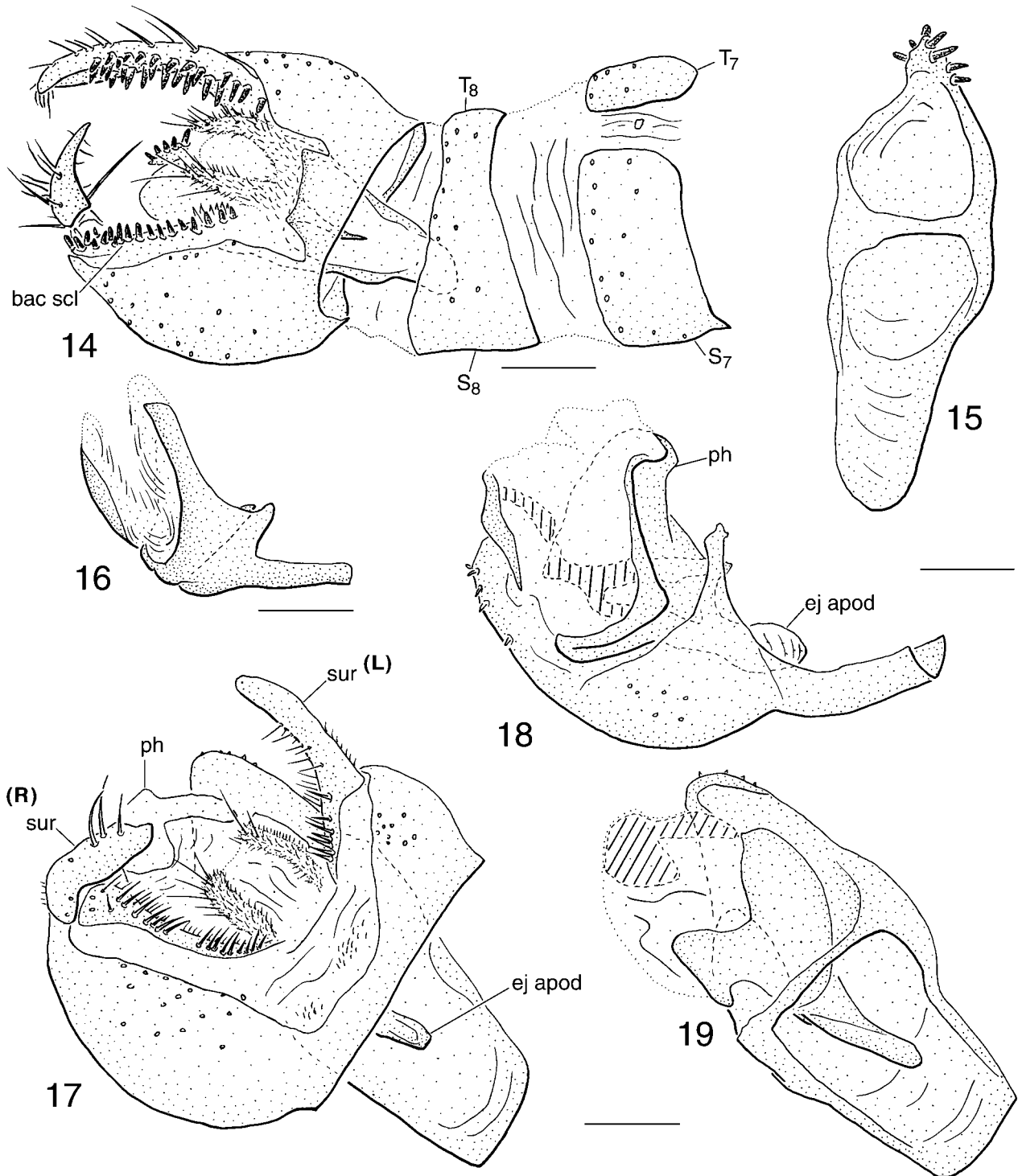
**Remarks.** There is also a dark form with 14–20 posteroventral spine-like setae on the fore tibia and the fore coxa is dark brown. The male terminalia are more darkly pigmented but otherwise identical to the paler form. Both forms are sympatric, collected from Crowea State Forest and are considered a result of intraspecific variation.

*Apterodromia minuta* n.sp.

Figs. 22, 35

**Material examined.** HOLOTYPE ♂, “AUSTRALIA: Tasmania/ NW 5km Renison Bell/ 180m, Berlese rainfor-/ est litter, 1|v|[19]87| N.I. Platnick *et al.*”; “HOLOTYPE/ *Apterodromia/ minuta/ Sinclair & Cumming* [red label] (ANIC). ALLOTYPE ♀, “AUST[ralia]: TAS[mania]: 7 km WNW/ Mt. Field/ 1.ii.1980/ Lawrence & Weir”; “ALLOTYPE/ *Apterodromia/ minuta/ Sinclair & Cumming* [red label]” (ANIC). PARATYPES: TASMANIA: ♂, same data as allotype (ANIC); ♀, Bubb’s Hill [42°07’S 145°46’E], W Victoria Pass, 28.iv.1987, berlese leaf litter, N.I. Platnick *et al.* (CNC); ♀, Mt. Rufus, Lk. St. Clair NP, berlese moss +





**Figures 14–19.** Male terminalia of *Apterodromia*. 14–16, *A. bickeli*: 14, postabdomen, ventrolateral view; 15, hypandrium, dorsal view; 16, phallus. 17–19, *A. evansi*: 17, terminalia, dorsal view; 18, hypandrium and phallus, lateral view; 19, hypandrium and phallus, dorsal view. Scale bars = 0.1 mm. Abbreviations: bac scl, bacilliform sclerite; ej apod, ejaculatory apodeme; L, left; ph, phallus; R, right; S, sternite; sur, surstylus; T, tergite.

rainfor. litter, 29.iv.1987, N.I. Platnick *et al.* (AMNH); ♀, Mt. Rufus, Lk. St. Clair NP, 29.iv.1987, berlese litter from beech eucalyptus for., N.I. Platnick *et al.* (AMNH); ♀, 0–10 km W Strathgordon, N. Mt. Sprent, 290 m, 27.iv.1989, berlese moss + litter wet rainfor., N.I. Platnick *et al.* (AMNH).

**Diagnosis.** Distinguished from the other apterous species by its yellowish-brown forelegs, yellowish tubercles at base of fore femur, and long right surstylus with an apical notch.

**Description.** Body length 1.8–2.0 mm.

**Male. Head.** Scape brown; pedicel yellowish-brown; first flagellomere and arista dark brown; first flagellomere pointed ovate.

**Thorax** entirely black. Proepisternum with 1 spine-like seta above fore coxa; notopleural seta stout. Mesopleuron, metapleuron and mediotergite black.

**Wings.** Absent. Halter absent.

**Legs.** Fore coxa pale yellow; lacking inner setae. Fore femur not strongly attenuated apically; basal half of posterior surface with dark brown band, tubercles of basal setae yellow; anterior basal spine-like seta less than twice length of posterior spine-like seta; lacking ventral row of spine-like setae. Fore tibia with 9 spine-like posteroventral setae. Fore tibia yellowish-brown, tarsal segments gradually darker apically. Mid and hind coxae yellowish-brown, becoming black basally. Mid and hind femora with broad brown band on basal half, more distinct on hindleg; remaining leg segments yellowish-brown gradually darkening on tarsal segments.

**Abdomen.** Sclerites heavily sclerotized (except sternites 1 and 2 which are weakly sclerotized); tergites 1 and 2 immovably fused together with intersegmental suture still obvious at lateral margin. Hypandrium with scattered, pointed, stout setae near apex. Posterior margin of epandrium deeply cleft, U-shaped. Left surstylus elongate, cylindrical, sparsely setose apically; inner dorsal margin near base with dense stout setae. Right surstylus nearly as long as left surstylus, geniculate near base, bearing long, stout basal and ventrolateral setae; from posterior view apex sharply constricted forming narrow tip. Right bacilliform sclerite elongate, bearing short stout setae along entire length. Cerci thinly sclerotized, unmodified and symmetrical (Fig. 22). Phallus with small oval flexible cap.

**Female.** Similar to male except mid and hindlegs yellowish-brown, banding not as distinct. Tergite 8 sclerotized along entire margin, not subdivided apically.

**Distribution.** This species is known from the wet forests of western Tasmania (Fig. 35).

**Biology.** This species was collected in leaf litter and moss samples which were first sifted and then extracted using berlese funnels.

**Etymology.** The specific name is derived from the Latin *minutus*, in reference to the very small size of this species.

### *Apterodromia monticola* n.sp.

Figs. 23, 34

**Material examined.** HOLOTYPE ♂, "QLD: Mt. Haig, 1150m/17.06S 145.36E, P./Zborowski, F.I.|malaise/ 1-xii-94-3-i-1995"; "HOLOTYPE/ Apterodromia/ monticola/ Sinclair & Cumming [red label]" (ANIC). ALLOTYPE ♀, "QLD: Hugh Nelson Range/ 1150 m, 17.27S 145.29E, P./ Zborowski, F.I.|malaise/ 3-i to 5-ii-1995"; "ALLOTYPE/ Apterodromia/ monticola/ Sinclair & Cumming [red label]" (ANIC). PARATYPE: QUEENSLAND: ♂, Longlands Gap, 17°28'S 145°29'E, 1150 m, 4.iv-2.v.1995, P. Zborowski (AMS).

**Diagnosis.** Distinguished from other winged species of *Apterodromia*, except *A. bickeli*, by a dark thorax and clear wings. Generally distinguishable from *A. bickeli* by the colouration of the scutum laterally, which is paler than the medial portion. In addition, unlike *A. bickeli*, the right bacilliform sclerite of the male lacks blunt spine-like setae on the apical half, and the female possesses a subdivided Y-shaped dorsoapical sclerite on tergite 8.

**Description.** Body length 2.0–3.0 mm.

**Male. Head.** Scape, pedicel and first flagellomere brown; first flagellomere conical.

**Thorax** brown to black, with some golden iridescence on margin of scutum at base of wing; scutum paler laterally, brownish-orange to brown. Proepisternum with 1 spine-like seta above fore coxa; notopleural seta stout. Mesopleuron, metapleuron and mediotergite brown to black.

**Wing** infusate, with dark band from tip of R<sub>1</sub> to tip of cell br; basal costal seta short; cell dm elongate, narrow, nearly twice length of basal cells; M<sub>2</sub> and CuA<sub>1</sub> faded prior to wing margin; cell cup longer than cell bm; CuA<sub>2</sub> convex.

**Legs** yellowish-brown, except mid and hind coxae tinged with black. Fore coxa slender, parallel-sided, lacking inner setae. Anterior basal spine-like seta of fore femur less than twice length of posterior spine-like seta; lacking ventral row of spine-like setae. Fore tibia with 14–15 spine-like posteroventral setae.

**Abdomen.** Sclerites thinly sclerotized and reduced in size. Hypandrium with crown of blunt, apical, spine-like setae. Posterior margin of epandrium uneven, sculptured. Left surstylus elongate, cylindrical, bearing blunt, spine-like setae along much of inner dorsal margin; right surstylus short, pointed, strongly arched. Right bacilliform sclerite elongate, bearing blunt, spine-like setae on basal half. Cerci thinly sclerotized, unmodified and symmetrical (Fig. 23). Phallus with broad lateral, flexible cap.

**Female.** Similar to male except setae of foreleg more pronounced. Tergite 8 weakly sclerotized on lateral margin subapically, with Y-shaped, dorsoapical sclerite bearing several pairs of lateral setae.

**Distribution.** Confined to high tablelands in the wet tropics region of northern Queensland near Cairns (Fig. 34).

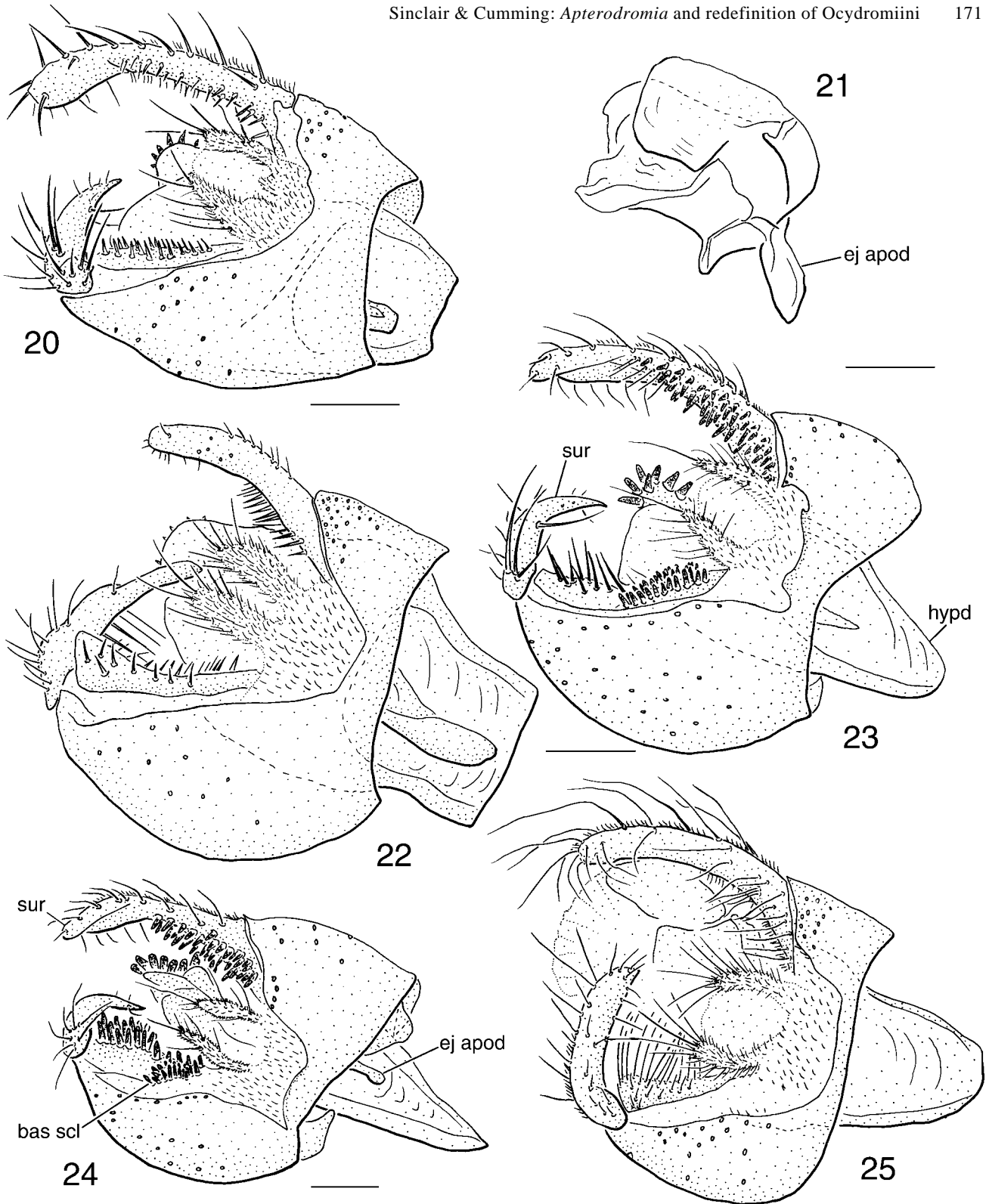
**Biology.** Collected in cool, submontane rainforests at 1150 m.

**Etymology.** A noun in apposition, derived from the Latin *monticola* (mountaineer), in reference to the montane habitat where this species is found.

### *Apterodromia pala* n.sp.

Figs. 10, 24, 33

**Material examined.** HOLOTYPE ♂, "AUST:QLD: Massey Ck./ 4.ii-6.iii.1995/P. Zborowski, 1000m/ 17°37'S 145°34'E/ ex. malaise trap"; "HOLOTYPE/ Apterodromia/ pala/ Sinclair & Cumming [red label]" (ANIC). ALLOTYPE ♀, "AUST:QLD: Massey Ck./ 5.iv-3.v.1995/ P. Zborowski, 1000m/ 17°37'S 145°34'E"; "ALLOTYPE/ Apterodromia/



**Figures 20–25.** Male terminalia of *Apterodromia*. 20–21, *A. irrorata*: 20, terminalia, dorsal view; 21, phallus. 22, *A. minuta*, dorsal view. 23, *A. monticola*, dorsal view. 24, *A. pala*, dorsal view. 25, *A. setosa*, dorsal view. Scale bars = 0.1 mm. Abbreviations: bac scl, bacilliform sclerite; ej apod, ejaculatory apodeme; hypd, hypandrium; sur, surstylus.

*pala*/ Sinclair & Cumming [red label]" (ANIC). PARATYPES: QUEENSLAND: ♂, 2 ♀, Hugh Nelson Range, 1150 m, 17°27'S 145°29'E, 1.xii.1994–3.i.1995, 3.i–5.ii.1995, 4.iv–2.v.1995, F.I. and malaise tps, P. Zborowski (AMS, ANIC); ♀, Longlands Gap, 17°28'S 145°29'E, 1150 m, 1.viii–1.ix.1995, malaise tp., L. Umbach (CNC);

3 ♂, 2 ♀, Massey Ck., 17°37'S 145°34'E, 1000 m, 4.ii–6.iii.1995, 3.v–4.vii.1995, 27.ii–26.iii.1996, malaise tp., P. Zborowski (ANIC); ♂, ♀, Mt. Edith, 17°06'S 145°37'E, 1050 m, 17.iii–6.iv.1995, 4–31.v.1995, malaise tp., P. Zborowski (AMS); ♂, Mt. Haig, 17°06'S 145°36'E, 1150 m, 4–31.v.1995, malaise tp., P. Zborowski (CNC);

♀, Mt. Lewis Rd. via Julatten, 1000 m, 10.x–11.xi.1987, rainfor. interc.tp., A. Walford-Huggins (ANIC).

**Diagnosis.** Distinguished from other winged species of *Apterodromia* by an almost entirely yellow to orange thorax and clear wings. The male terminalia are characterized by blunt, spine-like setae on the basal half of the left surstylus and entire length of the right bacilliform sclerite.

**Description.** Body length 2.5–3.5 mm.

**Male. Head.** Scape, pedicel and first flagellomere brown; first flagellomere conical.

*Thorax* almost entirely yellow to orange. Proepisternum with 1 spine-like seta above fore coxa; notopleural seta stout.

*Wing* infusate, with dark band from tip of  $R_1$  to tip of cell br; basal costal seta short; cell dm elongate, narrow, nearly twice length of basal cells;  $M_2$  and  $CuA_1$  faded prior to wing margin; cell cup longer than cell bm;  $CuA_2$  convex.

*Legs* yellowish-brown, except mid and hind coxae tinged with black. Fore coxa slender, parallel-sided, lacking inner setae. Anterior basal spine-like seta of fore femur twice length of posterior spine-like seta; lacking ventral row of spine-like setae. Fore tibia with 12 spine-like posteroventral setae.

*Abdomen.* Sclerites thinly sclerotized and reduced in size. Hypandrium with crown of blunt, apical, spine-like setae. Posterior margin of epandrium irregular. Left surstylus elongate, cylindrical, bearing blunt, inner dorsal spine-like setae on basal half; right surstylus short, pointed, strongly held inwards. Right bacilliform sclerite elongate, bearing blunt, spine-like setae along entire length. Cerci thinly sclerotized, unmodified and symmetrical (Fig. 24). Phallus with broad lateral, flexible cap.

**Female.** Similar to male except setae of foreleg more pronounced; fore tibia with 12–15 spine-like, posteroventral setae. Tergite 8 weakly sclerotized on lateral margin subapically, with Y-shaped, dorsoapical sclerite bearing several pairs of lateral setae (Fig. 10).

**Distribution.** Confined to high tablelands in the wet tropics region of northern Queensland near Cairns (Fig. 33).

**Biology.** Collected in cool, submontane rainforests (above 700 m).

**Etymology.** The specific name is derived from the Greek *pala* (gold nugget), in reference to the golden or orange colour of the thorax of this species.

#### *Apterodromia setosa* n.sp.

Figs. 25, 36

**Material examined.** HOLOTYPE ♂, "AUST[ralia]: TAS[mania]: Mt. Field/ N.P. Lyrebird Tr./ 17–19.ii.1994, 700m/ ex. yellow pans/ B.J. Sinclair"; "HOLOTYPE/ *Apterodromia/ setosa/ Sinclair & Cumming* [red label]" (AMS).

**Additional material.** TASMANIA: ♀, Mt. Rufus, Lk. St. Clair NP, 29.iv.1987, berlese litter from beech eucalyptus for., N.I. Platnick *et al.* (AMNH). This is possibly conspecific, but an associated male specimen is required for confirmation.

**Diagnosis.** Distinguished from the other apterous species by its reddish-brown forelegs, yellowish tubercles at base

of fore femur, and long setae on inner and outer faces of the surstyli and right bacilliform sclerite.

**Description.** Body length 2.0–2.5 mm.

**Male. Head.** Scape and pedicel yellowish-brown; first flagellomere and arista dark brown; first flagellomere pointed ovate.

*Thorax* entirely black. Proepisternum with 1 spine-like seta above fore coxa; notopleural seta stout. Mesopleuron, metapleuron and mediotergite black.

*Wings.* Absent. Halter absent.

*Legs.* Fore coxa pale yellow; lacking inner setae. Fore femur reddish-brown, basal half of posterior surface becoming darker basally, tubercles of basal setae yellow; not strongly attenuated apically; anterior basal spine-like seta less than twice length of posterior spine-like seta; lacking ventral row of spine-like setae. Fore tibia with 9 spine-like posteroventral setae. Fore tibiae reddish-brown, tarsal segments dull brown. Mid and hind coxae yellowish-brown, becoming black basally. Mid and hind femora with broad brown band on basal half, more distinct on hindleg; remaining leg segments yellowish-brown gradually darkening on tarsal segments.

*Abdomen.* Sclerites heavily sclerotized (except sternites 1 and 2 which are weakly sclerotized); tergites 1 and 2 immovably fused together with intersegmental suture still obvious at lateral margin. Hypandrium with scattered, pointed, stout setae near apex, right apicolateral margin with deep U-shaped notch. Posterior margin of epandrium deeply cleft, rectangular. Left surstylus elongate, cylindrical, bearing long, setae on outer margin, equal to half length of lobe; right surstylus slightly more than half length of left surstylus, blunt, geniculate near base, bearing long setae along outer margin. Right bacilliform sclerite elongate, bearing very long, slender setae along upper half. Cerci thinly sclerotized, unmodified and symmetrical (Fig. 25). Phallus with small oval flexible cap.

**Female.** Similar to male except banding of mid and hind legs less distinct. Tergite 8 sclerotized along entire margin, not subdivided apically.

**Distribution.** Known with certainty only from the holotype which was collected in yellow pans at an altitude of 700 m (Fig. 36).

**Biology.** The holotype of this species was collected in cool, moist forest with upper canopy of *Eucalyptus* sp. and lower canopy of *Nothofagus cunninghami*.

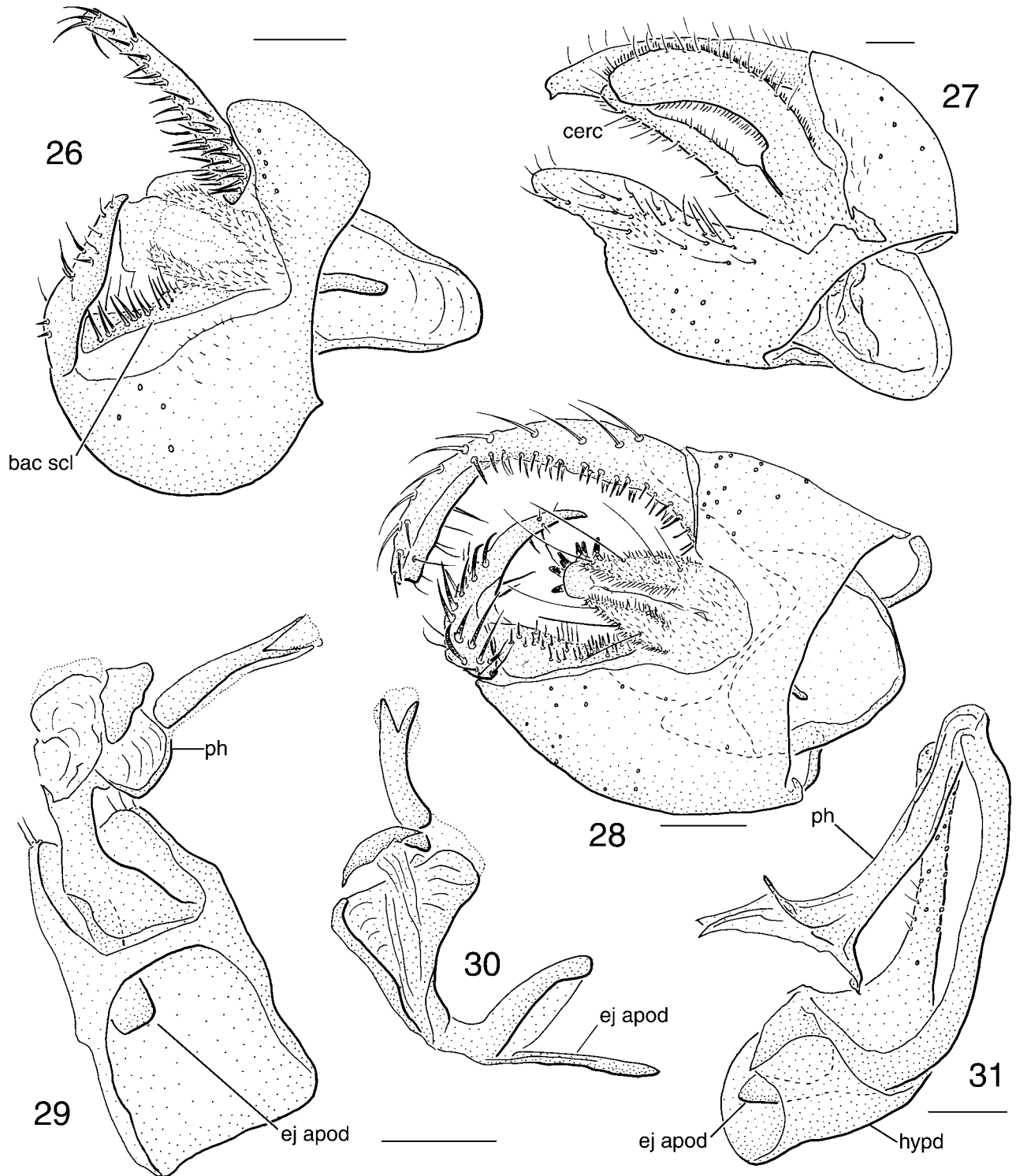
**Etymology.** The specific name is derived from the Latin *setosus*, meaning bristly, in reference to the long setae on the surstylus and right bacilliform sclerite.

#### *Apterodromia spilota* n.sp.

Figs. 5, 35

**Material examined.** HOLOTYPE ♀, "Hellyer River/ Gorge, NW Tas.[mania]/ 9.Feb.1971/ A. Neboiss"; "HOLOTYPE/ *Apterodromia/ spilota/ Sinclair & Cumming* [red label]" (MVM).

**Diagnosis.** Distinguished from all other winged species of *Apterodromia* by clouding surrounding the crossveins,



**Figures 26–31.** Male terminalia. 26, *Apterodromia tasmanica*, dorsal view. 27, *A. tonnoiri*, dorsal view. 28, *A. vespertina*, dorsal view. 29, *Leptodromia bimaculata*, hypandrium and phallus, dorsal view. 30, *L. bimaculata*, phallus, lateral view. 31, *Neotrichina* sp., hypandrium and phallus, oblique lateral view. Scale bars = 0.1 mm. Abbreviations: bac scl, bacilliform sclerite; cerc, cercus; ej apod, ejaculatory apodeme; hypd, hypandrium; ph, phallus.

presence of a ventral row of spine-like setae on the fore femur and an inner row of short stout setae on the fore coxa.

**Description.** Body length 4.5 mm.

**Female.** *Head.* Scape, pedicel, first flagellomere and arista dark brown; first flagellomere conical.

*Thorax* dark brown. Proepisternum with 2 spine-like setae above fore coxa; notopleural seta stout. Mesopleuron, metapleuron and mediotergite brown.

*Wing* (Fig. 5) infusate; basal costal seta lacking; dark cloudy patches surrounding crossveins and tips of major veins. Costa fading beyond  $M_1$ ; auxiliary crossveins between costa and  $R_{2+3}$  and  $R_{2+3}$  and  $R_{4+5}$ ; cell dm broad, shorter than cell bm;  $M_2$  and  $CuA_1$  reaching wing margin; cell *cup* short, two-thirds length of cell bm;  $CuA_2$  straight.

*Legs* yellowish-brown. Fore coxa slender, with inner row of short, stout setae. Anterior basal spine-like seta of fore femur equal in length to posterior spine-like seta; armed beneath with row of 8 spine-like setae mounted on short tubercles. Fore tibia with 12 spine-like posteroventral setae.

*Abdomen*. Sclerites brown, well sclerotized. Tergite 8 sclerotized along entire margin, not subdivided apically.

**Male.** Unknown.

**Distribution.** This species is known from only the type locality in northwestern Tasmania (Fig. 35).

**Etymology.** The specific name is derived from the Greek *spilotos*, meaning spotted, in reference to the dark cloudy patches on the wing.

#### *Apterodromia tasmanica* n.sp.

Figs. 26, 36

**Material examined.** HOLOTYPE ♂, “[Australia] 42.40S 145.58E/ Southwest Tasmania/ 19.iii.1976/ C. Howard, litter”; “HOLOTYPE/ *Apterodromia/ tasmanica/ Sinclair & Cumming* [red label]” (ANIC). ALLOTYPE ♀, “[Australia] 42.35'S 145.42'E/ Southwest Tasmania/ 29.i.1976/ C.Howard, litter”; “ALLOTYPE/ *Apterodromia/ tasmanica/ Sinclair & Cumming* [red label]” (ANIC). PARATYPE: TASMANIA: ♂, 42°40S 145°58E, 19.iii.1976, C. Howard, litter (ANIC).

**Diagnosis.** Distinguished from other apterous species by the yellowish-brown fore femur (which is evenly pigmented along its entire length), the lighter coloured (brown) first flagellomere, and long, slender right surstylus. The male terminalia are also characterized by long (subequal in length to width of surstylus) tapering, spine-like setae along the entire length of the left surstylus and the apical half of the right bacilliform sclerite.

**Description.** Body length 1.5–2.0 mm.

**Male. Head.** Scape and pedicel yellowish brown; first flagellomere and arista brown; first flagellomere pointed ovate.

*Thorax* entirely black. Proepisternum with 1 spine-like seta above fore coxa; notopleural seta stout. Mesopleuron, metapleuron and mediotergite black.

*Wings.* Absent. Halter absent.

*Legs.* Fore coxa pale yellow-brown; lacking inner setae. Fore femur entirely yellowish-brown, not strongly attenuated apically; anterior basal spine-like seta less than twice length of posterior spine-like seta; lacking ventral row of spine-like setae. Fore tibia with 6–8 spine-like posteroventral setae. Fore tibia and tarsomeres yellowish-brown. Mid and hind coxae yellow to brown, gradually

darkening to black basally. Mid and hindlegs yellowish-brown.

*Abdomen.* Sclerites heavily sclerotized (except sternites 1 and 2 which are weakly sclerotized); tergites 1 and 2 immovably fused together with intersegmental suture still obvious at lateral margin. Hypandrium with scattered, pointed, stout setae near apex. Posterior margin of epandrium deeply cleft, V-shaped. Left surstylus elongate, narrow and cylindrical, bearing long, tapering setae on inner dorsal margin near base; right surstylus greater than half length of left surstylus, tapered, slightly geniculate near base, bearing short setae. Right bacilliform sclerite elongate, bearing long, spine-like setae along entire length. Cerci thinly sclerotized, unmodified and symmetrical (Fig. 26). Phallus with small subrectangular cap.

**Female.** Similar to male except fore tibia with row of 9 spine-like posteroventral setae. Tergite 8 sclerotized along entire margin, not subdivided apically.

**Distribution.** Currently known only from southwestern Tasmania (Fig. 36).

**Biology.** This species was collected in litter samples.

**Etymology.** Refers to the distribution of this species, which is restricted to Tasmania.

#### *Apterodromia tonnoiri* n.sp.

Figs. 6, 27, 36

**Material examined.** HOLOTYPE ♂, “Tasm[ania]/ Launceston/ 15.x.1933, A. Tonnoir” (ANIC). “HOLOTYPE/ *Apterodromia/ tonnoiri/ Sinclair & Cumming* [red label]” (ANIC).

**Diagnosis.** Distinguished from all other winged species of *Apterodromia* by clouding surrounding the crossveins, presence of a ventral row of spine-like setae on the fore femur, and lack of inner row of stout setae on the fore coxa. The male terminalia appear unique (not known for the closely related *A. spilota*), characterized by a posteriorly directed epandrial lobe that covers the right surstylus, and elongate heavily sclerotized, asymmetrical cerci.

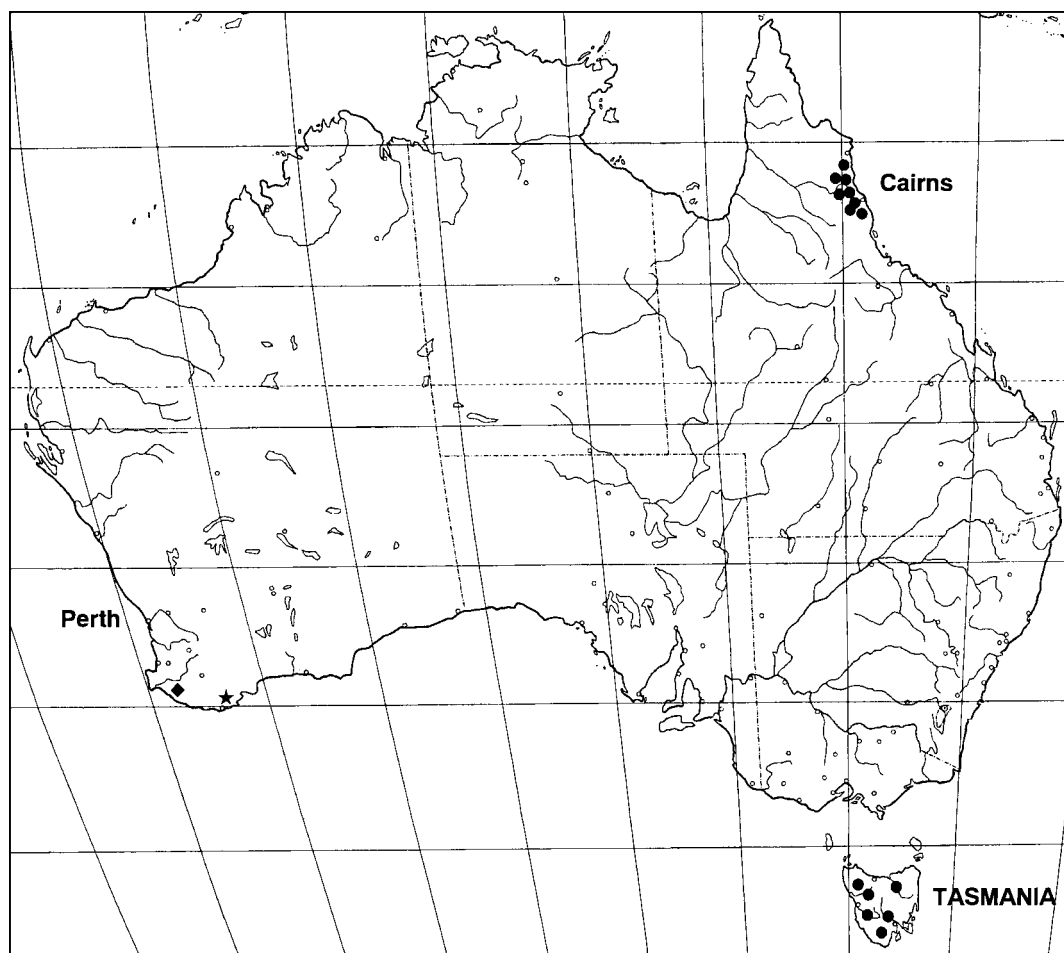
**Description.** Body length 4.0 mm.

**Male. Head.** Scape, pedicel, first flagellomere and arista dark brown; first flagellomere conical.

*Thorax* dark brown, nearly black. Proepisternum with 2 spine-like setae above fore coxa; notopleural seta stout. Mesopleuron, metapleuron and mediotergite dark brown.

*Wing* (Fig. 6) infusate; basal costal seta lacking; dark cloudy patches surrounding crossveins,  $M_1$ , and tips of major veins. Costa fading beyond  $M_1$ ; auxiliary crossvein between costa and  $R_{2+3}$ , but not between  $R_{2+3}$  and  $R_{4+5}$ ; cell dm broad, slightly shorter than cell bm;  $M_2$  and  $CuA_1$  reaching wing margin; cell *cup* short, two-thirds length of cell bm;  $CuA_2$  straight.

*Legs* brown. Fore coxa slender, lacking inner row of short, stout setae. Anterior basal spine-like seta of fore femur equal in length to posterior spine-like seta; armed beneath with row of 9 spine-like setae mounted on short tubercles. Fore tibia with 12 spine-like posteroventral setae.



**Figure 32.** Known distribution of species of *Apterodromia*. *Apterodromia* spp. eastern (●), *A. irrorata* (◆), *A. vespertina* (★).

**Abdomen.** Sclerites dark brown, well sclerotized. Hypandrium without stout or spine-like setae near apex. Posterior margin of epandrium ragged, with deep, narrow incision. Left surstylus elongate, lacking stout setae; right surstylus short, pointed, strongly held inwards (covered dorsally by posteriorly directed lobe of epandrium). Right bacilliform sclerite lacking stout setae. Cerci heavily sclerotized, asymmetrical, with left cercus expanded apically, curved over lower slender right cercus (Fig. 27). Phallus with subrectangular cap.

**Female.** Unknown.

**Distribution.** This species is known only from the type locality in northern Tasmania (Fig. 36).

**Etymology.** Named after A. Tonnoir, the collector of the single known specimen of this species.

**Remarks.** This species, which is known only from the male, is most closely related to *A. spilota*, which is known only from the female. However, the differences in setation of the fore coxae, wing venation, and wing patterning between these two are not indicative of conspecific secondary sexual characteristics observed in *Apterodromia*.

### *Apterodromia vespertina* n.sp.

Figs. 28, 32

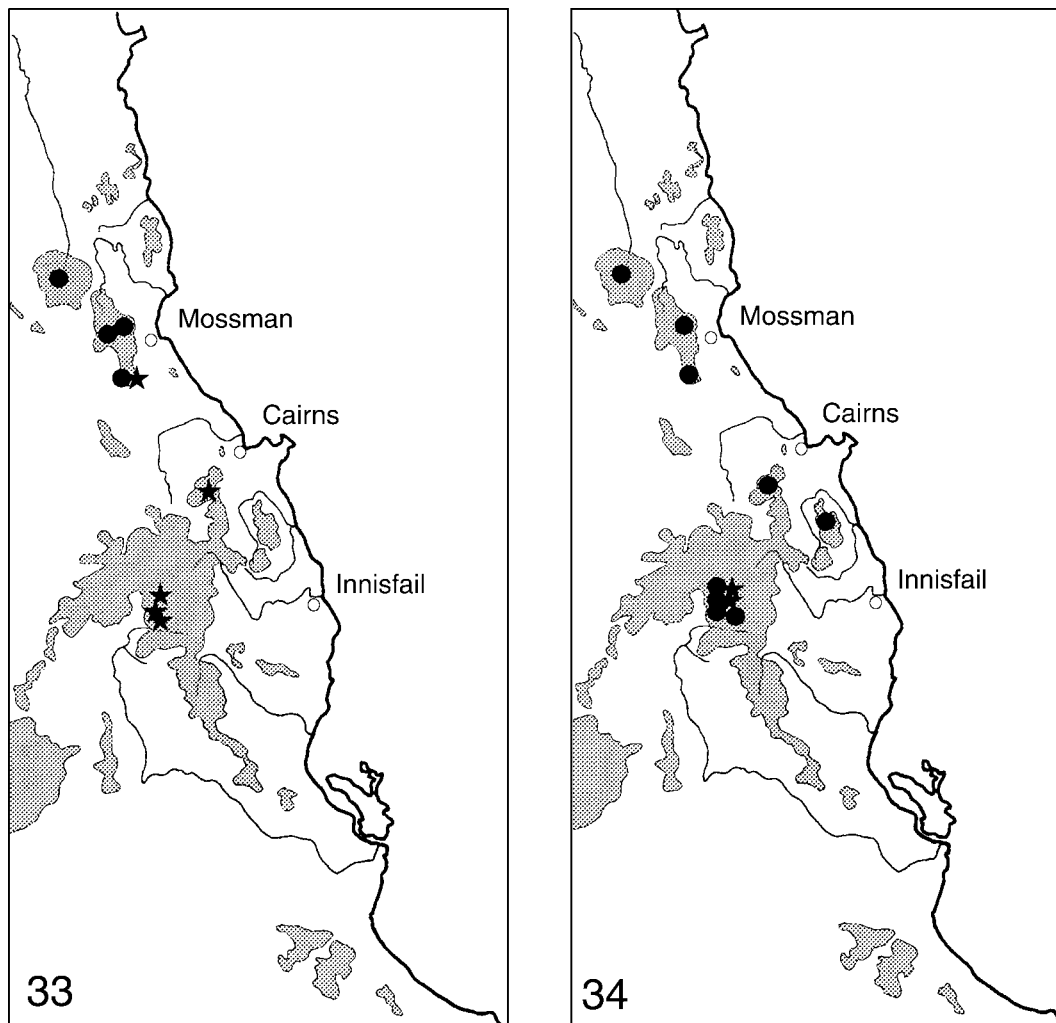
**Material examined.** HOLOTYPE ♂, “[AUST:WA]/ Porongorup NP, at Pass./ Devil’s Slide TR./ 4–5.Dec.1998/ B.J. Sinclair”; “HOLOTYPE/ *Apterodromia/ vespertina/ Sinclair & Cumming* [red label]” (WAM).

**Diagnosis.** Distinguished from all other winged species of *Apterodromia* by irrorated pattern on the wings, auxiliary crossvein from  $R_{2+3}$  to costa, and two spine-like proepisternal setae. The male terminalia are characterized by a very long, curved left surstylus with short setae on basal two-thirds and right bacilliform sclerite with slender setae.

**Description.** Body length 3.5 mm.

**Male. Head.** Scape, pedicel, first flagellomere and arista black; first flagellomere subtriangular. Vertex of head with median, brownish vitta from base of antennae to beyond occipital setae.

**Thorax.** Black. Proepisternum with 2 spine-like setae above fore coxa, upper one-quarter longer than lower; notopleural seta slender. Mesopleuron, metapleuron and mediotergite black.



Figures 33–34. Known distribution of species of *Apterodromia* in northern Queensland. 33, *A. aurea* (●), *A. pala* (★). 34, *A. bickeli* (●), *A. monticola* (★). Shaded areas indicate land above 700 m in altitude.

*Wing* infusate; basal costal seta slender, short; veins weakly undulating; numerous pale spots or irrorations: cell  $r_1$  with 3 broad spots, cell  $r_{2+3}$  with 5 round spots, cell  $r_{4+5}$  with ca. 12 spots, 3 spots in cell  $dm$ , 2 spots in cell  $m_1$ , cell  $m_2$  with 1 large spot, cell  $cua_1$  with 2 spots, cell  $cup$  with 1 apical spot. Auxiliary crossvein between costa and  $R_{2+3}$ ; cell  $dm$  narrow, ca. one-third longer than cell  $bm$ ;  $M_2$  and  $CuA_1$  faded prior to wing margin; cell  $cup$  longer than cell  $bm$ ;  $CuA_2$  convex.

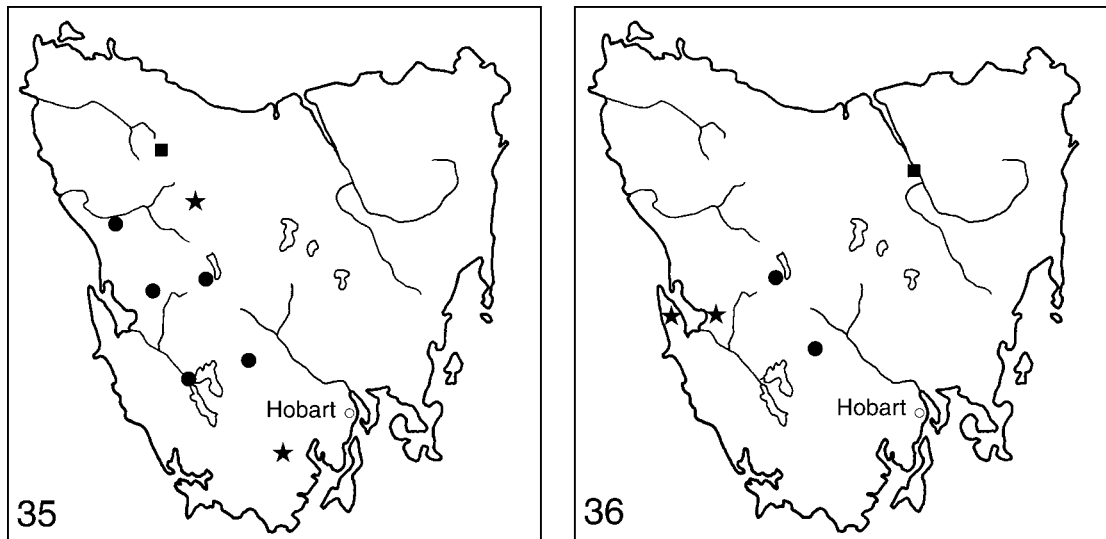
*Legs*. Fore coxa brownish-yellow; lacking inner setae. Fore femur brown on posterior face, tubercles of basal setae yellow; femur not strongly attenuated apically; anterior basal spine-like seta ca. equal in length to posterior spine-like seta; lacking ventral row of spine-like setae. Fore tibia with 14–16 spine-like posteroventral setae. Fore tibia and first tarsomere yellowish brown, remaining tarsal segments dull brown. Mid and hind coxae brown, becoming black basally. Ventral surface of mid and hind femora with basal fourth yellowish, remaining femora brown, darker towards apex; remaining leg segments brown gradually darkening on tarsal segments.

*Abdomen*. Sclerites lightly sclerotized. Hypandrium with scattered, pointed, stout setae near apex. Posterior margin of epandrium deeply cleft, U-shaped. Left surstylus elongate, arching beyond right surstylus; cylindrical, outer margin with long setae and pile of setulae; inner dorsal margin with dense stout setae, extending two-thirds length of surstylus; apex truncate, slightly notched. Right surstylus more than half length of left surstylus, geniculate near base, bearing long, stout basal setae extending beyond middle on apical margin; tapered to narrow apex. Right bacilliform sclerite elongate, bearing short, stout setae along entire length. Cerci thinly sclerotized, unmodified and symmetrical (Fig. 28). Phallus with oval flexible cap.

**Female.** Unknown.

**Distribution.** This species is known only from the type locality, a small eastern forest remnant, north of Albany (Western Australia), widely disjunct from the wet forests further west (Fig. 32).





Figures 35–36. Known distribution of species of *Apterodromia* in Tasmania. 35, *A. evansi* (★), *A. minuta* (●), *A. spilota* (■). 36, *A. setosa* (●), *A. tasmanica* (★), *A. tonnoiri* (■).

**Biology.** This specimen was collected along the edge of a seepage near the trail along Devil’s Slide. This is an intermittent seepage, as it dries up during the summer months. No specimens were collected in the Karri forest situated below Devil’s Slide.

**Etymology.** The specific name is derived from the Latin *vespertinus* (western), in reference to the distribution of this species in Western Australia.

**Remarks.** This species is most closely related to *A. irrorata*, with very similar male terminalia and wing pattern. However, it is considered a distinct species on the basis of its larger size, long, stout left surstylus arching beyond the right surstylus, stout setae of right surstylus extending well beyond base, two spine-like proepisternal setae, auxiliary crossvein present, and numerous small irrorations in cell  $r_{4+5}$ .

### Evolutionary history

#### Zoogeographic considerations

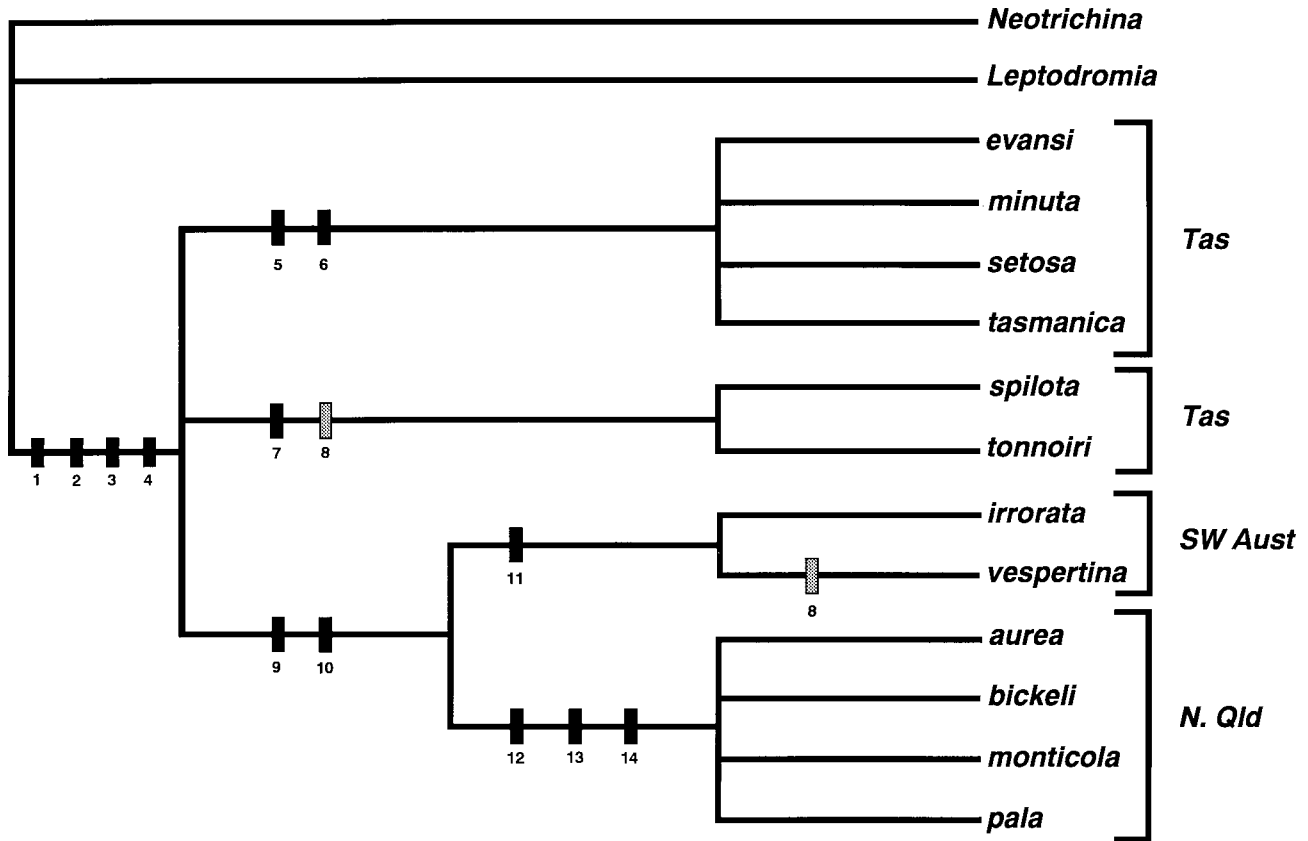
*Apterodromia* is an example of a Bassian faunal element (Spencer 1896), modified to include the temperate and tablelands rising from the tropical and subtropical lowlands of Northern Queensland (Nix, 1991). The Bassian subregion has a moist temperate climate, with vegetation ranging from southern rainforests and wet sclerophyll to alpine herb fields (Mackerras, 1970). Nix (1991) referred to the “islands” of cool, moist mountains in eastern Queensland as a mesotherm archipelago defined by a broad group of plants that have optimum temperatures for growth of 19–22°C, with a lower threshold of 5°C. These regions above 400 m are isolated from the mesotherm source area of southern Australia by warm temperatures and low rainfall (Nix, 1991, fig. 15). Although *Apterodromia* displays a Bassian pattern, this genus must be considered a relict taxon on the basis of the widely disjunct species. It is a remnant associated with

widespread Tertiary vegetation and the zoogeographic pattern is the result of extinction rather than speciation. The geographic distribution of *Apterodromia* is equivalent to many Gondwanan taxa and it is possible that with further collections using yellow pans that this genus may be recorded from southern Chile and possibly New Zealand.

The northern extension of this genus (the Tablelands west of Cairns) is common in southern temperate groups; e.g., *Scaptia* Walker (Tabanidae, Mackerras, 1970). Darlington (1961) observed several genera of the tribe Trechini (Carabidae) common in temperate southern Australia, whereas in the tropics these genera were confined to the Atherton Tableland (+600 m). Darlington assumed this distribution pattern was the result of ecological factors (e.g., cooler temperatures).

The disjunct pattern in eastern Australia (Northern Queensland and Tasmania) is also observed in the empidid genus *Hydropeza* Sinclair (Sinclair, 1999). In addition, Queensland Tablelands-Tasmania sister species pairs are known in *Clinocera* Meigen (Sinclair, 2000) and *Ceratomerus* Philippi (Sinclair, unpublished data).

*Apterodromia* is also characterized by high endemism in Tasmania, where a total of six species are recorded. In *Ceratomerus*, a genus generally confined to cool, moist forests and mountain streams, five of seven Tasmanian species are endemics (Sinclair, unpublished data). High Tasmanian endemism is also known in the aquatic orders Odonata, Plecoptera, and Trichoptera (Watson & O’Farrell, 1991; Hynes, 1976; Neboiss, 1991). The Odonata include several endemic cold-water genera, suggesting long isolation of stream faunas (Watson & O’Farrell, 1991). It can be assumed that the wet forests of Tasmania have also undergone a long period of isolation dating from middle Miocene when conditions on the continent started to become much drier (White, 1994). Although Tasmania was connected to the mainland during the Pleistocene, the land bridges were primarily low plains, providing routes primarily for lowland, warm adapted species (Hynes, 1976; White, 1994).



**Figure 37.** Hypothesized cladistic relationships of the species of *Apterodromia*. Numbers refer to characters discussed under “Phylogenetic relationships within *Apterodromia*”. Black rectangles = non-homoplastic apomorphies; shaded rectangles = homoplastic apomorphies. Abbreviations: N. Qld—Northern Queensland; SW Aust—Southwestern Australia; Tas—Tasmania.

**Phylogenetic position of *Apterodromia***

Oldroyd (1949) referred *Apterodromia* to the hybotid group of subfamilies or hybotid lineage (= Hybotidae sensu Chvála, 1983), specifically the subfamily Tachydromiinae. However, without male specimens, this placement has been doubted (Cumming, unpublished data). The discovery of both males and fully winged species of this genus has allowed us to analyse the subfamily placement with much more confidence.

On the basis of current subfamily and tribal divisions, the combination of a long arista, cell dm present and emitting three veins, simple hindlegs, and a single ejaculatory apodeme, suggests that this genus should be transferred to the Trichinini (Ocydromiinae). However, the above characters are symplesiomorphies and this tribe generally includes taxa that do not fit into any other lineage as currently defined (see below).

It could be also argued that the elongate cell cup (anal cell) resembles some Hybotinae, in contrast to the short, truncate cell cup common in the Ocydromiinae. Although the cell cup resembles some species of *Syneches* Walker (Smith, 1969, fig. 110), this probably represents the ground plan condition of the hybotid lineage. Especially when compared to relevant outgroups such as *Meghyperus* Loew (Steyskal & Knutson, 1981, fig. 47.17) and allied fossil

empidoids like *Phaetempis* Grimaldi & Cumming (1999, fig. 32) and *Trichinites* Hennig (1970, fig. 3).

In an effort to avoid possible homoplasmy through the interpretation of wing venation, we believe the main clues to the most plausible placement of *Apterodromia* is through the interpretation of the male terminalia. On the basis of a biarticulated phallus (apical articulated component or distiphallus), posterior margin of the hypandrium not deeply cleft, and absence of both postgonites and ventral apodeme (see Cumming & Sinclair, 1996; Sinclair, 1996), *Apterodromia* is herein transferred to the tribe Ocydromiini. A comparison of the genitalic figures of Collin (1961, figs. 93–5) and Chvála (1983, figs. 543–546, 553–555) illustrates the uniformity of the male terminalia in this tribe. In order to incorporate the inclusion of *Apterodromia*, the concept of the Ocydromiini is redefined below and included genera listed. A key to genera of Ocydromiini of the Southern Hemisphere is also included to aid identification.

The generic relationships within the Ocydromiini have not been analysed. The most plesiomorphic genus of this tribe appears to be *Neotrichina* n.gen. (see below) which has retained holoptic male eyes, with enlarged upper facets and three veins arising from cell dm that extend to the wing margin. On the basis of the configuration of the phallus, *Apterodromia* is hypothesized to be most closely related to an undescribed genus represented by “*Leptopeza*”

*bimaculata* White (1916) (*Leptodromia* n.gen., see below). The apex of the shaft of the phallus below the articulated apex is expanded or cup-shaped in both genera (c.f. Figs. 18, 29). All other genera appear to have a long, slender phallic shaft (Fig. 31), which is probably derived in comparison to the remaining groups in the hybotid lineage.

### Phylogenetic relationships within *Apterodromia*

The relationships within *Apterodromia* were analysed using PAUP Version 4.0b2 (Swofford, 1999) based on 14 informative characters (matrix in Table 1), with *Neotrichina* n.gen. and *Leptodromia* n.gen. (see below) used as outgroups. A heuristic search was performed, with stepwise addition resulting in one tree (Fig. 37) (tree length = 15; CI = 0.93; RI = 0.97; RC = 0.91).

*Apterodromia* is a distinctly monophyletic taxon within the *Ocydromiini* on the basis of the following characters: eyes with dense ommatrichia, fore femur with pair of long spine-like basal setae, fore tibia with ventral spine-like setae, and proepisternum with one spine-like seta (characters 1–4).

The apterous species of Tasmania are hypothesized to form a monophyletic group based on the loss of wings (character 5) and a modification of the base of the abdomen (character 6). In these species tergites 1 and 2 are immovably fused to form a plate over sternites 1 and 2, which are both virtually desclerotized and almost entirely membranous. Another character that may support this subgroup is a very narrow dorsal bridge connecting the two epandrial halves. It appears generally more slender compared to the winged species.

A row of spine-like setae on the fore femur and pair of proepisternal spines (characters 7 and 8) indicate the close relationship of the two fully-winged Tasmanian species. In addition, both species possess clouding along the crossveins of the wings that may also support this relationship, although

at least some degree of wing clouding is present in the other winged species of *Apterodromia*. A pair of proepisternal spines (character 8) appears to have arisen in *A. vespertina* independently from those seen in the fully-winged Tasmanian species.

A convex  $CuA_2$  and a lightly or weakly sclerotized abdomen (characters 9 and 10) support the sister group relationship between the western species group (*A. irrorata* and *A. vespertina*) and the northern Queensland species group. All Tasmanian species (i.e., winged and wingless) and outgroup taxa have well sclerotized abdomens. The western species group is considered monophyletic on the basis of irrorated wings (Fig. 3) (character 11). The four species found in Northern Queensland form a monophyletic group on the basis of blunt spines on the right bacilliform sclerite and left surstylus (Figs. 11, 14, 23, 24), an elongate cell dm (twice length of basal cells, Fig. 4), and a small dorsoapical sclerite partially separated from the apical margin of tergite 8 in the female terminalia (Figs. 8, 10) (characters 12–14).

### Ocydromiini

Type genus: *Ocydromia* Meigen

The tribe includes the following genera: *Abocciputa* Plant, *Apterodromia* Oldroyd, *Austropeza* Plant, *Hoplopeza* Bezzi, *Leptodromiella* Tuomikoski, *Leptozeza* Macquart, *Ocydromia* Meigen, *Oropezeza* Collin, *Pseudoscelolabes* Collin, *Scelolabes* Philippi, *Stylocydromia* Saigusa, plus all Neotropical species of *Trichina* sensu Collin (1933) and *Leptozeza bimaculata* Bezzi which are assigned to two new genera described below.

**Diagnosis.** This tribe is distinguished from the other major clades of the hybotid lineage by a short cell cup with truncate apex (except some *Apterodromia*), arista subequal or much longer than the first flagellomere, proboscis short, directed downwards or recurved, terminalia asymmetrical, rotated through 90°, phallus biarticulated, ventral apodeme and postgonites lacking, and epandrium with a pair of articulated surstyli.

**Table 1.** Data matrix of character states for the phylogenetic analysis of species of *Apterodromia*. Character numbers correspond to those in the text. 0, plesiomorphic state; 1, apomorphic state; ?, missing data; –, inapplicable (structure absent).

	characters													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
<i>Neotrichina</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Leptodromia</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>evansi</i>	1	1	1	1	1	1	0	0	0	0	–	0	–	0
<i>minuta</i>	1	1	1	1	1	1	0	0	0	0	–	0	–	0
<i>setosa</i>	1	1	1	1	1	1	0	0	0	0	–	0	–	0
<i>tasmanica</i>	1	1	1	1	1	1	0	0	0	0	–	0	–	0
<i>spilota</i>	1	1	1	1	0	0	1	1	0	0	?	0	0	0
<i>tonnoiri</i>	1	1	1	1	0	0	1	1	0	0	0	0	0	?
<i>irrorata</i>	1	1	1	1	0	0	0	0	1	1	1	0	0	0
<i>vespertina</i>	1	1	1	1	0	0	0	1	1	1	1	0	0	?
<i>aurea</i>	1	1	1	1	0	0	0	0	1	1	0	1	1	1
<i>bickeli</i>	1	1	1	1	0	0	0	0	1	1	0	1	1	1
<i>monticola</i>	1	1	1	1	0	0	0	0	1	1	0	1	1	1
<i>pala</i>	1	1	1	1	0	0	0	0	1	1	0	1	1	1

### Description

**Male. Head.** Eyes widely separated or closely approximated to holoptic; upper facets rarely enlarged. Antenna with small first flagellomere with style arista-like. Proboscis short, directed downwards; labrum and hypopharynx strongly arched at apex; pseudotracheae present.

**Thorax.** Slightly to strongly arched; acrostichal setulae usually present.

**Wings.** Costa generally ending at  $R_{4+5}$  or  $M_1$ ; cell dm emitting 2 or 3 veins, or short stump of  $M_1$ ; cell cup shorter than basal cells and apex truncate or longer than basal cells and apex convex.

**Legs.** Hindlegs generally elongate with variable chaetotaxy.

**Abdomen.** Terminalia asymmetrical, rotated through 90°; surstylus clearly articulated, asymmetrical; hypandrium with posterior margin not deeply cleft, lacking pair of apical lobes; phallus with long, flexible terminal appendage or

distiphallus; postgonites and ventral apodeme lacking; ejaculatory apodeme single.

**Female.** Similar to males except as follows: eyes similar to males, but not holoptic. Terminalia variable, with slender terminal cercus. Spermatheca unpigmented, simple, weakly sclerotized, slender, and tubular.

**Discussion.** As listed by Sabrosky (1999) the family-group name was first established by Schiner (1862) as Ocydromiinae, with the suffix later corrected by Melander (1908) to Ocydromiinae. Tuomikoski (1966) was the first to attempt to classify the subfamily into three monophyletic groups of genera. From these groupings, Chvála (1983) formally defined and characterized the tribe Ocydromiini.

With the inclusion of *Apterodromia* in the Ocydromiini, the only significant change in the present tribal definition is that cell dm emits three veins that reach the wing margin in the ground plan of the tribe. The Chilean and Patagonian species treated by Collin (1933) as *Trichina* Meigen are not congeneric with the northern hemisphere *Trichina* (Trichinini). These southern hemisphere species are also included in the Ocydromiini under a new genus (*Neotrichina*, see below), on the basis of the characteristic biarticulated phallus (Fig. 31; Collin, 1933, fig. 9).

Presence of a biarticulated phallus, plus loss of both the postgonites and ventral apodeme substantiates the monophyly of the Ocydromiini as currently defined. The relationships of the tribe to the remainder of the Ocydromiinae and the other subfamilies in the hybotid lineage (i.e., Hybotinae and Tachydromiinae) can only be partially resolved at present. Cumming *et al.* (1995, fig. 1) indicated that the Ocydromiinae is paraphyletic in relation to both the Hybotinae and Tachydromiinae. Using the Atelestinae as an outgroup, the Hybotinae (including *Bicellaria* Macquart, *Hoplocyrtoma* Melander, and *Leptocyrtoma* Saigusa), Tachydromiinae, Oedaleini, *Trichinomyia* Tuomikoski and *Trichina* appear to form a monophyletic group on the basis of two synapomorphies (Sinclair & Cumming, 1994; Cumming & Sinclair, 1996). The first is a modification of the ventral apodeme in which the separate paired rods seen in the Atelestinae appear to have fused together (see Sinclair, 1996, fig. 23), and the second is a modification of the phallus in the ground plan of each included lineage into a hood-like tip. The Ocydromiini by exclusion is therefore possibly the sister group to this diverse clade.

The Ocydromiini is distributed worldwide, and is the only tribe of the “Ocydromiinae” represented in southern South America, Australia, and New Zealand.

### *Neotrichina* n.gen.

Type species: *Trichina obscurata* Collin, 1933.

**Diagnosis.** Distinguished from all other genera of the Ocydromiini by three veins arising from cell dm reaching the wing margin, upper facets of male enlarged, and a long flexible distiphallus extending nearly the length of the shaft.

**Description.** Wing length 3.5–4.5 mm.

**Male.** *Head* dark, with extensive pruinescence. Eye bare, holoptic, upper facets enlarged. Face parallel-sided, width

equal to antennal sockets. Gena not extended below eye; postgena with sparse setae. Two pairs of fine ocellar setulae, directed forward. One pair of vertical and 1–2 pairs of upper occipital setae. Antennae inserted about middle of head; scape and pedicel subequal in length, scape devoid of setulae; pedicel cylindrical, with cirlet of short preapical setae; first flagellomere tapered to narrow apex, less than 2 times length of first and second segments combined; two-articled apical arista variable in length; first flagellomere and arista clothed in fine pubescence. Palpus tapered and flattened, pale, one-half to two-thirds length of proboscis; length of proboscis normally less than half height of head. Mouthparts as in other ocydromiines.

*Thorax* polished to thickly clothed in pruinescence; dark to orange-yellow in colour, occasionally with dark markings; slightly to strongly arched, postpronotal lobe and postalar callus well developed; prosternum separate from proepisternum; proepisternum with fine setae; antepnotum well developed, forming wide “neck”-like extension. Thoracic macrotrichia mostly slender and short; acrostichal setulae biserial, confined to anterior half; dorsocentral setulae uniserial; 1 postpronotal setula; 1 notopleural seta; 1 postalar seta; 1 pair of long, apical scutellar setae, with several pairs of outer marginal setulae. Meso- and metapleuron with patches of pruinescence.

*Wings* hyaline, broad, anal lobe well developed; microtrichia of equal length; costal setae short; basal costal seta short; costa fading beyond  $M_1$ ; Sc evanescent, extending to beyond  $R_{2+3}$  and  $R_{4+5}$  branching; stigma overlapping apex of  $R_1$ , occasionally extending to tip of  $R_2$ ; Rs long, arising proximal to middle of cell bm; cell dm broad, subequal to or longer than cell bm; 3 veins emitted from cell dm, each obtaining wing margin; cell cup approximately two-thirds or more length of cell bm. Halter pale to dark.

*Legs* yellow to dark; long and slender; some species with hind tibia dilated at apex and first and second tarsomeres dilated. Fore coxa short, less than twice length of other coxae; clothed in long, pale setae. Fore tibia with tubular gland near base. Femora and tibiae lacking stout anterodorsal and posterodorsal setae.

*Abdomen.* Tergites heavily sclerotized, darkly polished. Sternites less sclerotized, and generally more pale. Sclerites of segment 8 not fused, approximately one-third length of preceding segment. Hypopygium asymmetrical, rotated approximately  $90^\circ$  to right. Hypandrium short, quadrate, posterior margin either shallowly bilobed or lengthened into long slender process (Fig. 31); dorsal bridge V-shaped. Epandrium deeply cleft, strongly asymmetrical; right surstylus slender, generally strongly arched; right surstylus short to long, occasionally strongly arched. Bacilliform sclerites short, bearing several setae. Cercus unmodified, short, slender and thinly sclerotized. Phallic shaft long, gradually arched, cylindrical, not expanded apically; distiphallus bearing small cap membranously lengthened to near length of shaft; ejaculatory apodeme fused to base of phallus.

**Female.** Similar to male except as follows: eyes dichoptic, all facets of equal size; frons widely divergent; tergites 1 and 2 not fused; segments 1–7 broad, wider than long,

gradually tapered; tergites slightly more thickly sclerotized than sternites; sclerites of segment 8 separate, similar in length to preceding segment, not ovipositor-like; sclerites of segment 10 small triangular in shape, divided medially; cercus long and slender, well sclerotized, bearing long scattered setae.

**Distribution.** This genus is confined to southern South America, currently recorded from Argentina and Chile.

**Included species.** The genus includes all Neotropical species previously treated by Collin (1933) under *Trichina*, namely *Neotrichina abdominalis* (Collin) **n.comb.**, *Neotrichina digna* (Collin) **n.comb.**, *Neotrichina digressa* (Collin) **n.comb.**, *Neotrichina distincta* (Collin) **n.comb.**, *Neotrichina elegans* (Bigot) **n.comb.**, *Neotrichina fida* (Collin) **n.comb.**, *Neotrichina indiga* (Collin) **n.comb.**, *Neotrichina insignis* (Collin) **n.comb.**, *Neotrichina insons* (Collin) **n.comb.**, *Neotrichina laeta* (Collin) **n.comb.**, *Neotrichina media* (Collin) **n.comb.**, *Neotrichina obscurata* (Collin) **n.comb.**. The authors examined specimens of these species housed in the CNC, whereas the type specimens are located in the BMNH.

**Remarks.** The Neotropical species of this genus have long been considered not to be congeneric with *Trichina*, as first noted by Tuomikoski (1959) and later by Collin (1961) and Chvala (1983).

*Neotrichina* can be separated into two groups as delineated by Collin (1933). The first includes *N. digna* and allied species, characterized by a long straight labrum, weakly arched thorax, and hind tibia dilated towards tip, with partially dilated first and second tarsomeres. The second includes *N. obscurata* and allied species, characterized by a shorter, less conspicuous labrum, strongly arched thorax, and slender legs.

### *Leptodromia* n.gen.

Type species: *Leptopeza bimaculata* Bezzi, 1904.

**Diagnosis.** Distinguished from other genera of the *Ocydromiini* by a very short  $M_1$ , antennae inserted above middle of head, weakly developed anal lobe, and a long  $R_s$  vein.

**Description.** Wing length 3.5–4.5 mm.

**Male.** *Head* polished black. Eye bare, narrowly separated, all facets equally small. Face closely approximated; frons parallel-sided twice width of face. Gena not extended below eye; postgena with sparse setae. Two pairs of fine ocellar setulae, directed forward. One pair of vertical and 1–2 pairs of upper occipital setae. Antennae inserted above middle of head; scape and pedicel subequal in length, scape devoid of setulae; pedicel cylindrical, with circlet of short preapical setae; first flagellomere long and tapering to narrow apex, often 3 times length of first and second segments combined; two-articled apical arista nearly equal in length to first flagellomere; first flagellomere and arista clothed in fine pubescence. Palpus broad and flattened, pale, two-thirds

length of proboscis; length of proboscis less than half height of head. Mouthparts as in other *ocydromiini*.

*Thorax* polished orange-yellow, often with dark markings; not strongly arched, postpronotal lobe and postalar callus well developed; prosternum separate from proepisternum; proepisternum bare or with setulae; antepronotum well developed, forming wide “neck”-like extension. Thoracic macrotrichia mostly slender and short; acrostichal setulae biserial, confined to anterior half; dorsocentral setulae uniserial; 1 postpronotal setula; 1 notopleural seta; 1 postalar seta; 1 pair of long, apical scutellar setae, with several pairs of outer marginal setulae. Pruinescence confined to lateral margins; meso- and metapleuron generally devoid of pruinescence, except on laterotergite.

*Wings* hyaline to infusate, narrow, anal lobe weakly developed; microtrichia of equal length; costal setae short; basal costal seta long; costa fading beyond  $R_{4+5}$ ; Sc evanescent, extending to beyond  $R_{2+3}$  and  $R_{4+5}$  branching; stigma at apex of cell  $r_1$ ;  $R_s$  long, arising near middle of cell  $bm$ ; cell  $dm$  broad, shorter than cell  $bm$ ;  $M_1$  short, abruptly ending well before wing margin; cell  $cup$  approximately two-thirds length of cell  $bm$ . Halter pale.

*Legs* yellow to brown; long and slender, hind femur often with dark subapical band. Fore coxa short, less than twice length of other coxae; clothed in long, pale setae. Fore tibia with tubular gland near base. Femora and tibiae with stout, dark anterodorsal and posterodorsal setae.

*Abdomen.* Tergites heavily sclerotized, darkly polished. Sternites thinly sclerotized, pale. Sclerites of segment 8 not fused, approximately one-third length of preceding segment. Hypopygium asymmetrical, rotated approximately 90° to right. Hypandrium short, quadrate, posterior margin shallowly bilobed; dorsal bridge well sclerotized (Fig. 29). Epandrium deeply cleft, not strongly asymmetrical; right surstylus elongate, cylindrical, bearing setae; right surstylus short, more strongly arched. Bacilliform sclerites elongate, bearing several setae. Cercus unmodified, short, slender and thinly sclerotized. Phallic shaft short, expanded apically to form cup-shaped tip, bearing flexible cap and subapical process; ejaculatory apodeme fused to base of phallus (Figs. 29, 30).

**Female.** Similar to male except as follows: tergites 1 and 2 fused; segments 1–7 broad, wider than long; tergites heavily sclerotized and polished; sternites pale, thinly sclerotized; sclerites of segments 7 narrowly separated (appearing fused in dried specimens); sclerites of segment 8 separate, very slender, ovipositor-like, longer than 2 preceding segments; sclerites of segment 10 small triangular in shape, divided medially; cercus long and slender, well sclerotized, bearing long scattered setae.

**Distribution.** This genus is presently known only from Australia, widely distributed in wet eastern forests from Tasmania to northern Queensland and wet forests of southwestern Western Australia. Specimens are readily collected by sweep net or yellow pans.

**Included species.** The genus currently includes *Leptodromia bimaculata* (Bezzi) **n.comb.** from eastern Australia (NSW) and several undescribed species.

**Key to Southern Hemisphere Ocydromiini<sup>1</sup>**

- 1 Wings absent (Australia) ..... *Apterodromia* (in part)  
 — Wings present ..... 2
- 2 Cell dm lacking (Australia and Argentina) ..... undescribed genus A  
 — Cell dm present ..... 3
- 3 Three veins emitted from cell dm reaching wing margin ..... 4  
 — Two or fewer veins emitted from cell dm reaching wing margin ..... 5
- 4 Fore femur greatly swollen, with 2 long basal spine-like setae  
 (Australia) ..... *Apterodromia* (in part)  
 — Fore femur slender, lacking long basal setae (Chile) ..... *Neotrichina*
- 5 Eyes with ommatrichia (New Zealand) ..... *Abocciputa*  
 — Eyes bare ..... 6
- 6 Abdominal sclerites heavily sclerotized, punctate; legs with long  
 slender setae, 2–3 times width of leg segment (Australasian,  
 Neotropical, Oriental, and Palaearctic Regions) ..... undescribed genus B<sup>2</sup>  
 — Abdominal sclerites not heavily sclerotized, surface smooth;  
 chaetotaxy of legs variable ..... 7
- 7 Vein Rs short, arising near apex of cell bm ..... 8  
 — Vein Rs long, arising near middle of cell bm ..... 9
- 8 Hind tibia with at least one large anterior spur; hind femur banded;  
 epandrium usually with row of spines on inner right margin; hind  
 tibia not geniculate at base (Australasia, Chile) ..... *Hoplopeza*<sup>3</sup>  
 — Hind tibia with stout bristle, spur usually short and reduced; hind  
 femur not banded; epandrium lacking row of spines on inner right  
 margin; hind tibia generally geniculate at base (Australia, Chile) ..... *Scelolabes*<sup>4</sup>
- 9 Short M<sub>1</sub> vein arising from cell dm (Australia) ..... *Leptodromia*  
 — M<sub>1</sub> vein absent ..... 10
- 10 Anal lobe not developed, wing narrow; in doubtful cases antennal  
 inserted high on head ..... 11  
 — Anal lobe partially or strongly developed, wing broad; antennae  
 inserted near middle of head ..... 12

1 Key to the major lineages of Australian Empidoidea, including the Ocydromiini, follows this key.

2 This group may contain more than one genus and also includes the Palaearctic species *Leptopeza rugosiventris* Strobl (1910).

3 Also includes *Hoplopeza tachydromiaeformis* (Bezzi, 1904) **n.comb.** from eastern Australia (NSW). It is difficult to assign this species with full confidence because the description does not include an illustration of the wing and the type material is destroyed.

4 The generic separation of *Hoplopeza* and *Scelolabes* remains problematic. Revision of the genera comprising species from all regions is required, including details of female terminalia.

- 11 Acrostichal setulae present (Australasian, Neotropical, and Palearctic Regions) ..... *Oropezella*
- Acrostichal setulae absent (Malaysia) ..... *Stylocydrornia*<sup>1</sup>
- 12 First flagellomere oval; cell cup long, reaching near apex of cell bm (Afrotropical, Oriental, and Holarctic Regions) ..... *Ocydromia*
- First flagellomere conical; cell cup short, reaching only middle of cell bm ..... 13
- 13 Hind femur swollen (New Zealand) ..... *Pseudoscelolabes*
- Hind femur slender (Australia and New Zealand) ..... *Austropeza*

### Key to major lineages of Australian Empidoidea

The key to Subfamilies of the Empidoidea presented in the *Insects of Australia* (Colless & D.K. McAlpine, 1991: 760) lacks several major groups. An updated key (modified from Steyskal & Knutson (1981) and Bickel (1996)) to major lineages and unplaced genera (see Sinclair, 1999) is provided below to assist researchers in sorting and identification of Australian Empidoidea.

- 1 Wings present ..... 2
- Wings absent (Ocydromiini) ..... *Apterodromia* (in part)
- 2 Rs originating at or near level of crossvein h; crossvein r-m in basal fourth of wing; male terminalia rotated forward beneath preceding segments ..... 18
- Rs originating well distal to level of crossvein h; crossvein r-m distal to basal fourth of wing; male terminalia not rotated forward beneath preceding segments ..... 3
- 3 Cell dm absent, neither R<sub>4+5</sub> nor M forked; all veins running without branching to wing margin; cell cup usually lacking, but when present shorter than cells bm and br, and A<sub>1</sub> weak and faint ..... Tachydromiinae
- Cell dm present or absent; when this cell absent, R<sub>4+5</sub> or M or both forked, or R<sub>1+2</sub> forked, or cell cup slender, slightly shorter than cell bm, or foreleg raptorial, or hind first tarsomere with ventral spine-like setae ..... 4
- 4 Foreleg raptorial, located near head, and distant from others; fore coxa greatly lengthened, at least twice as long as other coxae; fore femur distinctly thickened with at least one row of spine-like setae beneath, never with pair of long, basal spines on short tubercles ..... Hemerdromiinae
- Foreleg not raptorial; fore coxa short, usually not twice length of other coxae; fore femur not greatly swollen; if leg appearing raptorial, then fore femur with pair of stout basal spines on short tubercles ..... 5

1 Saigusa (1986) distinguished *Stylocydrornia* from other Ocydromiini genera primarily on the basis of the greatly lengthened first flagellomere and the lack of acrostichals. However, certain species of *Oropezella* possess a similarly modified first flagellomere (see Plant, 1989), suggesting that the generic status of *Stylocydrornia* may have to be reevaluated. Although known only from just north of the Equator, *Stylocydrornia* is likely to be found much further south.

- 5 Cell cup absent; first flagellomere very large with pedicel inserted thumb-like on inner side at base; proboscis long and slender, arising from front of mouth-opening and slightly recurved ..... Ceratomerinae
- Cell cup present; first flagellomere normal in size, pedicel without thumb-like extension on inner side; mouthparts variable ..... 6
- 6 CuA<sub>2</sub> strongly recurved into A<sub>1</sub>; in doubtful cases, R<sub>4+5</sub> branched, or setae present on laterotergite; fore tibia gland lacking ..... 7
- CuA<sub>2</sub> forming distinct angle with A<sub>1</sub>; R<sub>4+5</sub> unbranched; setae lacking on laterotergite; fore tibial gland present on inner basal margin ..... 17
- 7 Costa with short, stout or fine erect setae on outer margin or dorsal face; anal lobe of wing not or only weakly developed, forming a broad obtuse angle; labellum sucker-like ..... Clinocerinae
- Costa without erect setae, if present (*Heterophlebus*) radial veins with setae; anal lobe well developed, usually forming an acute angle; labellum not sucker-like ..... 8
- 8 Laterotergite with group of setae; R<sub>1</sub> not swollen before joining costa ..... 9
- Laterotergite bare, if setose then R<sub>1</sub> distinctly swollen before joining costa ..... 10
- 9 Radial veins setose, with setae on at least dorsal surface of R<sub>1</sub> and ventral surface of R<sub>2+3</sub>; costa circumambient; female abdomen truncate, terminalia with acanthophorites (*Trichopezinae*) ..... *Heterophlebus Philippi*
- Radial veins lacking setae; costa usually ending at or slightly beyond R<sub>4+5</sub>; female abdomen pointed, terminalia with projecting cerci and no acanthophorites ..... Empidini s.l.
- 10 Labrum stout, curved posteriorly; fore coxa with numerous erect, spine-like setae; wing narrow with anal lobe weakly developed, forming a broad obtuse angle (*Ragas* group) ..... *Hydropeza Sinclair*
- Labrum slender or stout, not curved posteriorly; fore coxa lacking erect, spine-like setae; anal lobe of wing usually well developed, forming an acute angle ..... 11
- 11 CuA<sub>2</sub> little reflexed, apex of cell cup truncate ..... 12
- CuA<sub>2</sub> strongly reflexed; apex of cell cup rounded ..... 13
- 12 First flagellomere broadly ovate with short thick stylus (*Ragas* group) ..... *Hormopeza Zetterstedt*
- First flagellomere elongate, strap-like (known only from Tasmania) (possibly *Ragas* group) ..... new genus 1
- 13 R<sub>1</sub> distinctly swollen before joining costa; palpus arched forward beneath head; male with basitarsus of foreleg often enlarged or swollen; male terminalia with hypandrium keel-like, forming narrow hood over phallus along posterior margin ..... Hilarini



- $R_1$  not swollen before joining costa; palpus straight, projecting obliquely or parallel to proboscis; male with basitarsus of foreleg not swollen; male terminalia with broad hypandrium ..... 14
- 14 Subcosta complete or practically reaching costa (weakened at extreme apex); male eyes meeting above antennae (holoptic) with upper facets enlarged ..... 15
- Subcosta distinctly incomplete, fading out well short of costa; male eyes widely separated above antennae (dichoptic) without upper facets enlarged ..... 16
- 15 Proboscis short or long, if long projecting downwards; male terminalia held near horizontally; female abdomen truncate, terminalia with upright cerci and acanthophorites (*Trichopezinae*) ..... *Apalocnemis* Philippi
- Proboscis long and slender, projecting obliquely forward; male terminalia held upright, almost vertically; female abdomen pointed, terminalia with cerci projecting horizontally and no acanthophorites (often collected on blossoms) (*Iteaphila* group) ..... new genus 2
- 16 First flagellomere strap-like, elongate and thickened; apical flagellomeres style-like, shorter than first flagellomere (commonly found on rocks in streams and rivers) (probably *Trichopezinae*) ..... new genus 3
- First flagellomere short, pointed ovate; apical flagellomeres arista-like, longer than first flagellomere (known only from Tasmania) (*incertae sedis*) ..... new genus 4
- 17 Cell cup usually truncate, shorter than cell bm; if longer hind legs slender, not raptorial; eyes not meeting above antennae (dichoptic) in females and without upper facets enlarged ..... *Ocydromiini*
- Cell cup as long as or longer than cell bm, with apex arched to meet  $A_1$  at acute angle; eyes meeting above antennae (holoptic) in both sexes with upper facets enlarged ..... *Hybotinae*
- 18 Cell dm closed, crossvein bm-cu complete or nearly so; M forked, both branches reaching wing margin; costa circumambient; body generally black ..... *Microphorinae*
- Cells dm and bm confluent, crossvein bm-cu absent or distinctly abbreviated; if M forked then  $M_2$  not reaching wing margin; costa ending at  $R_{4+5}$  or  $M_1$ ; body generally yellow or green metallic ..... *Dolichopodidae*

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## References

- Adam, P., 1992. Australian Rainforests. In *Oxford Monographs on Biogeography*, eds. W. George, A. Hallam & T.C. Whitmore, no. 6. Oxford: Clarendon Press.
- Bezzi, M., 1904. Empididi Indo-Australiani raccolti dal Signor L. Biro. *Annales Musei Nationalis Hungarici* 2: 320–361.
- Bickel, D.J., 1994. The Australian Sciapodinae (Diptera: Dolichopodidae), with a review of the Oriental and Australian faunas, and a world conspectus of the subfamily. *Records of the Australian Museum, Supplement* 21: 1–394.
- Bickel, D.J., 1996. *Thinempis*, a new genus from Australia and New Zealand (Diptera: Empidoidea), with notes on the tribal classification of the Empidinae. *Systematic Entomology* 21: 115–128.
- Chvála, M., 1983. The Empidoidea (Diptera) of Fennoscandia and Denmark. II. General part. The families Hybotidae, Atelestidae and Microphoridae. *Fauna Entomologica Scandinavica* 12: 1–279.
- Colless, D.H., & D.K. McAlpine, 1991. Diptera (Flies) [Chapter] 39. In *The Insects of Australia*, ed. I.D. Naumann, vol. 2, 2nd edition, pp. 171–786. Carlton: Melbourne University Press.
- Collin, J.E., 1933. Empididae. *Diptera of Patagonia and South Chile* 4: 1–334.
- Collin, J.E., 1961. Empididae. In *British Flies*, vol. 6, pp. 1–782. Cambridge: University Press.
- Cumming, J.M., B.J. Sinclair & D.M. Wood, 1995. Homology and phylogenetic implications of male genitalia in Diptera—Eremoneura. *Entomologica Scandinavica* 26: 121–151.
- Cumming, J.M., & B.J. Sinclair, 1996. The higher-level phylogeny of Eremoneura (Diptera: Brachycera). *Proceedings of 20th International Congress of Entomology* (Firenze) 1996: 24.
- Darlington, P.J., 1961. Australian carabid beetles V. Transition of wet forest faunas from New Guinea to Tasmania. *Psyche* 68(1): 1–24.
- Grimaldi, D., & J. Cumming, 1999. Brachyceran Diptera in Cretaceous ambers and Mesozoic diversification of the Eremoneura. *Bulletin of the American Museum of Natural History* 239: 1–124.
- Hennig, W., 1970. Insektenfossilien aus der unteren Kreide. II. Empididae (Diptera, Brachycera). *Stuttgarter Beiträge zur Naturkunde* 214: 1–12.
- Hynes, H.B.N., 1976. Tasmanian Antarcticoperlaria (Plecoptera). *Australian Journal of Zoology* 24: 115–143.
- Mackerras, I.M., 1970. Composition and distribution of the fauna [Chapter] 9. In *Insects of Australia*, ed. CSIRO, pp. 187–203. Victoria: Melbourne University Press.
- McAlpine, J.F., 1981. Morphology and terminology—adults. [Chapter] 2. In *Manual of Nearctic Diptera*, vol. 1, eds. J.F. McAlpine *et al.*, pp. 9–63. Agriculture Canada Monograph 27: vi + 1–674.
- Melander, A.L., 1908. Family Empididae. In *Manual of North American Diptera*, ed. S.W. Williston, pp. 218–227. New Haven: J.T. Hathaway.
- Neboiss, A., 1991. Trichoptera (Caddis-flies, caddises) [Chapter] 40. In *The Insects of Australia*, ed. I.D. Naumann, vol. 2, 2nd edition, pp. 787–816. Carlton: Melbourne University Press.
- Nix, H.A., 1991. Biogeography: pattern and process. In *Rainforest Animals*, eds. H.A. Nix & M.A. Switzer, pp. 11–39. Kowari 1: xii + 112.
- Oldroyd, H., 1949. A wingless empid (Diptera) from Tasmania. *Entomologist's Monthly Magazine* 84: 278–279.
- Oldroyd, H., 1964. *The Natural History of Flies*. London: Weidenfeld & Nicolson.
- Plant, A.R., 1989. A revision of the Ocydromiinae (Diptera: Empidoidea: Hybotidae) of New Zealand with descriptions of new genera and species. *New Zealand Journal of Zoology* 16: 231–241.
- Pollet, M., & P. Grootaert, 1987. Ecological data on Dolichopodidae (Diptera) from a woodland ecosystem: I. Colour preference, detailed distribution and comparison of different sampling techniques. *Bulletin de L'Institut Royal des Sciences Naturelles de Belgique, Entomologie* 57: 173–186.
- Sabrosky, C.W., 1999. Family-group names in Diptera. An annotated catalog. *Myia* 10: 1–360.
- Saigusa, T., 1986. New genera of Empididae (Diptera) from eastern Asia. *Sieboldia* 5: 97–118.
- Schiner, I.R., 1862. *Fauna Austriaca*. 1(8): 657–674, i–lxxx.
- Sinclair, B.J., 1996. Review of the genus *Acarterus* Loew from southern Africa, with description of seven new species (Diptera: Empidoidea; Hybotinae). *Annals of the Natal Museum* 37: 215–238.
- Sinclair, B.J., 1999. Review of the genera *Dipsomyia* Bezzi, *Zanclotus* Wilder, and an allied new Gondwanan genus (Diptera: Empidoidea, Ragas-group). *Entomological Science* 2: 131–145.
- Sinclair, B.J., 2000. Revision of the genus *Clinocera* Meigen from Australia and New Zealand (Diptera: Empididae: Clinocerinae). *Invertebrate Taxonomy* 14: 347–361.
- Sinclair, B.J., & J.M. Cumming, 1994. Phylogenetic relationships within the Empidoidea (Diptera). *Third International Congress of Dipterology Abstract Volume*, ed. J.E. O'Hara, pp. 200–201. Guelph.
- Smith, K.G.V., 1969. The Empididae of southern Africa (Diptera). *Annals of the Natal Museum* 19: 1–342.
- Smith, K.G.V., 1989. 43. Family Empididae. In *Catalog of the Diptera of the Australasian and Oceanic Regions*, ed. N.L. Evenhuis, pp. 382–392. Bishop Museum Special Publication 86. Honolulu: Bishop Museum Press and E.J. Brill.
- Spencer, W.B., 1896. Summary of the zoological, botanical, and geological results of the expedition. In *Report on the Work of the Horn Scientific Expedition to Central Australia*. Part 1, ed. W.B. Spencer, pp. 139–199. London: Dulau.
- Steyskal, G.C., & L.V. Knutson, 1981. Empididae [Chapter] 47. In *Manual of Nearctic Diptera*, vol. 1, eds. J.F. McAlpine *et al.*, pp. 607–624. Agriculture Canada Monograph 27: vi + 1–674.
- Strobl, G., 1910. Die Dipterenfauna von Steiermark. II. Nachtrag. *Mitteilungen des Naturwissenschaftlichen Vereins für Steiermark* 46(1909): 45–293.
- Swofford, D.L., 1999. PAUP\*. Phylogenetic Analysis Using Parsimony (\*and other Methods). Version 4. Sunderland, Massachusetts: Sinauer Associates.
- Tuomikoski, R., 1959. Mitteilungen über die Empididen (Dipt.) Finnlands. VI. *Trichinomyia* gen.n., eine neue Ocydromiinengattung. *Annales Entomologici Fennici* 25: 103–110.
- Tuomikoski, R., 1966. The Ocydromiinae group of subfamilies (Diptera, Empididae). *Annales Entomologici Fennici* 32: 282–294.
- Watson, J.A.L., & A.F. O'Farrell, 1991. Odonata (Dragonflies and damselflies) [Chapter] 17. In *The Insects of Australia*, ed. I.D. Naumann, vol. 1, 2nd edition, pp. 294–310. Carlton: Melbourne University Press.
- White, A., 1916. The Diptera-Brachycera of Tasmania. Part III. Families Asilidae, Bombyliidae, Empidae, Dolichopodidae, & Phoridae. *Royal Society of Tasmania: Papers and Proceedings* 1916: 148–266.
- White, M.E., 1994. *After the Greening*. Kenthurst: Kangaroo Press.

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