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Hilarini (Diptera: Empididae) from the Auckland Islands New Zealand, the Homoplastic Loss of the Male Silk-Producing Basitarsus in Two Insular Species, and Notes on the Empidoidea of the Subantarctic Islands

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Abstract: The New Zealand taxa of the superfamily Empidoidea (minus Dolichopodidae) are briefly summarized. Two species, *Hilara ranui* n. sp. and *Hilarempis motumaka* n. sp. (Diptera: Empididae: Empidinae), from the Auckland Islands of New Zealand, where they appear to be common, are described. Both species show a homoplastic loss or reversal of the swollen, silk-producing, fore basitarsi characteristic of males in their respective genera. The environmental conditions of the Subantartic islands and their selective pressure on empidoid taxa are discussed.

Keywords: New Zealand; Subantarctic islands; Empididae; Hilarini; Dolichopodidae

1. Introduction

While examining Diptera holdings at the Bishop Museum, Honolulu, I found a drawer with some 1500 specimens of the family Empididae collected on the Auckland Islands, a small Tasman Sea archipelago some 460 km south of the South Island, New Zealand. This rugged, compact, island group has elevations reaching 710 m, with a cold temperate maritime climate characterised by almost continual overcast skies, wind, and rain squalls. The vegetation comprises low bushes and herbfields with trees in protected sites, and the soil is wet and peaty (see Figure 1a–f, and also Gressitt & Wise [1] for a comprehensive summary of Auckland Island geography, and Scott & Turnbull [2] for geology). The Auckland Islands specimens were sorted and found to comprise two distinct species in the tribe Hilarini (Empididae: Empidinae).

The New Zealand Empididae (now considered the superfamily Empidoidea, minus Dolichopodidae) were treated as a whole and keyed in 1928 by Collin [3]. This monograph utilized previous work and the holdings in the Natural History Museum London, primarily the collection of T. R. Harris made near Ohakune, just south of present day Tongariro National Park, central North Island. Of the 87 species treated by Collin, fully 55 were described only from Ohakune, and a further 15 from Ohakune and additional locales. One problem with this monograph is that many species were described from females only, whereas the male genitalia and male secondary sexual characters are essential for accurate species diagnosis and identification. For example, Collin described the new hilarine genus *Gynatoma* with five included new species from Ohakune, only two of which had an associated male. Nevertheless, if this work demonstrates the empidoid richness at a single New Zealand locale, one can only speculate on the potential taxonomic richness of the entire country.

Since then, the Empididae *s.l.* have been redefined and broken into five families—Atelestidae, Brachystomatidae, Hybotidae, Ragadidae, and Empididae *s.s.* [4]—and a number of taxa within the New Zealand fauna have received taxonomic treatment: Kerr & Tweed [5]; Kerr et al. [6]; Malloch [7,8]; Plant [9–18]; Plant & Didham [19]; Rogers [20];

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Sinclair [21–26]; Sinclair & Cumming [27]; Sinclair et al. [28]; Sinclair & McLellan [29]; and Smith [30]. Further, a revised key to New Zealand genera can be found in Sinclair [26].

However, the Hilarini have received little treatment since Collin's 1928 work, with only Plant's description of the monotypic genus *Hybomyia* [13] and two species of *Thinempis* by Bickel [31]. Currently the New Zealand fauna comprises 15 *Hilara* and 21 *Hilarempis* species, almost half of which were collected at the Ohakune site. Yet, based on unworked collections, the Hilarini are one of the most speciose empidoid groupings in New Zealand, dominated by the genera *Hilara* Meigen and *Hilarempis* Bezzi, into which the two new Auckland Islands species are described.

Figure 1. Landscapes, Auckland Island Group: (**a**) West coast sounds, Auckland I.; (**b**) East coast sounds, Auckland I.; (**c**) Rata forest (*Metrosideros umbellata*), Auckland I.; (**d**) Rata forest, interior, Auckland I.; (**e**) Hills in Carnley Harbour, Auckland I.; (**f**) Ocean and Ewing islands, viewed from Rose I. (All photographs courtesy of Adrian Plant).

2. Materials and Methods

The specimens used in this study are housed at the Bishop Museum, Honolulu (BPBM). Other institutions cited in the text include the Australian Museum, Sydney (AMS); the Canadian National Collection, Agriculture Canada, Ottawa (CNC); and the New Zealand Arthropod Collection, Auckland (NZAC).

Specimen photographs were made with a Leica M205A photomontage system. Morphological terminology follows Cumming & Wood [32] and Cumming et al. [33]. The hypopygium photographed in Figure 3d was cleared in KOH and mounted in glycerine gel. The body length of males is measured from the base of the antennae to the tip of the seventh abdominal segment. The position of features on elongate structures, such as leg segments, is given as a fraction of the total length, starting from the base. The relative lengths of the podomeres are representative ratios and not measurements, and they are given for each leg in the following formula and punctuation: trochanter + femur; tibia; tarsomere 1/ 2/ 3/ 4/ 5. The following abbreviations and terms are used: I, II, III: pro-, meso-, metathoracic legs; C, coxa; T, tibia; F, femur; MSSC, male secondary sexual character(s), those non-genitalic characters found only on the male body; ac, acrostichal setae; ad, anterodorsal; av, anteroventral; dc, dorsocentral setae; dv, dorsoventral; pd, posterodorsal; pv, posteroventral; t, tarsus; $t_{1–5}$, tarsomeres 1 to 5.

Differential diagnoses are provided for the two species, but the New Zealand Hilarini are very poorly known, and most described species have inadequate descriptions and lack illustrations. These two new species will be among the best documented for the New Zealand hilarine fauna.

3. Results

3.1. Hilara ranui Bickel n. sp. (Figure 2a–f)

Type material. NEW ZEALAND: **Auckland Islands:** holotype ♂, AUCKLAND ISLAND: Ranui Cove, 2 ♂♂, Malaise trap, 3 January 1963, J. L. Gressitt (BPBM); paratypes 523 ♂♂, 401 ♀♀, same but various dates, 27 December 1962–18 January 1963 (BPBM; specimens also deposited AMS, NZAC, and CNC).

Additional material. NEW ZEALAND: **Auckland Islands:** 84 ♂♂, 38 ♀♀, ADAMS ISLAND: Magnetic Cove, 2 m, 20 January 1966, 3 February 1966, J. L. Gressitt; west end of island, streamlet and seal wallows, 22 January 1966, K. A. J. Wise. AUCKLAND ISLAND: Crozier Point, 1–20 m, on *Poa* sp., 28 December 1962, J. L. Gressitt; Bivouac Mtn, 200–400 m, 18 January 1963, ex *Danthonia*, J. L. Gressitt; Webling Bay, 13 January 1963, J. L. Gressitt. ENDERBY ISLAND: 1–50 m, on mat plants above stream, 31 December 1963, J. L. Gressitt. OCEAN ISLAND: 1–18 m, 2 January 1963, sweep, J. L. Gressitt. ROSE ISLAND: 1–10 m, on *Carex* & *Polystichum* spp., 8 January 1963, J. L. Gressitt (all BPBM).

Description. **Male**: length: 2.4–2.5 mm; wing: 3.0 × 1.0 mm (Figure 2a).

Head (Figure 2b). Postcranium, vertex, frons, and face mostly dark brown, with dense grey pruinosity; setae black; some longer postvertical setae along posterior vertex followed by row of postocular setae along posterior eye margin, with irregular additional setae on dorsal and ventral postcrainum; field of short setae on ocellar triangle, with pair of diverging setae arising anteriad of lateral ocelli; frons broad, wider than ocellar triangle, and with row of 5–6 short black fronto-orbital setae along lateral margin adjacent to eyes; eyes notched laterad of antennae; face slightly wider than frons; eye with facets uniform; palp black, ovate, with some short apical and subapical setae; proboscis dark brown, labrum longer than head height, and with some whitish hairs along length; antenna dark brown; scape slightly longer than pedicel; pedicel with subapical corona of short setae; postpedicel subtriangular, tapering, with apical style.

Thorax (Figure 2d). Mostly dark brown and covered with dense grey pruinosity, with dark grey pruinose band between ac and dc rows; setae black; acrostichal setae comprising some 10–12 regular pairs, which extend onto posterior mesonotal slope; 3 long dorsocentral setae laterad of posterior mesonotal slope, and row continuing anteriad as 8 short setae; 1 postalar seta, 1 strong postsutural supra-alar seta, with shorter seta anteriad; presutural intra-alar setae absent; notopleuron with 4 posterior setae and short hairs anteriad; 1 strong postpronotal seta, with some shorter hairs on postpronotal lobe; 1 presutural supra-alar seta; prosternum with 4–5 short black setae; scutellum with four pairs of marginal setae; postnotum broad and slightly rounded; laterotergite bare.

Legs. All coxae and remainder of legs brown; coxae with grey pruinosity and black anteroapical setae; CI with rather short black anterior setae; CIII with group of black lateral setae; all tarsi with claws and short pulvilli; legs covered with short brownish vestiture and mostly bare of strong setae, except as noted: I: 3.1; 2.9; 1.3/ 0.7/ 0.4/ 0.3/ 0.6; It_1 unmodified, not swollen, and without modified ventral cuticle; II: 2.5; 2.8; 1.2/ 0.5/ 0.4/ 0.3/ 0.4; TII with short subapical corona of av and pv setae; III: 3.9; 3.8; 1.4/ 0.7/ 0.3/ 0.2/ 0.5; TIII with some short dorsal setae along length, but otherwise bare of major setae.

Wing (Figure 2f). Membrane faintly smoky; costa with strong basal ad setae, otherwise veins bare; Sc complete, gently curving distally to join costa; distal R_1 slightly dilated near costal join; stigma brown and diffuse; R_{2+3} unbranched and joining costa near 3/4; R_{4+5} branched, with R_4 in hemi-campanuliform (bell-shaped) curve to costa, and R_5 meeting costa at wing apex; discal cell with branches M_1, M_2, and M_3; crossvein closing anal cell (cell cup) strongly recurrent; vein CuA + CuP complete to margin; anal angle well developed; lower calypter dull whitish, with brownish marginal setae; halter brown.

Abdomen. Tergites dark brown, with dull grey prinosity; each tergite 1–5, with scattered short black setae and with row of longer black setae near posterior margin; sternite 8 forming base for brown hypopygium (Figure 2c); hypandrium enlarged, ovate, laterally compressed, and partially translucent in places; epandrium distally tapering; cercus short and digitiform.

Female (Figure 2e). Similar to male, except lacking MSSC, frons wider than width of ocellar triangle; thorax and leg podomere ratios similar, but leg setation not as strongly developed; oviscapt (tergite 10) unmodified, with long digitiform cerci projecting posteriorly.

Remarks. *Hilara ranui* appears to be abundant in the Auckland Group. The male basitarsis I is not swollen and shows no evidence of silk production (see Discussion). It is distinctly smaller than the sympatric *Hilarempis motumaka*.

Differential diagnosis. This species is distinguished from all other New Zealand *Hilara* by the combination of unmodified male basitarsus I; the elongated ovate and partially translucent hypopygium (Figure 2c); the hemi-campanuliform vein R_4; and the grey pruinose mesonotum, with darker grey pruinose bands between the ac and dc bands.

Etymology. The specific epithet *ranui* is a geographical place name from indigenous Maori languages and should be regarded as a noun in apposition.

3.2. *Hilarempis motumaka n. sp.* (Figure 3a–d)

Type material. NEW ZEALAND: **Auckland Islands:** holotype ♂, paratypes 10 ♂♂, 2 ♀♀, ADAMS ISLAND: Magnetic Cove, 2 m, 3 February 1966, Malaise trap near shore, K. A. J. Wise; paratype ♂, West End, Fairchild's Garden, 21 January 1966, K. A. J. Wise (BPBM).

Additional material. NEW ZEALAND: **Auckland Islands:** 2 ♂♂, 3 ♀♀, AUCKLAND ISLAND: 3 ♂♂, Crozier Point, 1–20 m, on *Poa* sp., 28 December 1962, J. L. Gressitt; 2 ♂♂, ♀, West Coast, below Stony Peak, 1–100 m, ex *Casinia* & *Danthonia* sp., 17 January 1963, J. L. Gressitt; 8 ♂♂, 2 ♀♀, Bivouac Mtn, 540 m, 14 January 1963, ex. tussock, J. L. Gressitt; ENDERBY ISLAND: 11 ♂♂, 4 ♀♀, 1–50 m, on *Casinia*, 31 December 1963, K. A. J. Wise; EWIG ISLAND: 3 ♂♂, SE Coast, sweeping sedges, 4–5 January 1964, J. L. Gressitt; OCEAN ISLAND: 5 ♂♂, 2 ♀♀, 1–18 m, 29 December 1962, ex. *Metrosideros*, J. L. Gressitt; ROSE ISLAND: 2 ♂♂, ♀, 1–10 m, ex. herb mat, 8 January 1963, J. L. Gressitt (BPBM; specimens also deposited AMS, NZAC, CNC).

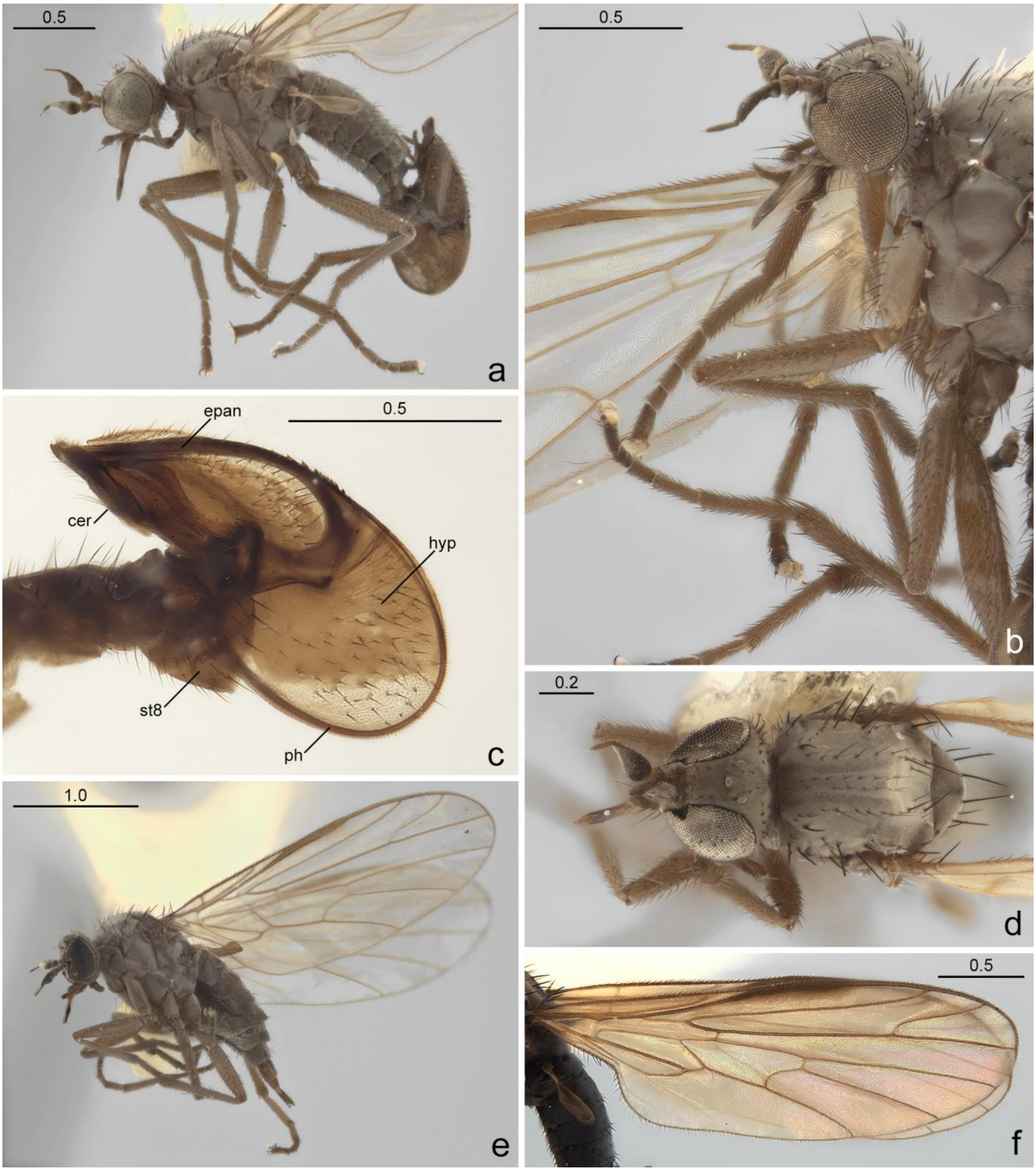

Figure 2. *Hilara ranui* n. sp.: (**a**) male habitus, left lateral; (**b**) male head, wing base, and legs, left lateral; (**c**) male postabdomen, left lateral; (**d**) male head and thorax, anterodorsal; (**e**) female habitus, left lateral; (**f**) male wing, dorsal. Legend: cer, cercus; sur, surstylus; el, epan, epandrium; hyp, hypandrium; ph, phallus; st 8, sternite 8.

Description. **Male**: length: 4.0–4.2 mm; wing: 4.3 × 1.6 mm (Figure 3a).

Head (Figure 3b). Postcranium, vertex, frons, and face mostly dark brown–black, with some grey pruinosity; setae black; group of postvertical setae along posterior vertex, row of long postocular setae along posterior eye margin, with irregular additional setae on dorsal and ventral postcrainum; field of short setae on ocellar triangle, with distinct strong ocellar setae; frons narrower than ocellar triangle, and with a row of 5–6 short black fronto-orbital setae along lateral margin adjacent to eyes; eyes notched laterad of antennae; face slightly wider than frons; eye with facets uniform; palp black, elongate, and curved, with abundant long ventral setae; proboscis dark brown, labrum longer than head height, and with some whitish hairs along length; antenna dark brown; scape slightly longer than pedicel; scape with dorsal and lateral setae, pedicle with some long subapical lateral setae; postpedicel subtriangular, tapering, with apical style.

Thorax (Figure 3c). Mostly dark brown, with brownish grey pruinosity over ac band, dc band, and humeral area, posterior mesonatal slope and dorsal scutellum, and chocolate brown bands between ac and dc rows and in stripe laterad of dc row; setae black; acrostichal setae comprising some 7–8 regular pairs, which extend onto the posterior mesonotal slope; 3–4 long dorsocentral laterad of posterior mesonotal slope, and w continuing anteriad as row of 8–9 slightly shorter setae; 1 postalar seta, 1 postsutural supra-alar seta; presutural intra-alar setae absent; notopleuron with strong posterior seta and 3 short setae anteriorly; 1 strong postpronotal seta, with some shorter hairs on postpronotal lobe; 1 presutural supra-alar seta; prosternum with 4–5 black setae; scutellum with four pairs of marginal setae; postnotum broad and slightly rounded; laterotergite bare.

Legs. All coxae and remainder of legs dark brown; coxae with grey pruinosity and black anteroapical setae; CI with abundant black anterior setae along length (Figure 2b); CIII with group of black lateral setae; all tarsi with strong claws and well developed pulvilli; legs mostly covered with short black vestiture, and with longer setae as noted; I: 5.5; 4.6; 2.0/ 1.4/ 0.8/ 0.3/ 0.8; FI covered with long dorsal, posterior, and ventral setae along length; TI with some 4–5 long spaced dorsal setae along length; It_1 with av-pv setal pair at base, and short dorsal and subapical setae, and unmodified, not swollen and without modified ventral cuticle; II: 4.5; 4.5; 1.8/ 1.1/ 0.6/ 0.3/ 0.6; FII with short vestiture and pv row of longer black setae; TII with 4 to 5 offset ad-pd setal pairs along length, and subapical corona of dorsal, ad, av, and pv setae; III: 5.0; 4.8; 1.8/ 1.2/ 0.7/ 0.3/ 0.7; FIII with some dorsal setae along length and some av setae along distal half; TIII with some spaced dorsal, ad, and anterior setae along length; IIIt_1 with basoventral seta and some short dorsal setae.

Wing. Membrane faintly smoky; costa with strong basal ad setae, otherwise veins bare; Sc straight and incomplete, ending well costa; distal R_1 slightly dilated near costal join; stigma brown and diffuse; R_{2+3} unbranched and joining costa near 3/4; R_{4+5} branched, with R_4 in gentle curve to costa, and R_5 meeting costa at wing apex; discal cell with branches M_1, M_2, and M_3; crossvein closing anal cell (cell cup) strongly recurrent; vein CuA + CuP complete to margin; anal angle well developed; lower calypter dull whitish, with black marginal setae; halter elongate and pale yellow.

Abdomen. Tergites dark brown, with dull grey prinosity; each tergite 1–5, with scattered short black setae and with row of longer black setae near posterior margin; hypopygium (Figure 3d) relatively small and ovate, and mostly dark brown; epandrium tapering to point; cercus relatively large and capitate.

Female. Similar to male, except lacking MSSC, frons wider than width of ocellar triangle; thorax and leg podomere ratios similar, but leg setation not as strongly developed; female oviscapt (tergite 10) unmodified, with long digitiform cerci projecting posteriorly.

Remarks. *Hilarempis motumaka* is common across the Auckland Group. Apart from hypopygial characters, males have strongly developed setation, ventrally along the palp and anterolaterally on coxa I (Figure 3b). In a manner similar to *Hilara ranui,* the male basitarsis I also is not swollen and shows no evidence of silk production (see Discussion).

Differential diagnosis. This species is distinguished from all other New Zealand *Hilarempis* by the combination of unmodified male basitarsus I; the rather compact hypopygium, with the rather large and capitate cercus (Figure 3d); and the highly setose head, coxa I, and mesonotum (Figure 3b,c).

Etymology. The specific epithet *motumaka* is the indigenous Maori name for the Auckland Islands and should be regarded as a noun in apposition. Archaeological evidence suggests that voyagers first discovered the Auckland Islands, leaving traces of settlement, possibly in the 13th century A.D. It is the southernmost known settlement by Polynesians.

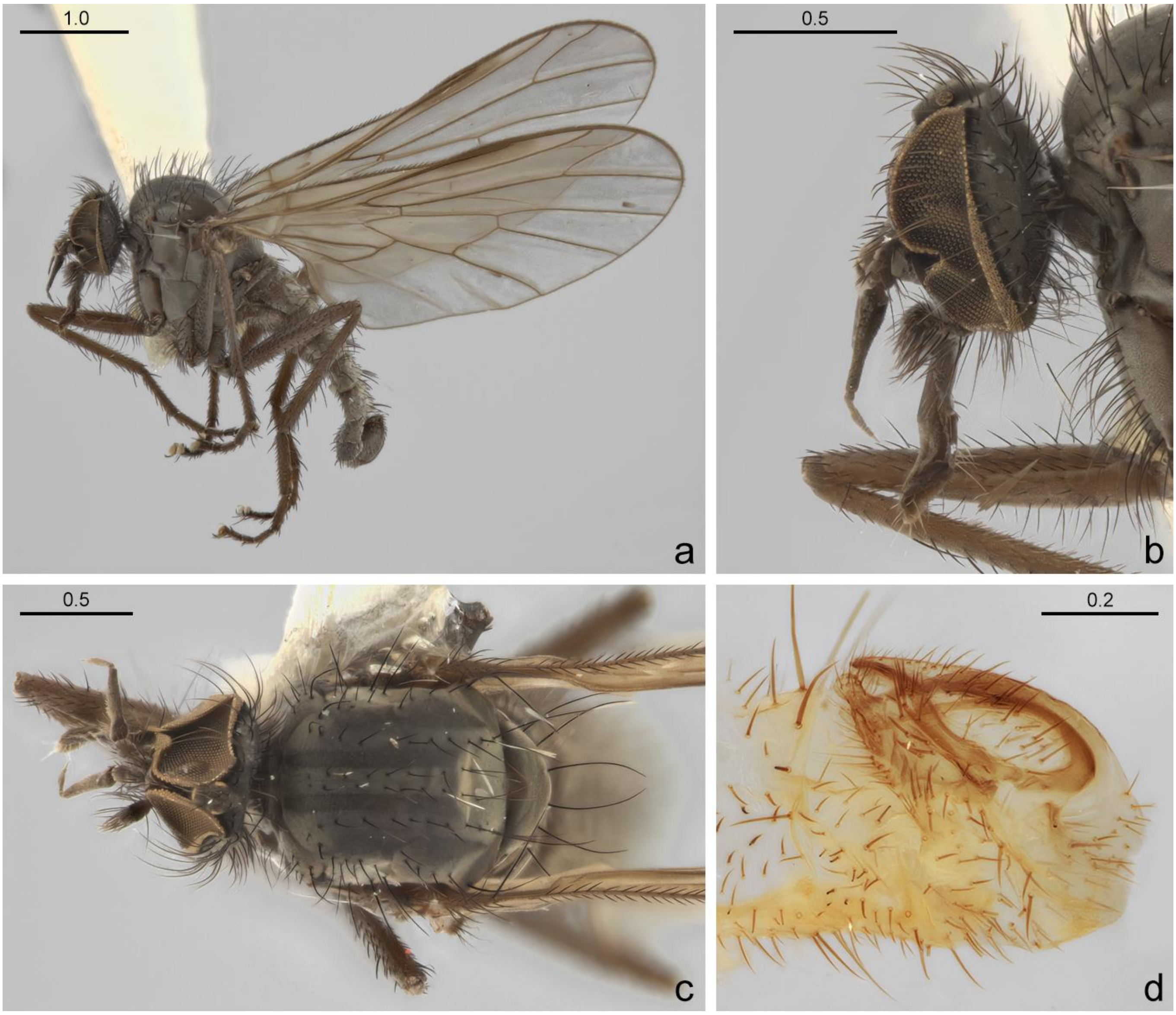

Figure 3. *Hilarempis motumaka* n. sp.: (**a**) male habitus, left lateral; (**b**) male head, left lateral; (**c**) male head and thorax, anterodorsal; (**d**) male postabdomen, left lateral.

4. Discussion

The two newly described species belong in the tribe Hilarini (Empididae: Empidinae), based on the characters listed for separating the Empidini from the Hilarini [31]. A generic grouping within the Hilarini, "the *Hilara* group of genera", has the male fore basitarsus swollen and comprises *Hilara* Meigen, *Hilarempis* Bezzi, *Atrichopleura* Bezzi, and *Hilarigona* Collin, with additional taxa awaiting description from the Southern Hemisphere. In the species that have been examined, this swollen basitarsus houses silk-producing glands [34,35], with the ventral surface covered by specialised hairs and tiny openings for silk extrusion. This is a readily observed morphological character, as well as being a strong de novo synapomorphy establishing the monophyly of this group. (In a remarkable convergence with the hilarine male leg I basitarsal silk glands, enlarged silk-producing glands are found on basitarsus I of both sexes, as well as larvae of the hemimetabolous webspinners, Order Embioptera [36]). From observations on the genus *Hilara*, the exuded silk is used for wrapping prey or debris, or in some cases, empty silken balloons are constructed, all to present as “nuptial gifts” to initiate mating with females. Many *Hilara* species have a low cruising flight, back and forth over ponds and backwaters along streams, where males attempt to pick up floating dead insects or debris from the surface to wrap in silk. The mating behaviour of *Hilara* is complex and often difficult to observe, but has been the subject of several reviews based on species from the Holarctic region [34,37–40].

However, the silk-producing capability of the swollen hilarine basitarsus has not been demonstrated across a wide range of taxa, i.e., the swollen basitarsus could be a male secondary sexual character in itself, with or without a glandular silk-producing function. As well, the swollen glandular male I basitarsus could also be absent, possibly as a secondary loss in species that otherwise would be included in these genera. This appears to be the case with the two new hilarine species treated here.

The two new Auckland Island species are described in separate genera, *Hilara* and *Hilarempis. Hilara* is a near cosmopolitan genus, with some 390 described species, while *Hilarempis* is a predominately southern temperate genus of some 110 described species [41]. Both genera have very large undescribed faunas, especially in the Southern Hemisphere. In keys, the two genera are traditionally separated by *Hilara* having vein Sc complete and reaching the costa, while *Hilarempis* has Sc incomplete, ending as a stub vein within the costal cell and not reaching the costa, a derived character state from the more plesiomorphic complete Sc. Although this character appears to have some use in distinguishing groups of species, it sometimes separates species that might be considered close based on other suites of characters. Further, in the Australian fauna, a specimen of an undescribed *Hilara* species has one wing with Sc complete and the other wing incomplete. Although this undoubtedly represents a developmental aberration within a single specimen, it suggests that the incomplete Sc may not be a deep synapomorphy and possibly easily derived. Nevertheless, both genera have a large burden of described species and several times more awaiting description. More accurate generic definition may prove difficult.

The presence on the Auckland Islands of two hilarine genera that both lack their characteristic male swollen fore basitarsi raises several questions: (1) Are these two species also present in probable ancestral source areas of the South Island or Stewart Island, but not yet collected or recognized there? (2) Is the homoplastic loss of swollen silk-producing basitarsi the result of similar insular environment selection against the mating behaviours associated with silk production, or had the loss occurred before the two species’ arrival on the Auckland Islands? It is not possible to answer these questions directly, but some background information should be reviewed.

The Auckland Islands supported ice caps during the Pleistocene period, until the Last Glacial Maximum some 21 thousand year ago. At this time, sea levels were some 150 m lower, exposing considerable areas of shelf around the islands which would have supported only periglacial habitats with low vegetation [2]. On cold windswept islands, especially those with overcast skies that block solar insolation, Diptera and other flying insects face the dual problem of flight muscle thermoregulation and the likelihood of being blown out to sea. One common evolutionary response to these factors is the loss of flight, with associated wing atrophy, i.e., having functional wings is a disadvantage and may not be selected for (review in Ref. [42]). Two empidoid Diptera on the Auckland Islands show marked wing size reduction. The strange flea-like dolichopodid *Apterachlachus borboroides* (Oldroyd) (see figure, p. 6 [43]) has totally lost both wings and halters. This species is also known from the Campbell Island, with either a conspecific or a closely related, undescribed, apterous species known from subalpine habitats above 1100 m on the Paparoa Range South Island, and above 600 m on Stewart Island. The flightless dolichopodid *Schoenophilus pedistris* (Lamb) has halters, but the wings are reduced to narrow straps (see Figure 1 [44]). It is known from the Auckland and Campbell islands, as well as the Australian Macquarie Island some 600 km to the southwest. The dispersal of such flightless Diptera between far-flung Subantarctic islands seems difficult to comprehend, but these species may have tolerated periglacial environments and occupied large areas exposed by lower sea levels at the Last Glacial Maximum, possibly facilitating such dispersal.

By contrast, both *Hilara ranui* and *Hilarempis motumaka* have normal-sized wings, without any indication of wing reduction or modification. This is also the case with the other Auckland Islands empidoid species, *Adipsomyia gressitti* Sinclair [25] and *Empidadelpha* nr. *propria* Collin [6], suggesting that these four species may have dispersed to the Auckland Islands well after the Last Glacial Maximum to a more ameliorated environment with greater vegetative diversity. On the other hand, the two flightless dolichopodid species might have been able to survive periglacial conditions and are therefore older residents of the islands.

However, there is still the problem of the homoplastic loss of the swollen, silk-producing, fore basitarsus in the *Hilara* and *Hilarempis* species from the Auckland Islands. If each is derived from South Island or Stewart Island congeners with swollen barsitarsi, is there a common selective pressure acting against the mating behaviour associated with silk production? Certainly, both genera are diverse in similar cold, rainy, southern temperate habitats (e.g., New Zealand's South Island, southern Chile, and Tasmania). Perhaps especially windy conditions on the Auckland Islands make the low skimming flight of males with silken "nuptial gifts" difficult, and therefore, silk production is not a selective advantage. Investigation of these species and their congeners in New Zealand would be of great interest.

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