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).


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 hemerodromines, 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 empidooids. 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

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**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.
first tarsomere with row of stout ventral setae; fore tibial gland present; propisternum with 1–2 spine-like seta(e) above fore coxa; three veins emitted from cell dm, A1 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; ommatridia 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 oval to conical, with long, two-articled apical arista. Palpus tapered to point, two-thirds length of proboscis; palpiifer 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, dorso-central setulae uniserial, increasing in length mostly slender and short; acrostichal setulae biserial; 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 oval to conical, with long, two-articled apical arista. Palpus tapered to point, two-thirds length of proboscis; palpiifer bearing pair of setae; labrum and hypopharynx strongly arched posteriorly; 4 pairs of pseudotracheae present (Fig. 7).

**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° 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. Phallosome with flexible, lateral cap lined with membrane; ejaculatory apodeme fused to base of phallosome.

**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, tracheal-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 .................................................. 4
   — 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. setosa*

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 .................................................. 9
   — Wing lacking auxiliary crossvein between R_{2+3} and R_{4+5} (Fig. 6); fore coxa without inner row of short stout setae .................................................. *A. spilota*

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 ............................................. \textit{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 ............................................. \textit{A. bickeli}

\textbf{Apterodromia aurea n.sp.}

Figs. 7–8, 11–13, 33

\textbf{Material examined.} \textit{HOLOTYPE} $\delta$, “AUSTRALIA: N[orthern]. Q[ueens]L[and]: 11 km up Mt. Lewis Rd. 900 m; 15–16.iv.1994; rainfor./ D.J. Bickel; ex. yellow/pans nr. creek; Stop I 16°36’S 145°17’E”; “\textit{HOLOTYPE/ Apterodromia/ aurea/ Sinclair \& Cumming [red label]}” (AMS). \textit{ALLOTYPES} $\varphi$, same data as holotype (AMS). \textit{PARATYPES: QUEENSLAND: \#1, Devil’s Thumb, 12 km NW Mossman, 1000 m, 5.ix.1992, I.D. Naumann (ANIC); 8 $\varphi$ 3 $\delta$, same data as holotype (ANIC, CNC); 4 $\delta$ 4 $\varphi$, 12 km up Mt. Lewis Rd., 860 m, 16°30’S 145°17’E, 15–16.iv.1994, D.J. Bickel (AMS); $\delta$, 25 km up Mt. Lewis Rd., 1000 m, 16°32’S 145°17’E, 16.iv.1994, B.J. Sinclair (CNC); $\varphi$, 25 km up Mt. Lewis Rd., 1000 m, 16°32’S 145°17’E, 21.iv.1994, M. Moulds (AMS); $\varphi$, Mt. Lewis at For. Hut, 1020 m, 16°36’S 145°16’E, 16.iv.1994, D.J. Bickel (ANIC); $\varphi$, Mt. Spurgeon, wet scler. for., tree trunks, 16°26’S 145°17’E, 19.iv.1994, D.J. Bickel (AMS); 2 $\delta$ 2 $\varphi$, 1400 m, 16°14’01”S 145°00’14”E, 17–18.iv.1994, D.J. Bickel (AMS).

\textbf{Diagnosis.} Distinguished from other winged species of \textit{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.

\textbf{Description.} Body length 2.5–3.0 mm.

\textbf{Male. Head.} Scape, pedicel and first flagellomere brown; first flagellomere conical.

\textit{Thorax} with dorsal orange except antepronotum and posterior third of notopleuron black; postpronotal lobe outlined in black. Proepisternum with 1 spine-like seta above posterior third of notopleuron black; lower half of mesopleuron black, upper half orange, extending to base of halter; laterotergite orange. Metapleuron and mediocercitg black.

\textit{Wing} infuscate, with dark band from tip of R$_{5}$ to tip of cell br; basal costal seta short; cell dm elongate, 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). Phallos with broad lateral, flexible cap (Fig. 12).

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

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

\textbf{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.

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

\textbf{Apterodromia bickeli n.sp.}

Figs. 4, 14–16, 34

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 mediatergite black.

Wing (Fig. 4) infuscate, 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* 1 and *CuA* 1 faded prior to wing margin; cell *cup* longer than cell *bn*; CuA 3 convex.


Abdomen. Sclerites thinly sclerotized and reduced in size. Hypantrium 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

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

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

Diagnosis. Distinguished from other apertus 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 mediatergite 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. Hypantrium 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** δ, "AUST[ralia]; WA [Western Australia] Pemberton/ Crowea St. For./ Nov.–Dec. 1979/ S.J. Curry"; "HOLOTYPE/ Apterodromia/ irrorata/ Sinclair & Cumming [red label]" (ANIC). **PARATYPE:** same data as holotype. **PARATYPES:** WESTERN AUSTRALIA: δ, Pemberton, 3.xii.1936, K.R. Norris (ANIC); 21 δ, 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); δ, 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 propisternal 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 mediopterite brown to black.

Wing (Fig. 3) infuscate; basal costal seta short, slender; veins weakly undulating; numerous pale spots or irrorations: cell r₁ with 3 broad spots, cell r₂+₃ with 4–5 round spots, cell r₄+₅ with 5 spots, 2–3 spots in cell dm, 2 spots in cell m₁, cell m₂ with 1 large spot, cell cu₄ with 2 spots, cell cu₅ with 1 apical spot. Auxiliary crossveins lacking; cell dm narrow, ca. one-third longer than cell bm; M₁ and CuA₁ faded prior to wing margin; cell cu₁ longer than cell bm; CuA₂ 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. 17). 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** δ, "AUSTRALIA: Tasmania/ NW 5km Renison Bell/ 180m, Berlese rainfor/- est litter, 1[4][19][87] N.I. Platnick et al."; "HOLOTYPE/ Apterodromia/ minuta/ Sinclair & Cumming [red label]" (ANIC). **PARATYPE:** same data as holotype. **PARATYPES:** TASMANIA: δ, same locality as holotype, xi–xii.1979, S.J. Curry (ANIC). **HOLOTYPE/ Apterodromia/ minuta/ Sinclair & Cumming [red label]" (ANIC). **PARATYPE:** "AUST[ralia]: TAS[mania]: 7 km WN/ Mt. Field/ 1.ii.1980/ Lawrence & Weir"; "ALLOTYPE/ Apterodromia/ minuta/ Sinclair & Cumming [red label]" (ANIC). **PARATYPES:** TASMANIA: δ, same data as holotype (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.

**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 posterovertetal setae. Fore tibia yellowish-brown, tarsal segments gradually darker apically. Mid and hind coxae yellowish-brown, spine-like setae. Fore tibia with 9 spine-like posterovertetal 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 yellow-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


**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.

### Apterodromia pala n.sp.

Figs. 10, 24, 33


of the thorax of this species.

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 apicodorsal margin with deep U-shaped notch. Posterior margin of epandrium deeply cleft, rectangular. Left surstyli elongate, cylindrical, bearing long, setae on outer margin, equal to half length of lobe; right surstyli slightly more than half length of left surstyli, blunt, geniculate near base, bearing long setae along outer margin. Right bacilliform sclerite elongate, bearing very long, slender setae along outer half. Cerci thin, immovably fused together with intersegmental suture still obvious, completely open, with very long, slender setae on inner faces of cerci, on outer faces of cerci, and on inner faces of cerci along outer margin. Cerci thin, symmetrical (Fig. 25). Phallosome 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. Know with certainty only from the holotype which 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 surstyli and right bacilliform sclerite.

Apterodromia spilota n.sp.

Figs. 5, 35


Diagnosis. Distinguished from all other winged species of Apterodromia by their reddish-brown forelegs, yellowish tubercles at base
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) infuscate; basal costal seta lacking; dark cloudy patches surrounding crossveins and tips of major veins. Costa fading beyond M₁; auxiliary crossveins between costa and R₁₊₂ and R₁₊₃ and R₄₊₅; cell bm broad, shorter than cell bm; M₁ and Cu₄₊₅ reaching wing margin; cell cup short, two-thirds length of cell bm; CuA₂ 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. Sclerotized 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


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 yellow-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 hind legs 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


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) infuscate; basal costal seta lacking; dark cloudy patches surrounding crossveins, M₁, and tips of major veins. Costa fading beyond M₁; auxiliary crossvein between costa and R₂₊₃, but not between R₂₊₃ and R₄₊₅; cell bm broad, slightly shorter than cell bm; M₂ and Cu₄ reaching wing margin; cell cup short, two-thirds length of cell bm; CuA₂ straight.

Legs. Fore coxa pale yellow-brown, 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.
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 surstylius elongate, lacking stout setae; right surstylius 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

“HOLOTYPE/ Apterodromia/ vespertina/ Sinclair & Cumming [red label]” (WAM).

Diagnosis. Distinguished from all other winged species of *Apterodromia* by irroration 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 surstylius 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 mediocorticite black.

Wing infuscate; 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 cu\(_{p}\) 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 cu\(_{p}\) 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).
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 r4+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 mesothermal 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 mesothermal 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 homoplasy 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*”
A convex CuA₂ 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 surstylist (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


**Diagnosis.** This tribe is distinguished from the other major clades of the hybotid lineage by a short cell cup with truncate apex (except *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.

**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 R₄₊₅ or M₁; cell dm emitting 2 or 3 veins, or short stump of M₁; 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°; surstylist clearly articulated, asymmetrical; hypandrium with posterior margin not deeply cleft, lacking pair of apical lobes; phallus with long, flexible terminal appendage or 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.
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 Ocydrominae, 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 Ocydromini.

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 Ocydromini in 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 setae, 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 setae; 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 proboscs; 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; antepronotum well developed, forming wide “neck”-like extension. Thoracic macrotrichia mostly slender and short; acrostichal setae biserial, confined to anterior half; dorsocentral setae uniserial; 1 postpronotal seta; 1 notopleural seta; 1 postalar seta; 1 pair of long, apical scutellar setae, with several pairs of outer marginal setae. Meso- and metapleura 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 M1; Sc evanescent, extending to beyond R5 and R6 branching; stigma overlapping apex of R5, occasionally extending to tip of R5; 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° 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 Chvála (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* †, antennae inserted above middle of head, weakly developed anal lobe, and a long Rs 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 ocydromines.

*Thorax* polished orange-yellow. often with dark markings; not strongly arched, postpronotal lobe and postalar callosity well developed; proepisternum 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 seta; 1 notopleural seta; 1 postalar seta; 1 pair of long, apical scutellar setae, with several pairs of outer marginal setae. Pruinosecence confined to lateral margins; meso- and metapleuron generally devoid of pruinoscence, except on laterotergite.

*Wings* hyaline to infuscate, narrow, anal lobe weakly developed; microtrichia of equal length; costal setae short; basal costal seta long; costa fading beyond *R* ‡; *Sc* evanescent, extending to beyond *R* ‡5; *Rs* long, arising near middle of cell bm; cell bm broad, shorter than cell bm; *M* † 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 anteradorsal and posteradorsal setae.

**Abdomen.** Tergites heavily sclerotized, darkly polished. Sternites thinly sclerotized, pale. Sclerites of segment 8 not fused, approximately one-third length of preceding segment. Hyponygmum asymmetrical, rotated approximately 90° to right. Hypantrum short, quadrated, posterior margin shallowly bilobed; dorsal bridge well sclerotized (Fig. 29). Epandum 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 9 small triangular in shape, divided medially; cercus long and slender, well sclerotized, bearing long scattered setae.

**Distribution.** This genus is currently 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 Ocydromiini¹

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 B²

   — 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*³

   — 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*⁴

9. Short M₁, vein arising from cell dm (Australia) ................................................... *Leptodromia*

   — M₁, 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

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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 Palaeartic Regions) ................................................................. Oropezella
—— Acrostichal setulae absent (Malaysia) ............................................................. Stylocydromia¹

12 First flagellomere oval; cell cu long, reaching near apex of cell bm (Afrotropical, Oriental, and Holarctic Regions) ........................................................... Ocydromia
—— First flagellomere conical; cell cu 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) ........................................................................................................ 2

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 R₄+₅ nor M forked; all veins running without branching to wing margin; cell cu usually lacking, but when present shorter than cells bm and br, and A₁ weak and faint ............................................................ Tachydromiinae
—— Cell dm present or absent; when this cell absent, R₄+₅ or M or both forked, or R₂+₃ forked, or cell cu 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 ................................................................................................................................. Hemerodromiinae
—— 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 Stylocydromia 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 Stylocydromia may have to be reevaluated. Although known only from just north of the Equator, Stylocydromia is likely to be found much further south.
<table>
<thead>
<tr>
<th>Step</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>5</td>
<td>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</td>
</tr>
<tr>
<td></td>
<td>—— Cell cup present; first flagellomere normal in size, pedicel without thumb-like extension on inner side; mouthparts variable ................................. 6</td>
</tr>
<tr>
<td>6</td>
<td>CuA₂ strongly recurved into A₁; in doubtful cases, R₄₊₅ branched, or setae present on laterotergite; fore tibia gland lacking ............................................................. 7</td>
</tr>
<tr>
<td></td>
<td>—— CuA₂ forming distinct angle with A₁; R₄₊₅ unbranched; setae lacking on laterotergite; fore tibial gland present on inner basal margin ............................................................. 17</td>
</tr>
<tr>
<td>7</td>
<td>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</td>
</tr>
<tr>
<td></td>
<td>—— 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</td>
</tr>
<tr>
<td>8</td>
<td>Laterotergite with group of setae; R₁ not swollen before joining costa ............................................................. 9</td>
</tr>
<tr>
<td></td>
<td>—— Laterotergite bare, if setose then R₁ distinctly swollen before joining costa ............................................................. 10</td>
</tr>
<tr>
<td>9</td>
<td>Radial veins setose, with setae on at least dorsal surface of R₁ and ventral surface of R₂₊₃; costa circumambient; female abdomen truncate, terminalia with acanthophorites (Trichopezinae) ............................. Heterophlebus Philippi</td>
</tr>
<tr>
<td></td>
<td>—— Radial veins lacking setae; costa usually ending at or slightly beyond R₄₊₅; female abdomen pointed, terminalia with projecting cerci and no acanthophorites .................................................. Empidini s.l.</td>
</tr>
<tr>
<td>10</td>
<td>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</td>
</tr>
<tr>
<td></td>
<td>—— 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</td>
</tr>
<tr>
<td>11</td>
<td>CuA₂ little reflexed, apex of cell cup truncate ............................................................. 12</td>
</tr>
<tr>
<td></td>
<td>—— CuA₂ strongly reflexed; apex of cell cup rounded ............................................................. 13</td>
</tr>
<tr>
<td>12</td>
<td>First flagellomere broadly ovate with short thick stylus (Ragas group) ............................................................. Hormoeza Zetterstedt</td>
</tr>
<tr>
<td></td>
<td>—— First flagellomere elongate, strap-like (known only from Tasmania) (possibly Ragas group) ............................................................. new genus 1</td>
</tr>
<tr>
<td>13</td>
<td>R₂ 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</td>
</tr>
</tbody>
</table>
— R₁ 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 arist-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 A₁ 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 M₁ not reaching wing margin; costa ending at R₄₅ or M₁; body generally yellow or green metallic .......... Dolichopodidae

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