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Article



The *Cycloneura* Marshall group of genera in New Zealand (Diptera: Mycetophilidae: Leiini)

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Table of contents

Abstract	2
Introduction	2
Material and methods	
Key to genera of Leiini s. str. in New Zealand	
Genus Paradoxa Marshall 1896	4
Paradoxa fusca Marshall 1896	6
Genus Sigmoleia Tonnoir & Edwards 1927	7
Key to species of Sigmoleia in New Zealand (males)	
Sigmoleia melanoxantha Edwards in Tonnoir & Edwards 1927	
Sigmoleia similis Jaschhof & Kallweit sp. n.	
Sigmoleia separata Jaschhof & Kallweit sp. n.	
Sigmoleia peterjohnsi Jaschhof & Kallweit sp. n.	
Genus Cycloneura Marshall 1896	19
Genus Paracycloneura Tonnoir & Edwards 1927	
Key to species of Paracycloneura (males)	
Paracycloneura apicalis Tonnoir in Tonnoir & Edwards 1927	
Paracycloneura inopinata Jaschhof & Kallweit sp. n.	
Paracycloneura sp	
Genus Tonnwardsia Jaschhof & Kallweit gen. n.	
Genus Cawthronia Tonnoir & Edwards 1927	
Cawthronia nigra Tonnoir in Tonnoir & Edwards 1927	
Genus Waipapamyia Jaschhof & Kallweit gen. n.	
Key to species of Waipapamyia (males)	
Waipapamyia dentata Jaschhof & Kallweit sp. n.	
Waipapamyia elongata Jaschhof & Kallweit sp. n.	
Waipapamyia truncata Jaschhof & Kallweit sp. n.	
Delineation of the Leiini in a strict sense	
Relationships of the genera of the Cycloneura group	
Acknowledgements	
References	

Abstract

The *Cycloneura* group of genera, as it is here defined, represents a significant component of the Leiini (Diptera: Mycetophilidae) in New Zealand. The group includes little known genera, such as *Cawthronia* Tonnoir & Edwards, *Cycloneura* Marshall, *Paracycloneura* Tonnoir & Edwards, *Paradoxa* Marshall and *Sigmoleia* Tonnoir & Edwards, which are reviewed, as well as two new genera, *Tonnwardsia* gen. n. and *Waipapamyia* gen. n., which are described here. The prominent feature of *Cycloneura*-like leiines is the peculiar course of the hind wing veins, CuA2 and A1. Typically, A1 approaches the sinuous course of CuA2, or the two veins even join each other, thereby forming a closed posterior cubital cell. In New Zealand the *Cycloneura* group is more speciose than previously thought. New species described in this paper are: *Paracycloneura inopinata* sp. n., *Sigmoleia peterjohnsi* sp. n., *Sigmoleia separata* sp. n., *Sigmoleia similis* sp. n., *Waipapamyia dentata* sp. n., *Waipapamyia elongata* sp. n., and *Waipapamyia truncata* sp. n. The New Zealand members of the *Cycloneura* group do not form a monophyletic group in themselves, but are variously related to extralimital taxa the majority of which is found in the southern Neotropics, South Africa, Australia, and New Caledonia. Possible relationships, with supporting arguments from adult morphology, are discussed.

Key words: taxonomy, morphology, Mycetophilidae, Leiini, new genera, new species, New Zealand

Introduction

According to Søli *et al.* (2000), the family Mycetophilidae is subdivided into two subfamilies, Mycetophilinae and Sciophilinae. Sciophilinae is the more diverse subfamily and includes five to six tribes. Leiini, one of the large tribes of Sciophilinae, comprises 25–28 extant genera (Bechev 2000, Blagoderov 2008). Our present understanding of the Leiini goes back to Edwards (1925: 575) who regarded the "genera of the *Leia* group" as the focal point to which further genera were assigned. The key characters of Edwards' Leiini were derived from wing venation, namely the short R1, being usually little if any longer than ta (r-m of Edwards), and the nearly horizontal inclination of ta. Edwards' argumentation was solid enough to survive practically unchallenged for almost 80 years to the present. Doubts on the monophyly of the Leiini sensu Edwards were expressed repeatedly (e. g., Søli 1997, Søli *et al.* 2000, Hippa *et al.* 2005), but a phylogenetic hypothesis more conclusive than Edwards' proposal is hitherto wanting. A phylogenetic analysis embracing all the genera is still fragmentary because relevant descriptive literature lacks sufficient detail and fresh material adequate to restudy their morphology, or even study their molecules, is hardly available. Contributing to these difficulties, many taxa are southern hemisphere in distribution, while most students of fungus gnats are, as is known, based in the north.

Among the little known southern hemisphere leiines are several genera endemic to New Zealand. Most exhibit wing vein patterns that deviate markedly from the ordinary, notably in that A1 closely approaches or even merges with CuA2, thereby forming a closed posterior cubital cell situated some distance from the wing margin. These *Cycloneura*-like leiines, as they are referred to here, appeared hitherto to be not diverse on the genus and species levels. The present article documents that such an impression results—as is so often the case with mycetophilids outside the Holarctic region—from too little study. No doubt the *New Zealand Fungus Gnats* by Tonnoir and Edwards (1927) is a classic among the literature on Australasian Sciaroidea. Yet our own studies of the last few years reveal, decades after this landmark paper appeared, how much is still to discover among the mycetophilids of the southwest Pacific. Here we describe two new genera and seven new species of the Leiini, and review the poorly known genera *Cawthronia* Tonnoir & Edwards, *Cycloneura* Marshall, *Paracycloneura* Tonnoir & Edwards, *Paradoxa* Marshall, and *Sigmoleia* Tonnoir & Edwards. Most of these taxa have not been subject of any further study since the time of their descriptions. From the viewpoint of adult morphology we discuss the arguments for possible interrelationships of the *Cycloneura*-like genera in New Zealand and elsewhere. Finally, we address the question of a more stringent definition for the Leiini, as its heterogenous nature is quite obvious. It is out of the question that southern hemisphere leiines

offer a perspective that is different from the prevailing, northern view. Even so, we do not aim to substitute Edwards' Leiini concept by an elaborate new hypothesis, rather we intend to contribute to developing it.

Material and methods

The following institutions in New Zealand provided specimens that, for the most part, were picked from unsorted Malaise and sweepnet samples taken during the past 30 years: New Zealand Arthropod Collection, Tamaki, Auckland (Dr T.K. Crosby); Landcare Research, Nelson (R. Toft); Department of Conservation, St Arnaud (through mediation by R. Toft); Canterbury Museum, Christchurch (P.M. Johns, Dr R.P. Macfarlane); University of Canterbury, Christchurch (Dr R.K. Didham); and School of Forestry, Christchurch (through mediation by P.M. Johns). The material provided by Dr Raphael K. Didham is exceptional as it was collected in the forest canopy, whereas the other samples were taken, as usual, close to the ground, mainly of forests. A large amount of specimens were collected by ourselves on various occasions during the years 2001–2003, with assistance by C. Jaschhof (Greifswald, Germany) and Dr A. Stark (Halle (Saale), Germany). Holotypes, most paratypes and further specimens are deposited in the New Zealand Arthropod Collection (NZAC). Some paratypes and voucher specimens are kept in the Senckenberg Naturhistorische Sammlungen, Museum für Tierkunde, Dresden, Germany (SMTD).

In addition to the species treated at length below, we studied one to five specimens of each of the following species of the Mycetophilidae (the country of collection in square brackets): *Acrodicrania* Skuse sp. [Australia]; *Allactoneura* Meijere sp. [Madagascar]; *Anomalomyia* Hutton spp. [New Zealand]; *Ateleia* Skuse sp. [Australia]; *Greenomyia baikalica* Zaitzev [Finland]; *Greenomyia mongolica* Laštovka & Matile [Germany]; *Leia cylindrica* (Winnertz) [Finland]; *Leia winthemi* Lehmann [Finland]; *Leiella* Enderlein sp. [Costa Rica]; *Mycetophila fungorum* (De Geer) [Finland]; *Paradoxa paradoxa* Jaschhof [South Africa]; *Procycloneura* Edwards sp. [Costa Rica]; *Rondaniella dimidiata* (Meigen) [Germany]; *Rondaniella* Johannsen sp. [Costa Rica]; and *Sigmoleia spinosistyla* Matile [New Caledonia]. These specimens came from the institutions listed above as well as from the University of Illinois, National Soybean Research Center, Urbana-Champaign (Dr M.E. Irwin); the Natal Museum, Pietermaritzburg (Dr M. Mostovski); and the Instituto Nacional de Biodiversidad (INBio), Santo Domingo de Heredia, Costa Rica (M. Zumbado).

Specimens marked with an asterisk (*) were mounted on microscope slides; other specimens were kept in 70% ethanol. For mounting in Canada balsam, specimens were macerated in warm 10% potassium hydroxide (KOH), neutralized in acetic acid, step-wise dehydrated in ethanol (50%, 100%), and eventually treated with beechwood creosote. For light microscope study and the preparation of drawings we used an Olympus BX50 microscope in combination with the U-DA drawing unit. Photographs were taken using a digital Olympus C-3030 camera attached to Olympus SZH10 and BH-2 microscopes. Morphological terminology, including abbreviations, follows largely Søli (1997). The thin apical portions of antennal flagellomeres are referred to as stalks (see Søli 1997), the thick basal portions as nodes. The outline of the mid-pleural pit and pleural apodeme is assessed according to Hippa and Vilkamaa (2005). The term "anteroapical depressed area" (Vockeroth 1981, Søli 1997) is substituted by "fore tibial organ", as its nature as a sensory organ is evident (Blaschke-Berthold 1994). Terms used for wing cells (anterior cubital cell, abbreviated and italized *cual*; posterior cubital cell, cup) are in accordance to McAlpine (1981). The structure termed "dorsal parameral apodeme" by Jaschhof and Didham (2002) is here referred to as the "anterior portion of the gonocoxal apodeme" (abbreviated antGA) in order to distinguish it from the "posterior portion" (postGA, see Fig. 64). The term "tegmen" is used for the sheath-like structure made of the merged parameters (see Figs 58, 77; Hippa & Vilkamaa 2005, character 68). "Macroseta" is used instead of "megaseta", as the latter word is a barbarism (Gagné, in litt.). Length measurements were taken of both slide-mounted and ethanol-preserved specimens. Two indices are applied to describe the shape of the thorax. The scutum index is the ratio of scutum length to height, with values close to 2 indicating a "high" thorax, and values close to 3 indicating a "flat" thorax. The episternum index is the ratio of height to length of preepisternum 2, with values near 0.7 indicating a "flat"

thorax, and values near 1 indicating a "high" thorax. The lengths of wing veins were assessed with the base of the stem vein as the basalmost point. The wing index, used to describe the shape of the wing, is the ratio of the wing length to its width, with values >2.1 indicating "long" wings. The tibial diameter was measured at the apex of the tibia.

For specimen localities, we applied the area code system proposed by Crosby *et al.* (1976, 1998). Codes with relevance to our specimens are as follows (ordered from north to south, and west to east): NO, North Island; ND, Northland; AK, Auckland; TO, Taupo; WN, Wellington; SO, South Island; NN, Nelson; SD, Marlborough Sounds; BR, Buller; KA, Kaikoura; WD, Westland; NC, North Canterbury; MC, Mid Canterbury; OL, Otago Lakes; SL, Southland. Other abbreviations are: F., for forest; F. P., Forest Park; L., lake; loc., locality; N. P., National Park; R., river; Res., reserve; Sc. Res., Scientific Reserve; S. F., State Forest; S. H., State Highway. Holotype data are given without abbreviations or codes. Abbreviations for type depositories are: NHM, for The Natural History Museum, London; NZAC, for New Zealand Arthropod Collection, Auckland; and SMTD, for Senckenberg Museum für Tierkunde, Dresden. For the description of habitats, we applied a gross classification into forest types, such as southern beech forest, podocarp/broadleaf forest, kauri forest, and exotic forest, as well as shrubland and grassland.

Key to genera of Leiini s. str. in New Zealand

2 4
ia gen. n.
n. & Edw.
nyia Hutt.
5
7
n. & Edw.
6
(Fig. 37).
ra Marsh.
margin of
ia gen. n.
xa Marsh.
. & Edw.

Genus Paradoxa Marshall 1896

Marshall 1896: 290 (description); Tonnoir & Edwards 1927: 823 (discussion); Jaschhof 2006: 233 (discussion). **Type species.** *Paradoxa fusca* Marshall 1896, by monotypy.

Diagnosis. The top of the head is rounded and situated above the level of the ventral margin of the mesonotum (Fig. 33). The lateral ocelli are far from the eye margins (Fig. 26). The third maxillary palpus segment lacks translucent sensilla, which is an unusual character state of Leiini but found also in *Procycloneura* sp. The scutum is rounded anteriorly, not protruding (Fig. 33). Sc is short and ends free; M is furcate, with short stem; and A1 joins CuA2 to form a closed *cup* (Fig. 13). *Paradoxa* has no recognizable autapomorphic characters. The diagnosis, and the generic redescription that follows, are based on the type species, *P. fusca*, and *P. paradoxa* Jaschhof 2006 from South Africa.

Redescription. Color. Dark brown with lighter legs. **Head.** Head capsule in lateral view higher than long, rounded on top. Foramen situated little above midheight of head. Frons mostly asetose except some lateral

setae. Antennae inserted at midheight of head. Scape little longer than pedicel, both setose. Fourteen flagellomeres; individual flagellomere slightly compressed, with very short stalk; node shorter or little longer than wide, longer in males than in females; short trichia of which the bases form polygon-like patterns, usually 1–3 short setae distally; apical flagellomeres with 2–3 short setae apically. Fine interommatidial setulae. Three ocelli in wide triangle on top of head, median ocellus smaller than laterals, the latter far from eye margins (the distance equates 3 times the ocellus width). 3–4 bristles in line behind upper eye margins, 1 pair of bristles behind median ocellus and 1 pair in front of lateral ocelli; all bristles directed anteriorly. Both face and clypeus subrectangular, setose. Labrum small, weakly sclerotized. Stipes strongly setose. Lacinia vestigial. Maxillary palpus 4- or 5-segmented; basalmost segment setose or asetose; second segment with few wartlike sensilla; third segment lacking translucent sensilla; apical segment longest. Prementum weak, asetose. Premental apodemes fused mesally, with 2 posterior processes. Labellum setose laterally; prestomal teeth forming long, dense mesal row.

Thorax. High, scutum index 2.05, episternum index 1.0. Postpronotum asetose. Suture between antepronotum and proepisternum weak; both sclerites with setae and bristles. Proepimeron situated posteroventrally of proepisternum, long and pointed, fitting into notch of preepisternum 2. Basisternum 1 asetose. Anepisternum smaller than preepisternum 2, with largely obscure suture between, both sclerites asetose like all other pleura. Preepisternum 2 covering basalmost portion of mid coxa. Anepimeron with narrow ventral portion occupying some space between preepisternum 2 and laterotergite. Mid-pleural pit well developed, its mound protruding, pleural apodeme funnel-shaped. Laterotergite ovate, bulging. Scutum rounded anteriorly, not protruding, with evenly distributed setae intermingled with bristles. Anterior parapsidal suture distinct. Prescutum not traceable. Scutellum setose, 2 lateral bristles. Mediotergite slightly arched. Wing. Long, wing index 2.6. Membrane with brown tinge, often darkened on anterior margin, with microtrichia on both sites and some setae close to posterior margin, or setae absent. Calypterous lobe developed, with setose margin. Dmp asetose. Anal lobe evenly curved. C extending much beyond apex of R5 and almost to wing apex, or ending clearly before wing apex. Sc very faint, short, ending free. One crossvein (Rs) between R1 and R5 in proximal half of wing. R1 shorter than ta, ending in distal half of wing. Apical portion of R5 curved alongside C. M furcate: M-stem and basalmost portion of either M1 or M2 weak, Mstem much shorter than fork; tines of fork evenly diverging towards wing apex. CuA1 long, free basally. CuA2 sinuous. A1 infraspecifically variable, joining CuA2 to form closed *cup* or fading out shortly before CuA2. CuP present as distinct fold. A2 slightly furcate, or absent. Dorsal setae on all veins except on h, Sc, Rs, CuP, and A2; tb with or without dorsal setae. Ventral setae on R1 and R5. Halter with light stem and dark knob. Legs. Hind margin of hind coxa protruding. Tibial and tarsal trichia irregularly arranged. Fore tibia shorter than femur, with very short setae arranged irregularly or in lines. Fore tibial organ with semicircular rim, with numerous pale trichia of which the distalmost form a comb. Mid and hind tibiae with 2–3 rows of setae, longest setae little longer than tibial diameter. Hind tibial apical comb of pale setae present or absent. Tibial spurs 1:2:2, with serrated rims; spurs on mid and hind tibiae of unequal length. Empodia wide, longer than pretarsal claws. Pulvilli, if correctly identified, reduced to form tiny sclerotized plates. Claws with 1 large and 2 small teeth.

Abdomen. Setose except sternite 1. Light, weakly pigmented lateral lines (folds?) on male tergites 2–5 and sternites 2–6, and on female tergites 2–6 and sternites 2–7.

Male terminalia. Large, usually rotated 90–180°. Sternite 9 absent, or present as small bare sclerite. Tergite 9 elongate, partly merged with gonocoxites. Gonocoxites capsule-like, with deep V- or U-shaped ventral emargination and lateral lobes to hold gonostyli. Both postGA and antGA long. Gonostylus inserted ventrolaterally on gonocoxal capsule, clasping in vertical direction. Aedeagus and parameres forming complex structure with large membranous and small sclerotized portions. Hypoproct setose. Cerci largely fused mesally, setose. **Female terminalia.** Tergite 8 moderately long, setose. Gonocoxite 8 narrowly rounded, with numerous large apical setae. Tergite 9 long, setose. Gonapophyses 9 sclerotized, merged to form common internal structure. Tergite 10 very short, setose. Sternite 10 setose, merged with tergite 10, or separate. Cercus setose, basicercus much longer than disticercus.

Paradoxa fusca Marshall 1896

(Figs 1, 2, 13, 26, 33, 40, 45-54)

Marshall 1896: 290 (description male), plt. XII, fig. 5 (line drawing habitus); Tonnoir & Edwards 1927: 823 (description female), plt. 62, fig. 71 (photo wing).

Holotype. Male, "Lincoln College" [= Lincoln, Mid Canterbury, South Island], in September [without year]. Specimen lost.

Diagnosis. This is the only species of the genus *Paradoxa* in New Zealand and thus recognizable readily by the generic characters. Differences between *P. fusca* and *P. paradoxa* are numerous (see Jaschhof 2006), including the wing membrane that is darkened along the anterior margin and asetose in *P. fusca* but not darkened and with setae along the posterior margin in *P. paradoxa*; the M1 that is distinct throughout in *P. fusca* but very weak or basally evanescent in *P. paradoxa*; the M2 that is very weak or basally evanescent in *P. paradoxa*; and the A2 that is absent in *P. fusca* but present in *P. paradoxa*.

Redescription. Male. **Head.** Fig. 26. Median convexity of postgenae not sclerotized. Frontal furrow complete. Frontal tubercle 2-pointed. Clypeus smaller than face. Nodes of antennal flagellomeres 0.6 times as long as wide (Figs 49, 52). Maxillary palpus 4-segmented, with 2 segments proximally of presumed third; basalmost segment asetose; apical segment less than twice the length of preceding segment.



FIGURES 1–4. Specimens in lateral view. 1: *Paradoxa fusca* Marshall, male. 2: *Paradoxa fusca* Marshall, female. 3: *Sigmoleia melanoxantha* Edwards, male. 4: *Sigmoleia melanoxantha* Edwards, female.

Thorax. Fig. 33. **Wing.** Fig. 13. Length 1.4–1.8 mm. Membrane darkened on anterior margin, without setae. C ending before wing apex. R1 of variable length, but always shorter than ta. M-stem weak, sometimes hardly discernible; basalmost portion of M2 very weak or evanescent. A2 absent. Tb setose. **Legs.** Fore coxa light, mid and hind coxae dark. Hind tibial apical comb of pale setae lacking.

Terminalia. Sternite 9 absent. Tergite 9 merged basally with gonocoxites, subrectangular, setose dorsally, ventrally a varying number of short, blunt macrosetae in subapical line (Figs 45, 46). Gonocoxites separate ventrobasally; ventral surface not bulging; apicodorsal lobes with numerous short, blunt mesal macrosetae and ordinary setae of various sizes (Figs 45, 47); a rounded setose lobe present mesally of gonostylus (Fig. 45). Gonostylus elongate, with large ventral setae (Fig. 45) and apicodorsal comb of blunt macrosetae plus 1 longer, pointed macroseta most apically (Fig. 47). Aedeagus/paramere complex with large membranous central portion, deeply incised mesally (Fig. 45), accompanied laterally by weakly sclerotized, tusklike processes (Fig. 51); process apices straight or hooked, smooth or serrate, which is subject of infraspecific variation (Fig. 48). Hypoproct setose apically (Fig. 51). Setae on cerci directed posteriorly (Fig. 45), not ventrally as in *P. paradoxa*.

Female. **Head.** Nodes of antennal flagellomeres 0.4 times as long as wide (Fig. 53), with 1–2 short setae among trichia.

Wing. Length 1.8–2.8 mm.

Terminalia. Fig. 40. Tergite 10 fused with sternite 10. Basicercus about twice as long as disticercus.

Distribution and phenology. Endemic to NZ: NO (TO), SO (NN, BR, KA, MC, OL, WD, SL). Very local in the North Island, widespread in the South Island. Adults captured in beech forest, podocarp forest (including kahikatea swamp forest) and mixed beech/podocarp forest, also in grassland and shrubland adjacent to woodland. Visits tree crowns of beeches and four species of podocarps up to a height of 21 m. Adult activity throughout the year except the winter period from May to July.

Material studied. NO. TO: 1 male, Pureora F., Waipapa Res., Jan. 1984, J. Hutcheson; 2 males, 2* females, same loc. but 20 Oct. 1983; 4* males, same loc. but 12 Jan. 1984; 1* female, same loc. but 15 March 1984; 3* males, 3* females, same loc. but 29 March 1983. SO. NN: 2 (1*) males, 2 females, Kahurangi N. P., Takaka R. valley (Cobb dam road), 31 Aug.-7 Oct. 2001, M. & C. Jaschhof; BR: 1 male, 1 female, Cass, Middle Bush, 17 Nov. 1998, P. M. Johns; 2* males, 1* female, same loc. but 9 April 1998; 1* female, same loc. but 11 April 1998; 21 (3*) males, 3 females, Ahaura, Granville S. F., Dec. 1994, J. Hutcheson; 8 males, Maruia F., Shenandoah Saddle, 25 Nov. 2001, M. Jaschhof & U. Kallweit; 9 females, same loc. but 9 Oct.-3 Nov. 2001, M. & C. Jaschhof; 1 female, same loc. but 3-25 Nov. 2001; 1* male, 1* female, L. Daniells Track 7 km E Springs Junction, 9 Nov. 2001, M. Jaschhof; 1 female, same loc. but 24 Nov.-26 Dec. 2001, M. & C. Jaschhof; 1 female, 5 km W Maruia Springs, 26 Nov.-25 Dec. 2001, M. & C. Jaschhof; 1 female, Lewis Pass, 26 Nov.-25 Dec. 2001, M. & C. Jaschhof; 2 females, Paparoa N. P., 5 km E Punakaiki, Inland Pack Track, 30 Sep.-5 Nov. 2001, M. & C. Jaschhof; KA: 11 (4*) males, 2 females, Blue Duck Sc. Res., 29 Nov. 1990-28 Feb. 1991, R.K. Didham; MC: 4 males, 1 female, Craigieburn F. P., Broken R. skifield road, 4 Dec. 2001, M. Jaschhof & U. Kallweit; OL: 15 (4*) males, 1 female, Fiordland N. P., Hollyford R. valley, S Divide Creek, 6-24 Jan. 2002, M. & C. Jaschhof; WD: 3 females, Westland N. P., SE Gillespies Beach, 14 Oct.-21 Nov. 2001, M. & C. Jaschhof; 2 females, Waiatoto, 16 Oct.-20 Nov. 2001, M. & C. Jaschhof; 1 male, same loc. but 20 Nov. 2001, U. Kallweit; SL: 4 males, 7 females, Catlins Coastal Rain F. P., Catlins R. valley, 27 Jan.-5 March 2002, M. & C. Jaschhof; 1* male, same loc. but 3 Jan. 2002, M. Jaschhof; 2 females, Catlins, Purakaunui Scenic Res., 27 Jan.-5 March 2002, M. & C. Jaschhof.

Genus Sigmoleia Tonnoir & Edwards 1927

Tonnoir & Edwards 1927: 826 (description); Matile 1993: 172 (discussion, New Caledonian species). **Type species.** *Sigmoleia melanoxantha* Edwards in Tonnoir & Edwards 1927, by original designation.

Diagnosis. Species of *Sigmoleia* have the following synapomorphies: the premental apodeme has 1 posterior process; the maxillary palpi are shortened (Fig. 27); the mesepisternum is setose (Fig. 34); the fore and mid tibiae are asetose; and the female hypoproct is enlarged. The male terminalia are rather uniform, with genus-specific character states as follows. The gonocoxites have a large ventral emargination and narrow lateral processes (Fig. 55); the gonostyli bear abundant short macrosetae (Fig. 55); the ejaculatory apodeme is absent (Fig. 58); and the parameres are fused to form a tegmen (Fig. 58). The top of the head is pointed and situated on the same level with the ventral margin of the mesonotum (Fig. 34). The lateral ocelli are far from the eye margins (Fig. 27). The scutum is strongly arched (Fig. 34). Preepisternum 2 and laterotergite are in touch ventrally (Fig. 34). Sc is short and ends free; the M-fork is shortened; ta is very short; CuA is furcate; CuA1 joins CuA2 to form a closed *cua1*; and A1 joins CuA2 to form a closed *cup* (Fig. 14).

Redescription. Color. Dark brown, abdominal tergites with light anterior margins. Head. Head capsule in lateral view higher than long, pointed on top, evenly setose. Foramen situated clearly above midheight of head. Median convexity of postgenae not or weakly sclerotized. Frons setose. Frontal furrow complete. Frontal tubercle 1-pointed. Antennae inserted below midheight of head. Scape little longer than pedicel, both setose. Fourteen flagellomeres; individual flagellomere cylindrical, with very short stalk; node in both sexes little shorter to little longer than wide, with short trichia, setae absent. Numerous fine interommatidial setulae. Three ocelli almost in line, situated frontally, median ocellus smaller than laterals, the latter far from eye margins. Face subrectangular, setose, with rows of setae along mesal eye margins. Clypeus rounded, smaller than face, setose. Labrum small, asetose. Stipes strongly setose. Lacinia absent. Maxillary palpus short, 3-segmented, with one segment proximally of presumed third; basalmost segment very small and asetose; third segment thick, with dorsomesal sensory pit; apical segment elongate. Prementum weak, asetose. Premental apodemes fused mesally, with 1 large posterior process. Labellum setose laterally; large prestomal teeth in long mesal row.

Thorax. High, scutum index 2.0, episternum index 1.0. Postpronotum asetose. Suture between antepronotum and proepisternum incomplete, both sclerites with setae of various sizes. Proepimeron situated posteroventrally of proepisternum, truncate, fitting into shallow excavation of anepisternum. Basisternum 1 asetose. Anepisternum slightly larger than preepisternum 2, with distinct suture between, with numerous short setae. Preepisternum 2 covering basalmost portion of mid coxa, with few fine dorsal setae. Anepimeron small, approaching laterotergite ventroposteriorly. Anterior basalare setose. Mid-pleural pit slit-like, its mound with membranous area. Laterotergite ovate, bulging, strongly setose, anteriorly in touch with preepisternum 2. Scutum slightly pointed and protruding anteriorly, markedly arched, with evenly distributed setae intermingled with lateral bristles. Prescutum not traceable. Scutellum setose. Mediotergite very slightly curved. Wing. Long, wing index 2.3. Membrane with light brown tinge; dark markings apically, along proximo-anterior margin, around ta and bend of CuA2; with microtrichia on both sites and some setae close to posterior margin. Calypterous lobe well developed, with setose margin. Dmp asetose. Anal lobe slightly angled. C extending much beyond apex of R5 and almost to wing apex. Sc short, ending free. One crossvein (Rs) present between R1 and R5 in proximal half of wing. Length of Rs variable, sometimes extremely short which results in R1 and R5 being almost in touch. R1 much longer than ta, ending in distal half of wing. R5 straight. M furcate, M-stem slightly shorter to longer than fork, tines of M-fork evenly diverging towards wing apex, or M1 strongly sinuous. CuA furcate. CuA2 angled twice; CuA1 joining CuA2 at anterior bend to form *cua1*, A1 joining CuA2 at posterior bend to form a closed *cup*. CuP foldlike, very short. A2 absent. Dorsal setae present on all veins except h, Sc, Rs, and CuP. Ventral setae present on R1, R5, and in some species also on ta and tb. Halter with light stem and dark knob. Legs. Hind coxa not widened subbasally. Tibial and most tarsal trichia irregularly arranged. Fore tibia shorter than femur. Fore tibial organ with semicircular rim, with numerous pale trichia of which the distalmost form a comb. Fore and mid tibiae asetose, hind tibia with row of setae, longest setae as long as tibial diameter. Mid tarsi with sole of 2 rows of short setae, hind tarsi with up to 4 rows of setae. Hind tibial apical comb of pale setae lacking. Tibial spurs 1:2:2, with serrated rims; spurs on mid and hind tibiae unequal in length. Empodia small. Pulvilli not traceable. Claws with each 1 large and small tooth.



FIGURES 5–8. Specimens in lateral view. 5: *Paracycloneura apicalis* Tonnoir, male. 6: *Tonnwardsia* gen. et sp. n., male. 7: *Tonnwardsia* gen. et sp. n., female. 8: *Cawthronia nigra* Tonnoir, male.

Abdomen. Setose except sternite 1. Male segment 8 very short. Light, weakly pigmented lateral lines (folds?) present on male tergites 2–6 and at least sternites 5–6, and female tergites 2–5 and at least sternite 5.

Male terminalia. Small, not rotated. Sternite 9 not traceable. Tergite 9 separate from gonocoxites, short and wide, consisting usually of 2 large sclerotized portions interconnected by narrow membranous portion, sclerotized portions setose. Gonocoxites broadly merged ventrobasally (= basal portion), with narrow ventrolateral processes projecting beyond gonostyli; each process with 1 short apical and 1 subapical seta. PostGA and antGA long. Gonostylus with large main body arising from basal stalk, the latter with dorsal setae, the former with numerous short, blunt macrosetae directed mesally. Ejaculatory apodeme absent. Parameres merged to form tegmen; parameral apodemes well developed, directed ventrolaterally. Hypoproct with 4 setae. Cerci largely fused, rounded apically, setose. **Female terminalia.** Short. Tergite 8 large, setose. Gonocoxite 8 rounded apically, with large setae. Tergite 9 not traceable. Gonapophyses 9 merged to form small, weakly sclerotized internal structure. Tergite 10 very short, setose. Sternite 10 very narrow, setose. Hypoproct unusually large, setose apically. Cercus setose, basicercus longer than disticercus.

Variation. The extent of infraspecific variation in *Sigmoleia* is remarkable, in particular with respect to body size, antenna length, and outline and relative length of Rs and M1. Unlike in the *Sigmoleia* species from

New Caledonia (see Matile 1993), interspecific differences in leg coloration are not apparent in the species from New Zealand.



FIGURES 9–12. Specimens in lateral view. 9: *Cawthronia nigra* Tonnoir, female. 10: *Waipapamyia dentata* **sp. n.**, female. 11: *Cycloneura* **sp.**, male. 12: *Cycloneura* **sp.**, female.

Key to species of Sigmoleia in New Zealand (males)

1	M1 sinuous
-	M1 straight
	M1 strongly sinuous, its basal portion running almost parallel to M2 (Fig. 14) melanoxantha Edw.
-	M1 moderately sinuous, its basal portion diverging from M2 (Fig. 15)similis sp. n.
3	Ventrolateral processes much longer than basal portion of gonocoxites, process apices curved mesally and thus
	approaching each other (Fig. 65)separata sp. n.

Identification. In the two New Caledonian species of *Sigmoleia*, *S. minuta* Matile 1993 and *S. spinosistyla* Matile 1993, M1 is not sinuous but straight, which applies also to *S. separata* and *S. peterjohnsi* from New Zealand. Matile's species differ from ours in that the M-fork is U-shaped, not V-shaped. Further interspecific differences are found in the male terminalia (see Matile 1993). Even so, comparison of *S. spinosistyla* and *S. peterjohnsi* reveals an extent of conformity that is astonishing, considering that New Caledonia and New Zealand are separated by 1,300 kilometres of insurmountable ocean or, in terms of geohistory, for a time span of about 40 million years (Stevens 1980).



FIGURES 13–18. Wings. 13: *Paradoxa fusca* Marshall, dorsal view. 14: *Sigmoleia melanoxantha* Edwards, ventral view. 15: *Sigmoleia similis* sp. n., ventral view. 16: *Sigmoleia separata* sp. n., dorsal view. 17: *Sigmoleia peterjohnsi* sp. n., ventral view. 18: *Cycloneura triangulata* Tonnoir, ventral view.

Sigmoleia melanoxantha Edwards in Tonnoir & Edwards 1927

(Figs 3, 4, 14, 55–62)

Tonnoir & Edwards 1927: 827 (description both sexes), plt. 61, fig. 65 (photo wing). *Holotype*. Sex unknown, Ohakune [Taupo, North Island], in May/July 1923, T.R. Harris leg. In NHM (specimen not seen).

Diagnosis. This species is distinguished from its congeners by the strongly sinuous M1 of which the basal portion runs almost parallel to M2 (Fig. 14). For a similar species, see below *S. similis*.

Redescription. Male. **Head.** Nodes of antennal flagellomeres 1.5–2.1 times as long as wide (Figs 60, 61). Apical segment of maxillary palpus as long as, or slightly longer than, preceding segment (Fig. 59).

Wing. Fig. 14. Length 1.6–3.0 mm. C almost reaching to wing apex. M-stem little shorter than M2. Outline of M1 variable, in large specimens more sinuous than in small specimens. Ventral setae on R1, R5, ta, and tb.

Terminalia. Sclerotized portions of tergite 9 interconnected by narrow sclerotized bridge; apical margin emarginate mesally (Fig. 57). Basal portion of gonocoxites large and setose; ventrolateral processes about as long as basal portion, curved mesally (Fig. 55). Stalk of gonostylus bulging, with large setae (Fig. 57). Tegmen apex narrow, rounded (Fig. 58).

Female. Head. Nodes of antennal flagellomeres 1.8–1.9 times as long as wide (Fig. 62).

Wing. Length 3.0 mm.

Distribution and phenology. Endemic to NZ: NO (ND, TO, WN), SO (NN, BR, KA, OL, WD, SL). Widespread in both the main islands. Adults captured abundantly in forests of beeches, podocarps, kauris as well as mixed forests, and in tussock grassland adjacent to woodland, up to an altitude of 800 m above sea level. Adult activity throughout the year.

Material studied. NO. ND: 3* males, 5 (3*) females, Waipoua F., along S. H. 12, 24 July–17 Aug. 2001, M. & C. Jaschhof; TO: 7 males, Pureora F., Waipapa Res., 3 Nov. 1983, J. Hutcheson; WN: 1 male, Tararua F. P., Blue Range Hut Track 10 km SW Mt Bruce, 2 Feb. 2002, M. Jaschhof. SO. NN: 28 males, 2 females, Kahurangi N. P., Takaka R. valley (Cobb dam road), 31 Aug.-7 Oct. 2001, M. & C. Jaschhof; BR: 76 (4*) males, 4 females, Maruia F., Shenandoah Saddle, 9 Oct.-25 Nov. 2001, M. & C. Jaschhof; 1 male, same locality but 25 Dec. 2001, M. Jaschhof & U. Kallweit; 17 males, 2 females, 5 km W Maruia Springs, 26 Nov.-25 Dec. 2001, M. & C. Jaschhof; 10 males, L. Daniells Track 7 km E Springs Junction, 24 Nov.-26 Dec. 2001, M. & C. Jaschhof; 2 males, 1 female, Lewis Pass, 26 Nov.-25 Dec. 2001, M. & C. Jaschhof; 23 (7*) males, Ahaura, Granville S. F., Dec. 1994, J. Hutcheson; 1 male, Paparoa N. P., 5 km E Punakaiki, Inland Pack Track, 30 Sept.-5 Nov. 2001, M. & C. Jaschhof; KA: 2 males, Blue Duck Sc. Res., 12 May-9 June 2001, M. & C. Jaschhof; OL: 6 males, 1 female, Fiordland N. P., Hollyford R. valley, S Divide Creek, 6-24 Jan. 2002, M. & C. Jaschhof; 6 males, 2 females, Moraine Creek Track, 5–24 Jan. 2001; M. & C. Jaschhof; 12 males, 7 females, Eglinton R. valley, Deer Flat, 4-24 Jan. 2002, M. & C. Jaschhof; WD: 1 male, Westland N.P., SE Gillespies Beach, 14 Oct.-21 Nov. 2001, M. & C. Jaschhof; SL: 3 (1*) males, Catlins, Purakaunui Scenic Res., 27 Jan.-5 March 2002, M. & C. Jaschhof; 25 males, 3 females, Catlins Coastal Rain F. P., Catlins R. valley, 27 Jan.-5 March 2002, M. & C. Jaschhof.

Sigmoleia similis Jaschhof & Kallweit sp. n.

(Figs 15, 34, 63–64)

Diagnosis. This species is distinguished from its congeners by the slightly sinuous M1 of which the basal portion diverges from M2 (Fig. 15). In *S. melanoxantha*, which is a closely similar species, the basal portion of M1 runs almost parallel to M2. Further differences between these two species are found in the male genitalic structures, particularly tergite 9, gonocoxites and gonostyli (see Figs 63–64 *versus* Figs 55–58).

Description. Male. **Head.** Nodes of antennal flagellomeres 1.5–1.8 times as long as wide. Apical segment of maxillary palpus longer than preceding segment.

Wing. Fig. 15. Length 1.3–2.3 mm. C almost reaching to wing apex. M-stem little shorter than M2. M2 slightly sinuous, diverging basally from M2. Ventral setae present on R1, R5, ta, and tb.

Terminalia. Sclerotized portions of tergite 9 barely in touch mesally (Fig. 64). Basal portion of gonocoxites short and setose; ventrolateral processes much longer than basal portion, strongly curved mesally with apices almost in touch (Fig. 63). Stalk of gonostylus flat, not bulging, with large setae (Fig. 64). Tegmen apex subtriangular with rounded edges (Fig. 63).

Female. Head. Nodes of antennal flagellomeres 1.9 times as long as wide.

Wing. Length 3.3 mm.

Distribution and phenology. Endemic to NZ: SO (NN, BR, OL, WD, SL). Confined to South Island where it is widespread. Adults, predominantly males, captured abundantly in beech, podocarp and mixed beech/podocarp forests between August and February.

Etymology. From Latin, similar, similar, referring to the similarity of this species to S. melanoxantha.

Types. *Holotype*. Male*, New Zealand, South Island, Buller, Maruia Forest, Shenandoah Saddle, 500 m, in beech forest, 9 Oct.–3 Nov. 2001, by Malaise trap, M. & C. Jaschhof (in NZAC). *Paratypes*. 6* males, same data as the holotype (in NZAC); 7* males, BR, Ahaura, Granville S. F., in forest of hard beech *Nothofagus truncata*, 170–250 m, Dec. 1994, by Malaise trap, J. Hutcheson (in NZAC); 4* males, SO, NN, Kahurangi N. P., Takaka R. valley (Cobb dam road), 450–800 m, in mixed podocarp/broadleaf forest, 31 Aug.–7 Oct. 2001, by Malaise trap, M. & C. Jaschhof (in SMTD).



FIGURES 19–25. Wings. 19: Paracycloneura apicalis Tonnoir, ventral view. 20: Paracycloneura inopinata sp. n., ventral view. 21: Tonnwardsia gen. et sp. n., ventral view. 22: Cawthronia nigra Tonnoir, ventral view. 23: Waipapamyia dentata sp. n., dorsal view. 24: Waipapamyia elongata sp. n., ventral view. 25: Waipapamyia truncata sp. n., ventral view. 25: Waipapamyia truncata sp. n., ventral view.

Other material. SO. NN: 37 males, Kahurangi N. P., Takaka R. valley (Cobb dam road), 31 Aug.–7 Oct. 2001, M. & C. Jaschhof; BR: 8 males, 2 females, same data as the holotype; 8 males, same loc. but 3–25 Nov. 2001; 2 males, same loc. but 25 Nov. 2001, U. Kallweit; 4 males, L. Daniells Track 7 km E Springs Junction, 9 Nov. 2001, M. Jaschhof; 2 males, same loc. but 24 Nov.–26 Dec. 2001, M. & C. Jaschhof; 1 male, same loc. but 27 Nov. 2001, U. Kallweit; 1 male, 5 km W Maruia Springs, 26 Nov.–25 Dec. 2001, M. & C. Jaschhof; 3 males, Lewis Pass, 26 Nov.–25 Dec. 2001, M. & C. Jaschhof; 2 males, Ahaura, Granville S. F., Dec. 1994, J. Hutcheson; 1 male, Paparoa N. P., 5 km E Punakaiki, Inland Pack Track, 30 Sep.–5 Nov. 2001, M. & C. Jaschhof; OL: 27 males, 6 females, Fiordland N. P., Hollyford R. valley, Moraine Creek Track, 5–24 Jan. 2002, M. & C. Jaschhof; 5 males, S Divide Creek, 6–24 Jan. 2002, M. & C. Jaschhof; 2 males, Eglinton R. valley, Deer Flat, 4–24 Jan. 2002, M. & C. Jaschhof; WD: 2 males, Waiatoto, 16 Oct.–20 Nov. 2001, M. & C. Jaschhof; 8 males, Westland N. P., SE Gillespies Beach, 14 Oct.–21 Nov. 2001, M. & C. Jaschhof; SL: 1 male, Catlins, Purakaunui Scenic Res., 27 Jan.–5 March 2002, M. & C. Jaschhof.



FIGURES 26–29. Head in frontal view. 26: *Paradoxa fusca* Marshall. 27: *Sigmoleia peterjohnsi* **sp. n.** 28: *Cawthronia nigra* Tonnoir. 29: *Waipapamyia dentata* **sp. n.** Length of scale bar = 0.1 mm.

Sigmoleia separata Jaschhof & Kallweit sp. n. (Figs 16, 65–68)

Diagnosis. This species differs from *S. peterjohnsi*, with identical wing venation, in details of the male terminalia, particularly tergite 9, gonocoxites, gonostyli, and tegmen (see Figs 65–67 *versus* Figs 69–70).

Description. Male. **Head.** Nodes of antennal flagellomeres 1.3 times as long as wide (Fig. 68 left). Apical segment of maxillary palpus little longer than preceding segment.



Wing. Fig. 16. Length 1.6–2.1 mm. C ending clearly before wing apex. M-stem longer than M2. M-fork V-shaped. Ventral setae present on R1 and R5.

FIGURES 30–33. Morphology of Leiini. 30: Head, in frontal view, of *Cycloneura* Marshall sp. 31: Head, in frontal view, of *Tonnwardsia* **gen. et sp. n.** 32: Head, in frontal view, of *Paracycloneura apicalis* Tonnoir. 33: Thorax, in lateral view, of *Paradoxa fusca* Marshall. Length of scale bar = 0.1 mm (for 30–32) and 0.25 mm (for 33).

Terminalia. Sclerotized portions of tergite 9 separated by weak membranous portion (Fig. 67). Basal portion of gonocoxites short, with few setae; ventrolateral processes very long, apices curved slightly mesally, widely separate from one another, with sparse, fine setae (Fig. 65). Stalk clearly distinguished from main body of gonostylus, with 1 short apical macroseta and large setae elsewhere (Fig. 67). Tegmen apex wide and blunt (Fig. 66).

Female. Head. Nodes of antennal flagellomeres 1.2 times as long as wide (Fig. 68 right).



FIGURES 34–37. Thorax, lateral view. 34: *Sigmoleia similis* **sp. n.** 35: *Waipapamyia dentata* **sp. n.** 36: *Cawthronia nigra* Tonnoir. 37: *Cycloneura* Marshall sp. Length of scale bar = 0.5 mm.

Wing. Length 1.5–2.0 mm.

Distribution and phenology. Endemic to NZ: NO (AK), SO (BR, KA, MC, OL, SL). Very local in the North Island, widespread in the South Island. Adults captured in beech, podocarp and mixed beech/podocarp forests from November to April. Visits tree crowns of black beech *Nothofagus solandri* and totara *Podocarpus totara* up to a height of 17 m.

Etymology. From Latin, *separatus*, separate, referring to the outline of ninth tergite.

Types. *Holotype.* Male*, New Zealand, South Island, Otago Lakes, Fiordland National Park, Eglinton River valley, Deer Flat, in beech forest, 4–24 Jan. 2002, by Malaise trap, M. & C. Jaschhof (in NZAC). *Paratypes.* 1* male, 2* females, same data as the holotype (in NZAC); 1* male, NO, AK, Huia, in native bush, Jan. 1981, by Malaise trap, B. Mau (in NZAC); 1* male, SO, KA, Blue Duck Sc. Res., 300–400 m, in mixed podocarp/beech forest, 29 Nov. 1990, by window trap in crown of a black beech *Nothofagus solandri* tree 15 m above ground, R.K. Didham (in NZAC); 1* male, same loc. but 6 Dec. 1990, 13.5 m above ground (in NZAC); 2* females, same loc. but 31 Jan. 1991, by window traps in crown of a totara *Podocarpus totara* tree 12 and 17 m above ground (in NZAC); 1* male, 1* female, SO, MC, Cass, Middle Bush, in forest of

black beech *Nothofagus solandri*, 9 April 1998, by Malaise trap, P.M. Johns (in NZAC); 1* male, same loc. but 10 Dec. 1998 (in SMTD); 2* males, 1* female, SO, BR, Ahaura, Granville S. F., 170–250 m, in forest of hard beech *Nothofagus truncata*, Dec. 1994, by Malaise trap, J. Hutcheson (in SMTD).

Other material. SO. SL: 1 male, 4 females, Catlins Coastal Rain F. P., Catlins R. valley, 27 Jan.–5 March 2002, M. & C. Jaschhof.



FIGURES 38–39. Thorax, lateral view. 38: *Tonnwardsia* gen. et sp. n. 39: *Paracycloneura apicalis* Tonnoir. Length of scale bar = 0.25 mm.

Sigmoleia peterjohnsi Jaschhof & Kallweit sp. n.

(Figs 17, 27, 69–70)

Diagnosis. This species differs from *S. separata* in several details of the male terminalia; the basal portion of the gonocoxites is larger and the ventrolateral processes are shorter (Fig. 69), the stalk of the gonostylus is not distinguished from the main portion (Fig. 70), and the tegmen apex is rounded (Fig. 69).

Description. Male. **Head.** Fig. 27. Nodes of antennal flagellomeres 1.1–1.2 times as long as wide. Maxillary palpus short; apical segment shorter than preceding segment.

Wing. Fig. 17. Length 1.3–2.2 mm. C ending clearly before wing apex. M-stem longer than M2. M-fork V-shaped. Ventral setae present on R1 and R5.

Terminalia. Sclerotized portions of tergite 9 interconnected by narrow membranous portion (Fig. 70). Basal portion of gonocoxites large, with few setae; ventrolateral processes as long as basal portion, strongly curved mesally and with apices approaching each other (Fig. 69). Stalk not distinguished from main portion of gonostylus, with 3–4 subbasal setae (Fig. 70). Tegmen apex rounded (Fig. 69).

Female. Head. Nodes of antennal flagellomeres 1.4 times as long as wide.

Wing. Length 1.8–2.0 mm.

Distribution and phenology. Endemic to NZ: SO (MC). Uncommon, confined to central South Island. Adults collected in beech forest in November/December and May.

Etymology. We name this species to honour Peter M. Johns, entomologist and research associate of the Canterbury Museum, Christchurch, who contributed to our study by providing a large number of specimens and adviced on many rewarding collection sites.

Types. *Holotype.* Male*, New Zealand, South Island, Mid Canterbury, Cass, Middle Bush, in forest of black beech *Nothofagus solandri*, 10 Dec. 1998, by Malaise trap, P.M. Johns (in NZAC). *Paratypes.* 7* males, 1* female, same loc. but 17 Nov. 1998 (in NZAC); 2* males, same loc. but 30 May 1998 (in SMTD); 2* males, 1* female, MC, Craigieburn F. P., Broken R. skifield road, in secondary beech forest, 4 Dec. 2001, by sweepnet, M. Jaschhof (in SMTD).

Other material. SO. MC: 3 males, same data as the holotype.



FIGURES 40–44. Female terminalia, lateral view. 40: *Paradoxa fusca* Marshall. 41: *Waipapamyia dentata* **sp. n.** 42: *Cawthronia nigra* Tonnoir. 43: *Cycloneura* Marshall sp. 44: *Tonnwardsia* **gen. et sp. n.** Length of scale bar = 0.05 mm (for 41) and 0.1 mm (for 40, 42–44).

Genus Cycloneura Marshall 1896

(Figs 11, 12, 18, 30, 37, 43)

Marshall 1896: 289 (description); Tonnoir & Edwards 1927: 823 (supplement to description). **Type species.** *Cycloneura flava* Marshall 1896, by original designation.

Diagnosis. The top of the head is pointed and situated on the same level with the ventral margin of the mesonotum (Fig. 37). The lateral ocelli are close to the eye margins (Fig. 30). The scutum is pointed and protruding anteriorly (Fig. 37). The proepimeron is enlarged (Fig. 37). The meron, if correctly identified, is present above the meeting point of preepisternum 2, mid coxa, anepimeron, and laterotergite (Fig. 37). Sc is short and ends free; M is one-branched; and A1 joins CuA2 to form a closed *cup* (Fig. 18). The hind margin of the hind coxa is strongly protruding (Fig. 37). The genus-specific combination of male genitalic character states includes the elongate, subtriangular tergite 9; the long gonocoxites with a deep, V-shaped ventral emargination; and the comparatively small gonostyli (Tonnoir & Edwards 1927: figs 236, 237). In females, gonocoxites 8 are excavated mesally and covered densely with large trichia.

Redescription. Color. Brown with lighter legs. **Head.** Figs 30, 37. Head capsule in lateral view higher than long, pointed on top. Foramen situated clearly above midheight of head. Median convexity of postgenae weakly sclerotized. Frons asetose. Frontal furrow complete. Frontal tubercle one-pointed. Antennae inserted below midheight of head. Scape little longer than pedicel, both setose. Fourteen flagellomeres; individual flagellomere cylindrical, with very short stalk; node much longer than wide, usually slightly longer in males than in females, covered densely with short trichia; setae largely absent except 2 on apical flagellomeres. Numerous fine interommatidial setulae. Three ocelli in wide triangle, situated frontally, median ocellus smaller than laterals, the latter almost in touch with eye margins. Three bristles in line behind upper eye margins, further bristles present in front of ocelli, all bristles directed anteriorly. Face subrectangular, with few fine setae. Clypeus subquadrate, with few fine setae. Labrum very small, subtriangular, asetose. Stipes setose. Lacinia sclerotized, bare. Maxillary palpus long, 5-segmented, with 2 segments proximally of presumed third; basalmost segment weak and asetose; second segment with wartlike sensilla; third segment longest, slender apically, with sensory pit. Prementum weak, asetose. Premental apodemes fused mesally, with 2 posterior processes. Labellum setose laterally; tiny prestomal teeth in long mesal row.

Thorax. Fig. 37. Flat, scutum index 2.9, episternum index 0.9–1.0. Postpronotum asetose. Antepronotum and proepisternum largely merged, with vestigial suture between; both sclerites with setae and bristles. Proepimeron extending along hind margins of antepronotum and proepisternum; ventroposterior process pointed, fitting into excavation of preepisternum 2. Basisternum 1 asetose. Anepisternum slightly smaller than preepisternum 2, with distinct suture between; asetose like all other pleural sclerites. Anepimeron large, with ventral portion narrow, fading away towards thorax margin. Mid-pleural pit well developed, its mound protruding, pleural apodeme funnel-shaped. Laterotergite bulging, rounded ventrally, subrectangular dorsally. Meron, if correctly identified, present as distinct, weakly sclerotized sclerite ventrally between preepisternum 2 and laterotergite. Scutum pointed and protruding anteriorly, with evenly distributed setae intermingled with bristles. Anterior parapsidal suture not traceable; median transverse suture present. Prescutum not traceable. Scutellum setose, 1 lateral bristle. Mediotergite very slightly curved. Wing. Fig. 18. Long, wing index 2.7. Membrane with light brown tinge, usually with dark markings subapically and near bend of CuA2; with microtrichia on both sites; setae absent. Calypterous lobe developed, with setose margin. Dmp asetose. Anal lobe very slightly angled. C extending much beyond apex of R5, ending before wing apex. Sc short, ending free. One crossvein (Rs) between R1 and R5 in proximal half of wing. R1 little shorter than ta, ending at or slightly beyond mid-wing. R5 straight. M one-branched, weak basally. CuA1 detached basally. CuA2 strongly sinuous. A1 joining CuA2 to form a closed *cup*. CuP very short. A2 absent. Dorsal setae on all veins except h, Sc, Rs, tb, and CuP. Ventral setae on R1 and R5. Halter with light stem and dark knob. Legs. Hind margin of hind coxa strongly protruding. Tibial trichia irregularly arranged. Tarsal trichia partly arranged in lines. Fore tibia shorter than femur, with few anterior setae. Fore tibial organ with semicircular rim, with numerous pale trichia of which the distalmost form a comb. Mid tibial bristles in 2, hind tibial bristles in 3 rows, most bristles clearly longer than tibial diameter. Hind tibial apical comb of pale setae present. Tibial spurs 1:2:2, with serrated rims, on mid and hind tibiae unequal in length. Empodia usually small, larger on fore legs in part of species. Pulvilli not traceable. Claws with 1 large and 1–2 small teeth.



FIGURES 45–54. *Paradoxa fusca* Marshall. 45: Male terminalia, ventral view; slightly pressed (0.1 mm). 46: Apical portion of tergite 9 to show variation in number of macrosetae, ventral view. 47: Gonostylus (a) and apicodorsal lobe of gonocoxite (b), mesal view; slightly distorted (0.05 mm). 48: Variation in apices of parameral processes in 4 specimens, ventral view (0.05 mm). 49: Male flagellomere 4, lateral view (0.05 mm). 50: Gonocoxites and tergite 9, dorsal view; slightly pressed (0.1 mm). 51: Aedeagus/paramere complex, ventral view (0.05 mm). 52: Male flagellomeres 1–5, lateral view (0.1 mm). 53: Female flagellomeres 1–5, lateral view (0.1 mm). 54: Gonocoxites and tergite 9, dorsal view; undisturbed (0.1 mm). Length of scale bar in parentheses.



FIGURES 55–64. Morphology in *Sigmoleia* spp. 55–62: *Sigmoleia melanoxantha* Edwards. 63–64: *Sigmoleia similis* **sp. n.** 55: Male terminalia, ventral view (0.1 mm). 56: Apex of gonocoxal process, dorsal view (0.05 mm). 57: Male terminalia, dorsal view (0.1 mm). 58: Tegmen, ventral view (0.05 mm). 59: Maxillary palpus, lateral view (0.05 mm). 60: Male flagellomere 4, lateral view (0.05 mm). 61: Male antennal flagellomeres 1–5, lateral view (0.1 mm). 63: Male terminalia, ventral view (0.1 mm). 64: Male terminalia, dorsal view (0.1 mm). antGA = anterior portion of gonocoxal apodeme, postGA = posterior portion of gonocoxal apodeme. Length of scale bar in parentheses.

Abdomen. Setose except sternite 1. Male segments 7 and 8 very short. Weakly pigmented lateral lines (folds?) traceable on tergites 2–6 in both sexes, absent on sternites.

Male terminalia. Large, not rotated. Sternite 9 not traceable. Tergite 9 merged basally with gonocoxites, elongate, subtriangular, evenly setose. Gonocoxites capsule-like, usually with V-shaped ventral emargination

and occasionally with complex lobes in various positions. GA short and wide, pointed anteriorly, not connected with parameres. Gonostylus small, inserted distoventrally on gonocoxal capsule, on mesal surface abundantly equipped with macrosetae of various sizes and shapes. Tegmen elongate, sclerotized. Ejaculatory apodeme not traceable. Hypoproct with 4 setae. Cerci largely fused. **Female terminalia.** Fig. 43. Tergite 8 very short dorsally, setose laterally. Apex of gonocoxite 8 pointed, with large setae, excavated and with innumerable large mesal trichia. Tergite 9 long, setose. Gonapophyses 9 sclerotized, merged to form common internal structure. Tergite 10 short, merged with sternite 10, both setose. Cerci setose, basicercus little longer than disticercus.

Species included. Our generic redescription is based on the two species named of *Cycloneura*, *C. flava* and *C. triangulata* Tonnoir 1927, and 6 unnamed species at our disposal. The taxonomy of these species will be treated in a separate paper (Jaschhof & Kallweit, in prep.).

Genus Paracycloneura Tonnoir & Edwards 1927

Tonnoir & Edwards 1927: 825 (description).

Type species. Paracycloneura apicalis Tonnoir in Tonnoir & Edwards 1927, by original designation.

Diagnosis. Synapomorphic character states of *Paracycloneura* are the mid tibial organ present in both sexes (which is exceptional among Leiini, cf. Väisänen 1986: 203), and the presumed male tergite 9 present as a narrow, sclerotized bridge on the basal gonocoxal margin (Fig. 71). The top of the head is pointed and situated on the same level with the ventral margin of the mesonotum (Fig. 39). The lateral ocelli are situated close to the eye margins (Fig. 32). The scutum is pointed anteriorly and protruding (Fig. 39). Preepisternum 2 and laterotergite are in touch ventrally (Fig. 39). Sc is short and ends free; M is one-branched; CuA2 is slightly bent, not sinuous; and A1 runs almost parallel to and separate from CuA2 (Fig. 19).

Redescription. Color. Brown with lighter legs. **Head.** Head capsule in lateral view higher than long, pointed on top. Foramen situated clearly above midheight of head. Median convexity of postgenae not sclerotized. Frons asetose. Frontal furrow complete. Frontal tubercle 1-pointed. Antennae inserted below midheight of head. Scape little longer than pedicel, both setose. Fourteen flagellomeres; individual flagellomere cylindrical, with very short stalk; node much longer than wide, densely covered with short trichia; setae largely absent except 2–3 on apical flagellomeres. Numerous fine interommatidial setulae. Three ocelli almost in line, situated frontally, median ocellus slightly smaller than laterals, the latter almost in touch with eye margins. A row of 3 strong bristles behind upper eye margins, 1 pair of strong bristles directed anteriorly between lateral ocelli. Face subrectangular, weakly sclerotized, with few fine setae. Clypeus ovate, with few fine setae. Labrum very small, weakly sclerotized. Stipes setose. Lacinia vestigial. Maxillary palpus long, 5-segmented, with 2 segments proximally of presumed third; basalmost segment weak, asetose; third segment with sensory pit; apical segment longest, twice as long as preceding segment. Prementum weak, asetose. Premental apodemes fused mesally, with 2 posterior processes. Labellum setose laterally; prestomal teeth in long, dense row.

Thorax. High, scutum index 2.2, episternum index 1.1. Postpronotum asetose. Suture between antepronotum and proepisternum incomplete; both sclerites setose. Proepimeron situated posteroventrally of proepisternum, long and pointed, fitting into notch of preepisternum 2. Basisternum 1 asetose. Anepisternum smaller than preepisternum 2, with distinct suture between, asetose like all other pleural sclerites. Ventral portion of anepimeron subtriangular, not reaching to ventral thorax margin. Mid-pleural pit well developed, pleural apodeme funnel-shaped. Laterotergite bulging, asetose, rounded ventrally, narrowed dorsally, anteroventrally in touch with preepisternum 2. Scutum pointed and protruding anteriorly, with evenly distributed setae intermingled with bristles. Prescutum not traceable. Scutellum setose, 2 lateral bristles. Hind margin of mediotergite almost straight.



FIGURES 65–70. Morphology in *Sigmoleia* spp. 65–68: *Sigmoleia separata* **sp. n.** 69–70: *Sigmoleia peterjohnsi* **sp. n.** 65: Male terminalia, ventral view. 66: Tegmen, ventral view. 67: Terminalia, dorsal view. 68: Flagellomeres 1–5, lateral view, male left, female right. 69: Male terminalia, ventral view. 70: Male terminalia, dorsal view. Length of scale bar = 0.05 mm (for 66) and 0.1 mm (for 65, 67–70).

Wing. Long, wing index 2.5. Membrane with light brown tinge and dark subapical transverse fascia, or apex completely dark, with microtrichia on both sites and usually some setae along posterior margin. Calypterous lobe developed, with large setae along margin. Dmp asetose. Anal lobe evenly rounded. C extending much beyond apex of R5 and up to wing apex. Sc short, ending free. One crossvein (Rs) between R1 and R5 in proximal half of wing. R1 longer than ta, ending in distal half of wing. R5 straight. M one-branched, straight. CuA1 short, detached basally. CuA2 slightly bent before half-length. CuP short. A1 weak, running almost parallel to and reaching to level of bend of CuA2. A2 present, slightly furcate. Dorsal setae on

all veins except h, Sc, Rs, and CuP. Ventral setae on R1 and R5. Halter with light stem and dark knob. **Legs.** Hind coxa not widened subbasally. Tibial and tarsal trichia irregularly arranged. Fore tibia shorter than femur, with 1 ventral seta. Fore tibial organ with semicircular rim, with numerous trichia of which the distalmost form a comb. Mid tibia with 4 rows of setae; in both sexes with dorsomesal groove of fine, pale translucent sensilla intermingled with very dense microtrichia, this mid-tibial organ occupies one third of tibia length. Hind tibia with 5 rows of setae, longest setae little longer than tibial diameter; apical comb of pale setae present. Tibial spurs 1:2:2, with serrated rims, on mid and hind tibiae unequal in length. Empodia small. Pulvilli not traceable. Claws with each 1 large and small tooth.

Abdomen. Segments 1–8 setose. Male segments 7 and 8 very short, both tergites and sternites bearing large setae arranged in long rows along distal margins. Tergites and sternites in both sexes without weakly pigmented lateral lines.

Male terminalia. Rotated 90°. Sternite 9 present as small membranous protrusion between gonocoxites. A narrow, sclerotized, subrectangular bridge on basal gonocoxal margin presumedly represents tergite 9 or a composite structure involving parts of it. Gonocoxites capsule-like, deeply emarginated ventrally, with large membranous dorsal portion; with apicoventral, mesal and apicodorsal lobes. Gonocoxal apodemes interconnected by weakly sclerotized bridge; postGA and antGA short. Gonostylus long and slender, largely hidden among gonocoxal lobes, inserted ventrally on gonocoxal capsule. Aedeagus and parameres forming complex, partly sclerotized structure. Hypoproct incised apicomesally, membranous, with 1 seta on either side. Cerci largely merged, rather small-sized, with apical and ventral setae. **Female terminalia.** Only 1 specimen in poor shape. Gonocoxite 8 with numerous large apical setae. Cercus setose, basicercus 1.5 times as long as disticercus, the latter elongate ovate.

Key to species of Paracycloneura (males)

1	Wing membrane with dark subapical fascia (Fig. 19) apicalis Tonn.
-	Wing membrane with dark portions at apex and around CuA (Fig. 20)
2	Aedeagus/paramere complex covered by pubescent ventral lobe (Fig. 79) inopinata sp. n.
-	Aedeagus/paramere complex without pubescent lobe, with strongly sclerotized, subtriangular tegmen
	Paracycloneura sp.

Paracycloneura apicalis Tonnoir in Tonnoir & Edwards 1927

(Figs 5, 19, 32, 39, 71-77)

Tonnoir & Edwards 1927: 825 (description both sexes), plt. 61, fig. 62, plt. 62, fig. 73 (photos wing), plt. 75, fig. 238 (line drawing male terminalia).

Holotype. Male, Waiho [Westland, South Island], 21 Jan. 1922, A.L. Tonnoir leg. In NZAC (specimen seen).

Diagnosis. This species is distinguished from its congeners by the dark subapical fascia on the wing membrane (Fig. 19) and in details of the male terminalia (see below under *P. inopinata*).

Redescription. Male. **Head.** Fig. 32. First and occasionally second antennal flagellomeres light. Node of fourth flagellomere 2.2–2.5 times as long as wide (Figs 73, 76).

Wing. Fig. 19. Length 2.4–3.0 mm. Membrane with dark subapical fascia, with some setae close to posterior margin.

Terminalia. Gonocoxites with setae of various sizes including 3 large ventromesal setae and 2 very long, pale setae on interior ventromesal margin; ventrobasal surface mesally with numerous tiny warts; apicoventral lobe with 6 lateral bristles and 2 large, pale setae, and 5 short, blunt apical macrosetae of which the most apical one is largest (Fig. 74); mesal lobe long and narrow, with 1 large pale apical seta, 1 smaller pale mesal seta and 3 ordinary subbasal setae (Fig. 75); apicodorsal gonocoxal lobe directed mesally, strongly flattened, with rasplike surface, comblike dark lamella on ventromesal margin, and 1 sabre-like, pointed macroseta

dorsosubapically (Figs 71, 72). Basal portion of gonostylus thick, with 2 mesal setae; apical portion slender, usually winding, with 1 fine subapical seta and some tiny setulae (Figs 75). Aedeagus/paramere complex with subtriangular, sclerotized tegmen (Fig. 77).



FIGURES 71–79. Morphology in *Paracycloneura* spp., males. 71–77: *Paracycloneura apicalis* Tonnoir. 78–79: *Paracycloneura inopinata* **sp. n.** 71: Terminalia, dorsal view (0.1 mm). 72: apicodorsal lobe of gonocoxite, ventral view, apical macroseta broken (0.05 mm). 73: Flagellomere 4, lateral view (0.05 mm). 74: Terminalia, ventral view (0.1 mm). 75: Gonostylus, apicoventral and mesal lobes of gonocoxite, mesal view, mesal lobe broken and separate (0.1 mm). 76: Flagellomeres 1–5, lateral view (0.1 mm). 77: Aedeagus/paramere complex, ventral view, presumed aedeagus stippled (0.05 mm). 78: Gonostylus, apicoventral and mesal lobes of gonocoxite, mesal view (0.1 mm). 79: Aedeagus/paramere complex, ventral view, presumed aedeagus stippled (0.05 mm). a = apicodorsal lobe of gonocoxites, b = mesal lobe of gonocoxites, c = apicoventral lobe of gonocoxites, d = gonostylus, e = presumed tergite 9, f = presumed sternite 9, g = tegmen. Length of scale bar in parentheses.

Remark. In their description of *P. apicalis*, Tonnoir and Edwards (1927: 825) mention "a male paratype from Cass [with] the wing-tip completely brownish"; this specimen, which we have not seen, should belong to our *P. inopinata*, or to even another *Paracycloneura* species not named here (see below).

Distribution and phenology. Endemic to NZ: SO (NN, BR, KA, WD). Confined to northern South Island. Adults, exclusively males, captured in beech and mixed podocarp/beech forests from November to February. A few specimens trapped in a beech tree crown in a height of 13.5 m.

Material studied. SO. BR: 2* males, L. Daniells Track 5 km E Springs Junction, 9 Nov. 2001, M. Jaschhof; KA: 3* males, Blue Duck Res., 24 and 31 Jan. 1991, R.K. Didham.

Paracycloneura inopinata Jaschhof & Kallweit sp. n.

(Figs 20, 78–79)

Diagnosis. *Paracycloneura inopinata* is extremely similar to *P. apicalis*. It differs in the more extensively dark portions of the wing membrane, including the wing apex (Fig. 20), and in several details of the male terminalia (see below).

Description. Male. **Head.** First antennal flagellomere light. Node of fourth flagellomere 2.3 times as long as wide.

Wing. Fig. 20. Length 3.1 mm. Apex and a portion around CuA dark. Some setae present close to posterior margin, or setae absent.

Terminalia. Very similar to that in *P. apicalis* with differences as follows. Gonocoxites with 4–5 large ventromesal setae and ordinary setae elsewhere, setae along ventromesal margin very dense; warts on ventrobasal surface larger and more numerous; apicoventral lobe with 5 lateral bristles and 5–6 short blunt apical macrosetae plus 1 larger pointed macroseta; mesal lobe (Fig. 78) shorter, with 1 large pale apical seta and 1 smaller pale mesal seta, lacking ordinary setae; sabre-like macroseta on apicomesal gonocoxal lobe inserted on short process. Gonostylus shorter, apical portion not winding, with 1 tiny subapical setula (Fig. 78). Aedeagus/paramere complex more elongate, approximately subrectangular, covered by pubescent ventral lobe (Fig. 79).

Female. Unknown.

Distribution and phenology. Endemic to NZ: SO (BR). Only known from an old-growth beech forest where it was collected together with *P. apicalis* in November.

Etymology. From Latin, *inopinatus*, unexpected.

Types. *Holotype*. Male*, New Zealand, South Island, Lake Daniells Track 7 km E Springs Junction, in mixed forest of red beech *Nothofagus fusca* and silver beech *N. menziesii*, 24 Nov. 2001, by sweepnet, M. Jaschhof (in NZAC). *Paratypes*. 1* male, same locality but 9 Nov. 2001 (in SMTD); 1* male (only terminalia preserved), same locality but 27 Nov. 2001, U. Kallweit (in SMTD).

Paracycloneura sp.

A male specimen we studied has the wing as extensively dark as is found in *P. inopinata*, while the first antennal flagllomeres are dark with light bases. The slide-mount of this specimen is in poor shape, which makes assessment of genitalic characters difficult. It differs from *P. inopinata*, at least, in details of the vestiture on the gonocoxal lobes, and in the aedeagus/paramere complex that includes a strongly sclerotized, pointed tegmen. Adequately prepared specimens are needed in order to be certain as to the specific characters of this apparently new species.

Material studied. SO. WL: 1* male, 1* female, Westland N. P., Fox Glacier Village, 23 Oct. 2001, M. Jaschhof.

Genus Tonnwardsia Jaschhof & Kallweit gen. n.

(Figs 6, 7, 21, 31, 38, 44)

Type species. Cycloneura aberrans Tonnoir in Tonnoir & Edwards 1927, hereby designated.

Diagnosis. The top of the head is pointed and situated on the same level with the ventral margin of the mesonotum (Fig. 38). The lateral ocelli are close to the eye margins (Fig. 31). The scutum is slightly protruding anteriorly (Fig. 38). The presumed meron is present above the meeting point of preepisternum 2, mid coxa, anepimeron, and laterotergite (Fig. 38). A part of the microtrichia on the wing membrane are more clearly arranged in lines than in most other Leiini. Sc is short and ends free; M is one-branched; CuA2 is sinuous; and A1 is not in touch with CuA2 (Fig. 21). Male sternite 9 bears large, variform processes, which is a synapomorphic character state of *Tonnwardsia*. The female terminalia are peculiar for the unusually broad basal portions of gonocoxites 8 (Fig 44).

Tonnwardsia is sufficiently different from *Cycloneura*, its presumed sister group, to warrant distinct generic status. Differences between the two genera include the hind coxa that is very broad in *Cycloneura* but not so in *Tonnwardsia*; the cell *cup* that is closed in *Cycloneura* and open in *Tonnwardsia*; the male sternite 9 that is not traceable as a separate sclerite in *Cycloneura* but distinct and equipped with large processes in *Tonnwardsia*; and the female gonocoxite 8 that is of ordinary shape in *Cycloneura* but with very broad basal portion in *Tonnwardsia*.

Description. Color. Dark brown. Head. Figs 31, 38. Head capsule in lateral view higher than long, pointed on top. Foramen situated clearly above midheight of head. Median convexity of postgenae large but weakly sclerotized. Frons asetose. Frontal furrow complete. Frontal tubercle 2-pointed. Antennae inserted below midheight of head. Scape little longer than pedicel, both setose. Fourteen flagellomeres; individual flagellomere cylindrical, with very short stalk; node longer than wide in males and as long as wide in females, covered densely with short trichia; setae largely absent except 2 on apical flagellomeres. Numerous fine interommatidial setulae. Three ocelli in wide triangle, situated frontally, median ocellus smaller than laterals, the latter almost in touch with eye margins. A row of 3 bristles behind upper eye margins plus several bristles behind lateral ocelli and alongside median ocellus, all bristles directed anteriorly. Face subrectangular, weakly sclerotized. Stipes setose. Lacinia not tracable. Maxillary palpus long, 5-segmented, with 2 segments proximally of presumed third; basalmost segment weak and asetose; third segment with sensory pit; apical segment longest, slender. Prementum weak, asetose. Premental apodemes fused mesally, with 2 posterior processes. Labellum setose laterally; tiny prestomal teeth in mesal row.

Thorax. Fig. 38. Comparatively high, scutum index 2.3, episternum index 0.98. Postpronotum asetose. Suture between antepronotum and proepisternum complete; both sclerites with setae and bristles. Proepimeron situated posteroventrally of proepisternum, long and pointed, fitting into excavation of preepisternum 2. Basisternum 1 asetose. Anepisternum smaller than preepisternum 2, asetose like all other pleura. Anepimeron large; ventral portion narrow, fading away towards thorax margin. Mid-pleural pit well developed, its mound protruding, pleural apodeme funnel-shaped. Laterotergite bulging, rounded ventrally, subrectangular dorsally. Presumed meron present as weakly sclerotized distinct sclerite ventrally between preepisternum 2 and laterotergite. Scutum truncate anteriorly, little protruding, with evenly distributed setae intermingled with bristles. Anterior parapsidal suture not traceable. Median transverse suture weak. Prescutum not traceable. Scutellum setose, with 1–2 lateral bristles. Mediotergite very slightly curved.

Wing. Fig. 21. Long, wing index 2.6. Membrane with light brown tinge and usually dark markings subapically, on part of anterior margin and near apex of A1; with microtrichia on both sites, those on posterior margin and near apex arranged in lines; setae absent. Calypterous lobe developed, with setose margin. Dmp asetose. Anal lobe slightly angled. C extending little beyond apex of R5, ending well before wing apex. Sc short, ending free. One crossvein (Rs) between R1 and R5 in proximal half of wing. R1 shorter than ta, ending little beyond mid-wing. R5 straight. M one-branched, weak basally. CuA1 detached basally. CuA2 strongly

sinuous. A1 ending free, not in touch with CuA2. CuP very short. A2 absent. Dorsal setae on all veins except h, Sc, Rs, tb, and CuP. Ventral setae on R1 and R5. Halter with light stem and dark knob. **Legs.** Hind coxa only slightly widened subbasally. Tibial trichia irregularly arranged. Fore tibia shorter than femur, with few anterior setae. Fore tibial organ with semicircular rim, with numerous trichia of which the distalmost form a comb. Mid and hind tibiae with 1 row of large and small bristles, large bristles longer than tibial diameter. Hind tibial apical comb of pale setae present. Tibial spurs 1:2:2, with serrated rims, on mid and hind tibiae unequal in length. Empodia small. Pulvilli not traceable. Claws with 1 large and 1–2 small teeth.

Abdomen. Setose except sternite 1. Male sternites 7 and 8 elongated, as long as sternite 6 and much longer than corresponding tergites. In both sexes weakly pigmeted lateral lines (folds?) on tergites traceable, weaker in females than in males, lacking on sternites.

Male terminalia. Rotated at least 90°. Large, thick, capsule-like. Sternite 9 with posterior pair of large, strongly sclerotized processes of variform outline. Tergite 9 indistinguishably merged with dorsal portions of gonocoxites. Ventral portions of gonocoxites short, separate mesally, with sternite 9 between, with large, strongly sclerotized mesal processes. PostGA rather long and narrow. AntGA short and wide. Gonostylus elongate, inserted ventrolaterally on gonocoxal capsule, clasping vertically. Aedeagus and parameres forming complex elongate, sclerotized structure. Hypoproct larger than cerci, incised apicomesally, with large microtrichia and apical setae. Cerci largely merged, setose apically. **Female terminalia.** Fig. 44. Tergite 8 very short dorsally, setose apically. Gonocoxite 8 with very broad basal portion, apically pointed and with numerous large setae. Tergite 9 short, setose. Gonapophyses 9 sclerotized, merged to form large common internal structure. Tergite 10 short, setose. Sternite 10 narrow, setose. Cerci setose, 2-segmented, basicercus little longer than disticercus.

Species included. Our generic description is based on the type species, *Tonnwardsia aberrans* (Tonn.), and 6 unnamed species at our disposal. These species will be treated together with those of the genus *Cycloneura* in a separate paper (Jaschhof & Kallweit, in prep.).

Etymology. We name this genus to honour the merits of the authors of *New Zealand Fungus Gnats*, André L. *Tonn*oir (1885–1940) and Frederick W. Edwards (1888–1940). Gender is feminine.

Genus Cawthronia Tonnoir & Edwards 1927

Tonnoir & Edwards 1927: 825 (description).

Type species. Cawthronia nigra Tonnoir in Tonnoir & Edwards 1927, by monotypy.

Diagnosis. The top of the head is rounded rather than pointed and situated slightly above the level of the ventral margin of the mesonotum (Figs 8, 36). The lateral ocelli are far from the eye margins (Fig. 28). The thorax is flat, mainly due to preepisternum 2 that is truncate ventrally (Fig. 36). The scutum is rounded anteriorly, not protruding (Fig. 36). Sc is long and joins C; the M-fork is evenly diverging towards the wing apex; and A1 is curved posteriorly (Fig. 22). The dorsal wall of the male gonocoxites is desclerotized (Fig. 85), which is an autapomorphic character state.

Redescription. Color. Dark brown. Head. Head capsule in lateral view little higher than long, rounded on top. Foramen situated little above midheight of head. Median convexity of postgenae sclerotized. Frons setose. Frontal furrow complete. Frontal tubercle 2-pointed. Antennae inserted below midheight of head. Scape little longer than pedicel, both setose. Fourteen flagellomeres; individual flagellomere slightly compressed, with very short stalk; node little shorter to longer than wide in males, much shorter than wide in females, covered densely with short trichia of which the bases form polygon-like patterns; setae absent in males, 2 setae present on apical flagellomeres of females. Numerous fine interommatidial setulae. Three ocelli in wide triangle on top of head, median ocellus little smaller than laterals, the latter far from eye margins. Postcranium and frons densely covered with setae of various sizes including 4–5 large setae behind ocelli. Face subrectangular, setose. Clypeus rounded, smaller than face, setose. Labrum very small, weakly

sclerotized, asetose. Stipes strongly setose. Lacinia not traceable. Maxillary palpus long, 4-segmented, with 1 segment proximally of presumed third; basalmost segment weak, asetose, lacking wartlike sensilla; third segment with sensory pit; apical segment long, slender. Prementum weak, asetose. Premental apodemes fused mesally, with 2 posterior processes. Labellum with lateral setae and prestomal teeth in long, dense mesal row.

Thorax. Flat, scutum index 2.49, episternum index 0.68. Postpronotum asetose. Suture between antepronotum and proepisternum complete; both sclerites with setae and anteriorly directed bristles. Proepimeron situated posteroventrally of proepisternum, long and pointed, fitting into notch of preepisternum 2. Basisternum 1 asetose. An pisternum and preepisternum 2 subequal in size, with distinct suture between, both sclerites asetose like all other pleura. Preepisternum 2 covering basalmost portion of mid coxa. An epimeron large; ventral portion narrow, occupying a space between preepisternum 2 and laterotergite. Mound of mid-pleural pit flat, pleural apodeme funnel-shaped. Laterotergite ovate, bulging, darker than pleura. Scutum rounded, not protruding anteriorly, with evenly distributed setae intermingled with bristles on lateral margin. Anterior parapsidal suture indistinct. Prescutum not traceable. Scutellum with setae and 2 lateral bristles. Mediotergite slightly arched. Wing. Long, wing index 2.2. Membrane with brown tinge, a portion above media darkened; with microtrichia on both sites and some setae close to posterior margin and on apex. Calypterous lobe developed, with setose margin. Dmp asetose. Anal lobe angled. C extending much beyond apex of R5, ending clearly before wing apex. Sc long, joining C. One crossvein (Rs) between R1 and R5 in proximal half of wing. R1 longer than ta, ending in distal half of wing. Apical portion of R5 approaching C. M furcate; M-stem shorter than fork; tines of M-fork evenly diverging towards wing apex. CuA1 long, basally evanescent. CuA2 sinuous. CuP present as short fold. A1 not reaching wing margin, curved strongly posteriorly. A2 absent. Dorsal setae on all veins except h, Sc, Rs, tb, and CuP. Ventral setae on R1 and R5. Legs. Hind margin of hind coxa slightly protruding. Tibial and tarsal trichia irregularly arranged. Fore tibia shorter than femur, with very short setae. Fore tibial organ with semicircular rim, with numerous pale trichia of which the distalmost form a comb. Mid and hind tibiae with 2-3 rows of setae, longest setae longer than tibial diameter. Hind tibial apical comb of pale setae absent. Tibial spurs 1:2:2, with serrated rims, on mid and hind tibiae unequal in length. Empodia as long as pretarsal claws. Pulvilli not traceable. Claws with 1 large and 2 small teeth.

Abdomen. Setose except sternite 1. Male segments 7 and 8 very short and telescoped. Light, weakly pigmentd lateral lines (folds?) on tergites and sternites 2–6 in both sexes.

Male terminalia. Large, not rotated. Sternite 9 absent as separate sclerite. Tergite 9 short, separate from gonocoxites. Gonocoxites elongate, broadly merged ventrobasally, with V-shaped ventral emargination; dorsal portions desclerotized and asetose. PostGA reduced. AntGA moderately long. Gonostylus small, simple. Aedeagus/paramere complex with large membranous and very small sclerotized portions; ejaculatory apodeme long, weakly sclerotized. Hypoproct setose. Cerci largely merged, setose. **Female terminalia.** Tergite 8 moderately long, setose. Gonocoxite 8 pointed apically, with some large apical setae. Tergite 9 very short, setose. Gonapophyses 9 sclerotized, merged to form internal common structure. Tergite and sternite 10 merged, setose. Cerci setose, 2-segmented.

Cawthronia nigra Tonnoir in Tonnoir & Edwards 1927

(Figs 8, 9, 22, 28, 36, 42, 80-89)

Tonnoir & Edwards 1927: 826 (description female), plt. 62, fig. 72 (photo wing). *Holotype*. Female, Nelson [South Island], 1 Nov. 1923, A.L. Tonnoir leg. In NZAC (specimen seen).

Diagnosis. This is the only species of *Cawthronia* and thus recognizable readily by the generic characters.

Description. Male. **Head.** Fig. 8. Nodes of antennal flagellomeres 0.9–1.2 times as long as wide (Figs 86, 89). Apical segment of maxillary palpus less than twice the length of preceding segment.

Thorax. Fig. 36. Wing. Fig. 22. Length 1.9–2.3 mm.



FIGURES 80–89. *Cawthronia nigra* Tonnoir. 80: Gonostylus, ventral view (0.05 mm). 81: Gonostylus, mesal view (0.05 mm). 82: Gonostylus, dorsal view (0.05 mm). 83: Male terminalia, ventral view (0.1 mm). 84: Aedeagus/tegmen complex, ventral view (0.1 mm). 85: Male gonocoxites and cerci, dorsal view (0.1 mm). 86: Male flagellomeres 1–5, lateral view (0.1 mm). 87: Female flagellomeres 1–5, lateral view (0.1 mm). 88: Male tergite 9, dorsal view (0.1 mm). 89: Male flagellomere 4, lateral view (0.05 mm). Length of scale bar in parentheses.

Terminalia. Tergite 9 subtriangular, vaguely 2-pointed, with slight apicomesal depression, with setae of various sizes including very large apical and basolateral setae (Fig. 88). Gonocoxites apically with 1 large dorsomesal seta and 2 smaller ventromesal setae, and setae of various sizes elsewhere (Figs 83, 85). Gonostylus with setae of various sizes including 1 very large dorsomesal seta, and 1 flat, subtriangular apical spine (Figs 80–82). Parameres emarginate apicoventrally, sclerotized and finely serrate apicolaterally (Fig. 84). Ejaculatory apodeme slightly shorter than parameres, with weakly sclerotized, circular apical extension (Fig. 84).

Redescription. Female. **Wing.** Length 1.9–2.5 mm. **Head.** Nodes of antennal flagellomeres 0.5 times as long as wide (Fig. 87).

Terminalia. Basicercus longer than disticercus, both segments with numerous short, thick dorsal setulae (Fig. 42).

Distribution and phenology. Endemic to NZ: SO (NN, BR, NC, MC, SL). Confined to South Island. Adults collected in beech, podocarp and mixed beech/podocarp forests up to an altitude of 800 m above sea level. Adult activity almost throughout the year, but no findings known from February, March and July.

Material studied. SO. NN: 6 (4*) males, Kahurangi N. P., Takaka R. valley (Cobb dam road), 31 Aug.–7 Oct. 2001, M. & C. Jaschhof; BR: 18 (2*) males, 9 (3*) females, Cass, Middle Bush, 9 April 1998, P.M. Johns; 4* males, 4* females, same loc. but 11 April 1998; 3 males, 1 female, same loc. but 30 May 1998; 1* male, Maruia F., Shenandoah Saddle, 3–25 Nov. 2001, M. & C. Jaschhof; NC: 3 males, Arthur's Pass N. P., Bealey Spur, Waimakariri Track, 19 May–13 June 2001, M. & C. Jaschhof; MC: 1* male, Craigieburn F. P., Broken R. skifield road, 4 Dec. 2001, M. Jaschhof; SL: 1 male, Catlins, Purakaunui Scenic Res., 30 Jan. 2002, M. Jaschhof.

Genus Waipapamyia Jaschhof & Kallweit gen. n.

Type species. Waipapamyia dentata sp. n., hereby designated.

Diagnosis. This is the only leiine genus, in New Zealand and elsewhere, with the combination of a sinuous CuA2 and two short crossveins (Rs and R4) between R1 and R5 (Fig. 23). The top of the head is rounded and situated above the level of the ventral margin of the mesonotum (Figs 10, 35). The lateral ocelli are far from the eye margins (Fig. 29). Postocular bristles are present (Fig. 29). The scutum is rounded anteriorly (Fig. 35). The mediotergite is angled (Fig. 35). Sc is long and ends in C; the tines of the M-fork diverge towards the wing apex, M2 is detached basally; CuA2 is sinuous; and A1 is not in touch with CuA2 (Fig. 23). Outline of the male terminalia is uniform and distinctive, including the genus-specific combination of the following characters. The long gonocoxites have a very deep V-shaped ventral emargination (Fig. 90); the gonostylus is equipped with an apical spine and abundant macrosetae of various sizes and in species-specific arrangements (Figs 90, 91); and tergite 9 bears 2 very large apical setae projecting ventrally (Fig. 92). The closest relatives of *Waipapamyia* remain obscure for the time being.

Description. Color. Thorax and abdomen brown, legs light. Head. Head capsule in lateral view higher than long, rounded on top. Foramen situated above midheight of head. Median convexity of postgenae not sclerotized. Frons asetose. Frontal furrow complete. Frontal tubercle 2-pointed. Antennae inserted at midheight of head. Scape little longer than pedicel, both setose. Fourteen flagellomeres; four proximal flagellomeres slightly compressed, others subcylindrical, with very short stalks; nodes longer than wide, in males longer than in females; covered densely with trichia of which the bases form polygon-like patterns, longest trichia little shorter than width of node; each flagellomere usually with 1–3 short setae distally; apical flagellomeres of females with 2, those of males without apical setae. Numerous fine interommatidial setulae. Three ocelli in wide triangle on top of head; median ocellus little smaller than laterals, the latter far from eye margins (the distance equates about 3 times the ocellus width). Postocular bristles 8–10 in row. Face setose, dorsal margin subtriangular. Clypeus smaller than face, setose. Labrum elongate subtriangular, asetose. Stipes strongly setose. Lacinia absent. Maxillary palpus long, 4-segmented; one segment proximally of presumed third; basalmost segment weak, asetose; third segment strongly swollen, with innumerable translucent sensilla on dorsomesal surface; apical segment long, slender. Prementum weak, asetose. Premental apodemes fused mesally, with 2 posterior processes. Labellum enlarged, with large lateral setae and large prestomal teeth in long mesal row.

Thorax. Comparatively high, scutum index 2.79, episternum index 1.00. Postpronotum asetose. Suture between antepronotum and proepisternum incomplete posteriorly; both sclerites with setae and bristles. Proepimeron situated posteroventrally of proepisternum, long and truncate, fitting into notch of preepisternum 2. Basisternum 1 asetose. Anepisternum smaller than preepisternum 2, with weak suture between, both

sclerites asetose like all other pleura. Preepisternum 2 covering basalmost portion of mid coxa. Anepimeron large; ventral portion narrow, occupying a space between preepisternum 2 and laterotergite. Mid-pleural pit poorly developed. Laterotergite ovate, bulging, darker than pleura. Scutum rounded, not protruding anteriorly, with evenly distributed lateral setae intermingled with bristles. Anterior parapsidal suture indistinct. Prescutum not traceable. Scutellum with setae and 2 lateral bristles. Mediotergite protruding, sharply arched. Wing. Long, wing index 2.8. Membrane with brown tinge and dark markings above M; with microtrichia on both sites and some posterior setae. Calypterous lobe developed, with setose margin. Dmp asetose. Anal lobe very slightly angled. C extending much beyond apex of R5 and almost to wing apex. Sc weak, long, ending in C. Two crossveins (Rs and R4) between R1 and R5 in far distance from one another, Rs situated in proximal half of wing, R4 in distal half of wing. R1 much longer than ta, ending in distal half of wing. Apical portion of R5 approaching C. M 2-branched; M1 and M2 evenly diverging towards wing apex; M2 reaching wing margin or not, detached basally; M-stem shorter than fork. CuA1 long, evanescent basally. CuA2 sinuous. A1 long, fading out before reaching CuA2, straight or curved posteriorly. CuP present as distinct fold. A2 absent. Dorsal setae on all veins except h, Sc, Rs, R4, tb, and CuP. Distal section of R1 with some ventral setae. Legs. Hind margin of hind coxa slightly protruding. Tibial and tarsal trichia irregularly arranged. Fore tibia shorter than femur, with very short, irregularly arranged setae. Fore tibial organ with semicircular rim, with numerous pale trichia of which the distalmost form a comb. Mid tibia with 3 rows of setae, hind tibia with 2 rows, longest setae little longer than tibial diameter. Hind tibial apical comb of pale setae absent. Tibial spurs 1:2:2, with serrated rims, on mid and hind tibiae unequal in length. Empodia narrow, shorter than pretarsal claws. Pulvilli not traceable. Claws with 1 large and 2 small teeth.

Abdomen. Setose except sternite 1. Male segments 6–8 very short, telescoped. Light, weakly pigmented lateral lines (folds?) present on male tergites 2–6 and sternites 3–6, and on female tergites and sternites 2–6.

Male terminalia. Large, not rotated. Sternite 9 not traceable. Tergite 9 subtriangular, broadly merged with gonocoxites, with dorsal setae of various sizes and 2 very large apical setae directed ventrally. Gonocoxites long, capsule-like, almost separate ventromesally, with 1 very large seta each ventromesally and dorso-subapically. PostGA very short. AntGA long, thin, largely unsclerotized. Gonostylus flattened, its mesal surface excavated, with apical spine, 2 sabre-like macrosetae ventromesally and 7–8 long pointed macrosetae dorsomesally. Aedeagus, ejaculatory apodeme and parameres forming complex structure of variable outline. Hypoproct very weak, with 2 setae. Cerci merged mesally, setose. **Female terminalia.** Tergites 8 and 9 moderately long, setose. Gonocoxite 8 rounded apically, with some very large apical setae. Gonapophysis 8 very large. Gonapophyses 9 sclerotized, merged to form common internal structure. Tergite 10 very short, merged with sternite 10, both setose. Cercus setose, basicercus longer than disticercus.

Etymology. The name is composed of Waipapa, the locality where most specimens were collected, and *myia*, the Greek word for fly or gnat. Gender is feminine.

Key to species of Waipapamyia (males)

1	Thorax almost entirely dark. Gonostylus with short apical process ending in blunt spine (Figs 100, 103)
	truncata sp. n.
-	Thorax with dark and light portions. Gonostylus with pointed apical spine
2	Preepisternum 2 bicolored, light dorsally and dark ventrally. Gonocoxites twice as long as gonostylus (Fig. 90).
	Parameres present as 2 large, tusklike processes (Fig. 93) dentata sp. n.
-	Preepisternum 2 completely light. Gonocoxites 3 times as long as gonostylus (Fig. 97). Parameres vestigial (Fig. 99)
	elongata sp. n.

Waipapamyia dentata Jaschhof & Kallweit sp. n.

(Figs 10, 23, 29, 35, 41, 90-96)

Diagnosis. Preepisternum 2 is bicolored, not entirely light or dark as in the other two species. The gonostyli in *W. dentata* resemble that in *W. elongata* in having a pointed apical spine, whereas the aedeagus/paramere complexes in these two species differ greatly (see Fig. 93 *versus* 99).

Description. Male. Head. Fig. 29. Antennal flagellum as in Figs 94 and 95.

Thorax. Fig. 35. Scutum mainly light. An pisternum 2, upper portion of preepisternum 2 and an epimeron 2 light, lower half to two thirds of preepisternum 2 dark. Laterotergite and mediotergite darker than pleura and scutum.

Wing. Fig. 23. Length 1.8–2.2 mm. A1 almost straight.

Terminalia. Gonocoxites as in Fig. 90. Gonostylus with strong, slightly curved, pointed apical spine and 7 macrosetae along dorsomesal margin (Figs 90, 91). Ejaculatory apodeme notched apically, with 2 pairs of mesolateral processes and barblike subbasal structure (Fig. 93). Parameres present as tusklike processes directed posteriorly; parameral apodemes directed dorsolaterally (Fig. 93).

Female. Thorax. As in male.

Wing. Length 2.1 mm.

Distribution and phenology. Endemic to NZ: NO (TO). Known from only one locality, a podocarp forest, where adults were captured in December and January.

Etymology. From Latin, *dentatus*, toothed, referring to the strong spine on gonostylus apex.

Types. *Holotype*. Male*, New Zealand, North Island, Taupo, Pureora Forest, Waipapa Reserve, in podocarp forest, 570 m, 15 Dec. 1983, by Malaise trap, J. Hutcheson (in NZAC). *Paratypes*. 1* female, same data as the holotype (in NZAC); 6* males, same data as the holotype but Dec. 1983 (in NZAC); 1* male, same data as the holotype but 1 Dec. 1983 (in SMTD); 1* male, same data as the holotype but 29 Dec. 1983 (in SMTD); 1* male, same data as the holotype but 29 Dec. 1983 (in SMTD); 1* male, same data as the holotype but 12 Jan. 1984 (in SMTD).

Other material. 5 males, same data as the holotype but Jan. 1984; 7 males, same data as the holotype but 12 Jan. 1984.

Waipapamyia elongata Jaschhof & Kallweit sp. n.

(Figs 24, 97-99)

Diagnosis. Preepisternum 2 in *W. elongata* is light, while it is dark in *W. truncata* and bicolored in *W. dentata*. The male gonocoxites are longer than in the other two species (Fig. 97). The parameres are vestigial (Fig. 99), while they are large, tusk-shaped in the other two species.

Description. Male. **Thorax.** Scutum mainly dark. An pisternum 2, preepisternum 2 and an epimeron 2 light. Laterotergite darker than pleura and scutum. Ventral half of mediotergite pale.

Wing. Fig. 24. Length 2.0 mm. A1 slightly curved.

Terminalia. Gonocoxites strikingly long (Fig. 97). Gonostylus small in relation to gonocoxites (Fig. 97); apex subtriangular, with pointed spine; on dorsomesal margin 7 macrosetae in line plus 1 macroseta in some distance (Fig. 98). Aedeagus/paramere complex elongate; parameres vestigial; apex of ejaculatory apodeme axe-shaped (Fig. 99).

Female. Unknown.

Distribution and phenology. As in *W. dentata*.

Etymology. From Latin, *elongatus*, elongate, referring to the long gonocoxites.

Types. *Holotype*. Male*, New Zealand, North Island, Taupo, Pureora Forest, Waipapa Reserve, in podocarp forest, 570 m, 15 Dec. 1983, by Malaise trap, J. Hutcheson (in NZAC). *Paratype*. 1* male, same data as the holotype but 29 Dec. 1983 (in SMTD).



FIGURES 90–96. *Waipapamyia dentata* **sp. n.** 90: Male terminalia, ventral view. 91: Gonostylus, mesal view. 92: Gonocoxites and tergite 9, dorsal view. 93: Aedeagus/paramere complex, ventral view. 94: Male flagellomere 4, lateral view. 95: Male flagellomeres 1–5, lateral view. 96: Female flagellomeres 1–5, lateral view. Length of scale bar = 0.05 mm (for 94) and 0.1 mm (for 90–93, 95–96).

Waipapamyia truncata Jaschhof & Kallweit sp. n. (Figs 25, 100–103)

Diagnosis. Preepisternum 2 is entirely dark. The gonostylus bears a winding apical process ending in a blunt spine (Figs 100, 103), whereas the apical spine in the other two species is pointed.

Description. Male. **Thorax.** Scutum mainly dark. Anepisternum 2, preepisternum 2, anepimeron 2, laterotergite, and mediotergite entirely dark.

Wing. Fig. 25. Length 2.0 mm. A1 slightly curved.

Terminalia. Gonostylus with winding apical process ending in blunt spine, on dorsomesal margin 7 macrosetae in line plus 1 macroseta in some distance (Fig. 103). Apex of ejaculatory apodeme widened, with minute trichia, 2 pairs of mesolateral processes and barblike subbasal structure (Fig. 101). Parameres present as tusklike processes directed posterolaterally; parameral apodemes directed dorsolaterally (Fig. 101).



FIGURES 97–103. Male terminalia of *Waipapamyia* spp. 97–99: *Waipapamyia elongata* **sp. n.** 100–103: *Waipapamyia truncata* **sp. n.** 97: Ventral view. 98: Gonostylus, mesal view. 99: Aedeagus/paramere complex, ventral view. 100: Gonostylus, ventral view. 101: Aedeagus/paramere complex, ventral view. 102: Ventral view. 103: Gonostylus, mesal view. Length of scale bar = 0.05 mm (for 99) and 0.1 mm (for 97–98, 100–103).

Female. Unknown.

Distribution and phenology. Endemic to NZ: NO (TO), SO (BR). Occurs in both the main islands, in North Island concurrently with *W. dentata* and *W. elongata*. Adults captured in podocarp and beech forests in summer.

Etymology. From Latin, truncatus, truncate, referring to the blunt structure on gonostylus apex.

Types. *Holotype*. Male*. New Zealand, North Island, Taupo, Pureora Forest, Waipapa Reserve, in podocarp forest, 570 m, 12 Jan. 1984, by Malaise trap, J. Hutcheson (in NZAC). *Paratypes*. 2 (1*) males, SO, BR, L. Daniells Track 7 km E Springs Junction, in forest of red beech *Nothofagus fusca* and silver beech *N. menziesii*, 24 Nov. 2001, by sweepnet, U. Kallweit & A. Stark (in SMTD).

Delineation of the Leiini in a strict sense

Our search for the closest relatives of the New Zealand members of the Cycloneura group led inevitably to the issue of the stricter definition of the Leiini, as it became obvious that for instance Tetragoneura, which we found to be well represented in New Zealand by some 20 species, had little in common with Cycloneura-like leiines. We screened representatives from a wide range of genera traditionally classified with the Leiini, including the Cycloneura-like genera in New Zealand, and identified a set of common characters as follows: (1) the premental apodeme bears two posterior processes (except in *Sigmoleia* with one such process); (2) the pleural thoracic sclerites are asetose (except in *Sigmoleia* with setose anepisternum and preepisternum 2); (3) the mediotergite is asetose; (4) the wing is long with the wing index >2.1; (5) the microtrichia on the wing membrane are irregularly arranged and equal in size (except in *Tonnwardsia* with the microtrichia partly arranged in lines); (6) setae on the wing membrane are absent, or at most sparsely present near the posterior margin and apex; (7) the wing membrane bears dark markings; (8) one crossvein, presumably Rs, is present between R1 and R5 (except in Waipapamyia with two crossveins); (9) CuA1 is typically proximally free (except in Sigmoleia where it joins CuA2); and (10) CuA2 is sinuous (except in Paracycloneura where it is slightly bent). The combination of these characters, putatively both plesiomorphic and apomorphic, is, according to our analysis, qualified to mark Leiini in a strict sense, even though one may find many leiines that do not exhibit the complete set. Character (10), the sinuous CuA2, may be considered a synapomorphy of Leiini sensu stricto, which must be substantiated by more rigorous testing. The significance of that character state was pointed out earlier by Baxter and Poinar (1994). A slightly sinuous CuA2 is also present in some non-leiine sciophiline mycetophilids, but those deviate considerably from the characters referred to above. Based on our results, the following extant genera should be regarded as Leiini in a strict sense: Acrodicrania, Allactoneura, Anomalomyia, Ateleia, Cawthronia, Clastobasis, Cycloneura, Greenomyia Brunetti, Indoleia Edwards, Leia, Leiella, Neoclastobasis Ostroverkhova, Paracycloneura, Paradoxa, Paraleia Tonnoir, Procycloneura, Rondaniella, Sigmoleia, Sticholeia, Thoracotropis Freeman, Tonnwardsia, and Waipapamyia. Genera, such as Caledonileia Matile, Docosia Winnertz, Garrettella Vockeroth, Megophthalmidia Dziedzicki, and Trichoterga Tonnoir & Edwards, very probably belong here as well, even though their CuA2 is not or only slightly sinuous. Limitation of apomorphies to only a part of a supposed monophyletic group was found to weaken a strictly phylogenetic argumentation also in the case of the Gnoristini (Väisänen 1986: 205), so appears to be a general problem in Mycetophilidae.

The two leiine characters identified by Edwards (1925), shortness of R1 and horizontal inclination of ta, are indeed met in many Leiini, but there are also a number of exceptions, including *Sigmoleia*, in which R1 is much longer than ta, and/or ta is not in alignment with R5. For this and other reasons genera, such as *Aphrastomyia* Coher & Lane, *Gracileia* Matile, *Mohelia* Matile, *Novakia* Strobl, and *Tetragoneura* Winnertz, should in our opinion be excluded from the Leiini. In these genera Sc tends to run into R, not into C, which is typical of many Gnoristini to which they are rather affiliated. Gnoristini is another sciophiline tribe that requires a more stringent definition (Väisänen 1986, Søli *et al.* 2000), which again requires deeper knowledge of the relevant southern hemisphere genera, including several undescribed (personal observation).

Relationships of the genera of the Cycloneura group

Presence of a closed, or almost closed, posterior cubital cell is a striking feature of leiine genera, such as the New Zealand *Cycloneura*, *Paradoxa*, *Sigmoleia* and *Tonnwardsia*, and the Neotropical *Procycloneura*. One is inclined to value this character as an synapomorphy gathering a 'closed-cell-bearer' group of genera, but as soon as other putatively apomorphic features are taken into account, there appear various affiliations to 'open-cell-bearers' occurring in New Zealand and elsewhere, in particular *Allactoneura*, *Cawthronia*, *Leiella*, *Paracycloneura*, *Sticholeia* and *Waipapamyia*. All these genera share two or all of the following apomorphic character states: Sc ends free; Sc-r is lacking; and A2 is lacking. This we regard as evidence for a monophyletic *Cycloneura* group of genera within the Leiini *sensu stricto* as defined above. Additional evidence is discussed below. The *Cycloneura* group is primarily of southern hemispheric distribution, a fact that we regard as an argument supporting our assumption of monophyly. None of the fossil Leiini described by Baxter and Poinar (1994) and Blagaderov and Grimaldi (2004) appear to be members of the *Cycloneura* group.

Some possible intergeneric relationships within the *Cycloneura* group, and the putatively synapomorphic characters on which they are based, are outlined in the following. Presence of the one-branched M is shared among the apparently monophyletic subgroup comprising Cycloneura, Paracycloneura and Tonnwardsia (all of which are New Zealand endemics), with Cycloneura and Tonnwardsia being sister groups. It is worth noting the variable outline of CuA2/A1 within this subgroup. Sigmoleia appears to hold an isolated position within the Cycloneura group due to its many peculiarities, including the short M-fork and the sinuous M1. In *Procycloneura*, the M-fork tends towards shortening (shown by the fact that M1 is shortened and detached basally) and M1 is sinuous, which might indicate that the venation in Sigmoleia is just at the extreme end of a transformational series not yet fully unveiled. Absence of translucent sensilla on the maxillary palpus of both Procycloneura and Paradoxa might serve as an argument for the closer relationships between these two genera, which is supported by other similarities, such as the gonostylus clasping in a vertical direction and the very long ninth tergite of males. Postocular bristles, in the sense of Hippa et al. (2005), are present in Allactoneura, Leiella, Procycloneura, Sticholeia and Waipapamyia, which is of interest insofar as a close affiliation among Allactoneura, Leiella and Sticholeia has already been argued (Søli 1996). We agree with Søli that Allactoneura is properly placed within the Leiini, and Allactoneura and Leiella are sister groups. In Allactoneura, Leiella and Procycloneura, preepisternum 2 is truncate ventrally, thereby giving the thorax a flat appearance; this character, in turn, is shared with Cawthronia. Allactoneura and Leiella correspond with Waipapamyia in that the mediotergite is angled, not slightly arched as is the ordinary condition in Leiini. The proepimeron is enlarged in, again, Allactoneura, Leiella and Sticholeia, and further in Cycloneura, Waipapamyia and the Australian Ateleia. Admittedly our hypotheses of intergeneric relationships remain untested, but it is our opinion that the Cycloneura group is monophyletic. For further progress in elucidating Leiini phylogeny, we argue to intensify alpha-taxonomic (descriptive) work rather than to expand cladistic analyses of the known taxa, because it is only a small fraction of southern hemisphere leiines that is described. A small collection of Australian Mycetophilidae we have at our disposal yielded two Cycloneura-like leiines that shall deserve new generic status.

The relationships between the genera of the *Cycloneura* group and those Leiini with a more plesiomorphic type of venation are still obscure to us. One such genus, *Leia*, includes some 150 species known from all the world biogeographic regions (Bechev 2000), and should first be the focus of extensive taxonomic revision and character re-assessment. At present we do not regard it reasonable to discuss possible relationships on the basis of just one or two randomly chosen representatives of *Leia*. *Anomalomyia*, with 13 species endemic to New Zealand and New Caledonia, has no obvious affinities to the *Cycloneura* group. Marshall (1929) regarded *Anomalomyia* as closely allied to *Leia*, *Ateleia*, *Acrodicrania* and *Coelosia* Winnertz (the last genus classified presently with the Gnoristini); Tonnoir and Edwards (1927) regarded it as closely related to *Acrodicrania*. The Australian genus *Ateleia* is, according to what we have seen, not monotypic but speciose

and diverse, and this might apply also to other leiine genera still regarded as species-poor. At this stage, the inadequate knowledge of Australian Leiini is a particularly obstructive!

To summarise, New Zealand Leiini appear to belong to two different lineages, the genus *Anomalomyia*, which is essentially plesiomorphic in its wing vein characters, and the *Cycloneura* group of genera, exhibiting derived vein patterns. The New Zealand genera of the *Cycloneura* group do not form a monophyletic group in themselves, but are variously related to extralimital taxa the majority of which is found in today distant land masses, the southern Neotropics, South Africa, Australia, and New Caledonia. The *Cycloneura* group appears to be of ancient, Gondwanan origin. Its sister group, as well as possible affiliations to the Leiini of presumed northern origin, remain obscure for the time being.

Acknowledgements

The study eventually leading to this paper was made possible through grants by the Deutsche Forschungsgemeinschaft for M.J. (JA 1020/1–1 and –2) and U.K. (EM 91/1–3). We thank all our New Zealander colleagues and their institutions listed in the Material section for providing specimens for our study as well as for various advice and support of our own field work. Peter M. Johns authorised us to collect Diptera specimens under his permit (#9900/142/3/04). Several institutions on various occasions provided access to their facilities—collections, laboratories and libraries, namely the Department of Zoology, University of Canterbury, Christchurch (represented by Dr Raphael K. Didham); the New Zealand Arthropod Collection, Auckland (Dr Trevor K. Crosby); and the Nelson Branch of Landcare Research New Zealand (Richard Toft). Catrin Jaschhof, Greifswald, Germany, gave broad technical assistance which expedited our study considerably. We thank Dr Raymond J. Gagné, research entomologist emeritus with the Systematic Entomology Laboratory, USDA, National Museum of Natural History, Washington, D.C., for reading and commenting on an earlier version of this manuscript. We thank the two reviewers unknown to us whose comments and suggestions led to a considerable improvement of the contents and the readability of the text.

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