

Description and natural history of the first micropterous *Meteorus* species: *M. orocrambivorus* sp. n. (Hymenoptera, Braconidae, Euphorinae), endemic to New Zealand

Helmuth Aguirre^{1†}, Scott R. Shaw^{1‡}, Jocelyn A. Berry^{2§}, Claudio de Sassi^{3,1}

1 University of Wyoming Insect Museum, Department of Ecosystem Science and Management (3354), 1000 East University Avenue, Laramie, Wyoming 82071 USA **2** Heaton House, Brooklyn, Wellington, New Zealand **3** Centre for International Forestry Research, PO Box 0113 BOCBD, Bogor 16000 Indonesia

† <http://zoobank.org/4D9AE3B6-BE69-484B-AD64-5BBFD04AF4FB>

‡ <http://zoobank.org/B4DCD509-07A6-45E1-AF25-296430A49EED>

§ <http://zoobank.org/DB32AAB2-13D9-4795-8AD2-BDCC1BBC4590>

| <http://zoobank.org/94E5A871-66E2-48B9-B9D2-40D259FAEDF2>

Corresponding author: *Helmuth Aguirre* (haguirre@uwyo.edu)

Academic editor: *Gavin Broad* | Received 1 March 2014 | Accepted 14 May 2014 | Published 12 June 2014

<http://zoobank.org/E025D630-ECA2-45A4-8815-E164AD6BEFEC>

Citation: Aguirre H, Shaw SR, Berry JA, de Sassi C (2014) Description and natural history of the first micropterous *Meteorus* species: *M. orocrambivorus* sp. n. (Hymenoptera, Braconidae, Euphorinae), endemic to New Zealand. *Journal of Hymenoptera Research* 38: 45–57. doi: 10.3897/JHR.38.7403

Abstract

Wing reduction is well known in the cyclostome lineage of Braconidae, but very unusual in non-cyclostome groups. A new species from New Zealand, *Meteorus orocrambivorus*, the first micropterous species of the non-cyclostome and cosmopolitan genus *Meteorus*, is described. Phylogenetic analysis places it close to *M. versicolor*, a macropterous parasitoid of macrolepidoptera. Details about its host relationships, plant associations and habitat suggest that the necessity of succeeding in cryptic environments may explain the wing modification. A possible case of Batesian mimicry with ants could explain the extreme sexual dimorphism.

Keywords

Wing reduction, sexual dimorphism, alpine habitat, parasitoid, *Orocrambus*

Introduction

Wing reduction is relatively common within the New Zealand braconid fauna. Iqbal et al. (2003) pointed out that 75% of doryctine species displaying wing reductions occur in the Australasian Region, and this proportion is steadily increasing (Austin and Jennings 2009, Belokobylskij and Kula 2012, Belokobylskij and Austin 2013). Several hypotheses, some of them overlapping, have been proposed to explain the origins of wing reduction in groups where it is considered an exception to the general rule, i.e. taxa mainly composed of winged species, such as the Braconidae. Such taxa rely on flight for dispersal to accomplish mating, foraging and colonization of new habitats. Roff (1990) reviewed the prevalent knowledge about the evolution of wing reduction, and sorted the possible causes into four groups: 1) potential tradeoffs between flight capacity and fecundity, whereby the development of wings, wing muscles, and the energetic budget to keep them are negatively correlated with the egg load; 2) relatively stable and cold environments may boost the selection of flightless forms because migration is not required. Stable environments are characterized by a small variability in resource supply in time and space (Roff 1990). Under such conditions, females do not need to travel long distances, and the flight apparatus is reduced in favor of increasing reproduction; 3) increases in latitude and altitude are positively correlated with stable environments (for example, alpine habitats), and as a consequence, they lead to wing reduction; 4) a tight association with concealed, protected, and narrow niches drives the loss of wings because such structures can become a handicap to moving into small and cryptic habitats.

Wing reduction is displayed in varying degrees, from the total loss of structures associated with wings, including the tegula, to wings being structurally well-developed but too short to perform flight. To describe this variability, Iqbal et al. (2003) used the following terminology for parasitoid wasps: 1) macropterous, for specimens having the fore wings fully developed and reaching, or almost so, the abdominal apex; 2) brachypterous, for specimens with the fore wing tips reaching beyond the posterior propodeum but not the second metasomal tergite; 3) micropterous, for specimens whose fore wing tips do not reach the posterior propodeum; and 4) apterous, for specimens with a total absence of wings or, at most, manifesting as small scales no longer than the tegula.

The family Braconidae (Hymenoptera) is mainly comprised of winged species. However, wing reduction is a well-known phenomenon among the cyclostome lineage of Braconidae, since 90 species in 44 genera (1.2%) have been reported showing it (Belokobylskij and Kula 2012). In contrast, only 19 non-cyclostome species in six genera (0.2%) are known with this character (Belokobylskij and Kula 2012). The non-cyclostome euphorine clade (Euphorinae+Meteorinae+Neoneurinae) (Belshaw and Quicke 2002) is represented by three species in the genus *Cosmophorus* Ratzeburg (Belokobylskij and Kula 2012). In *Cosmophorus* only the male is apterous, and this extreme sexual dimorphism is particularly remarkable in *C. laricio* Shaw, a parasitoid of the bark beetle *Pityogenes bistridentatus* (Eichoff) (Shaw 2009).

Meteorus Haliday (Euphorinae: Meteorini) is a cosmopolitan genus of koinobiont parasitoids of Coleoptera and Lepidoptera larvae. Its most remarkable characteristic is the distinctive pendant (meteor-like) cocoon constructed by the last larval instar (Shaw 1997). Around 326 species have been described worldwide (Yu et al. 2012). Huddleston (1986) studied the New Zealand fauna and reported seven species. Berry and Walker (2004) added *M. pulchricornis* (Wesmael) to the list, an exotic species first detected in 1996. All the New Zealand *Meteorus* species currently known are macroppterous. This paper describes the first micropterous *Meteorus* species and provides information about its biology and habitat.

Methods

The sampling location was Glynn Wye station at Lewis Pass (42°22.78'S, 172°24'E), North Canterbury Region, New Zealand (Fig. 14). The Lewis Pass traverses the Southern Alps, which run north-south along much of the South Island of New Zealand. It is the most northern and lowest (907m) of the three main alpine passes which allow access between the west and east coasts.

All the *Meteorus* specimens were reared as solitary parasitoids of caterpillars of *Orocrambus ramosellus* Doubleday, *O. simplex* Butler (Lepidoptera: Crambidae) and *Merophyas leucaniana* (Walker) (Tortricidae). The caterpillars were collected by Claudio de Sassi from four locations (42°36.73'S, 172°27.78'E; 42°36.88'S, 172°27.62'E; 42°36.72'S, 172°26.58'E; 42°38.83'S, 172°22.17'E) at three elevations (650 m, 800 m, 1000 m) from November 2008 to January 2009. The sample sites comprise alpine and subalpine habitats dominated by a mixture of tussock grasses (*Poa* and *Festuca*), representing the native flora component, and exotic pastures accounting for the non-native component (Barratt et al. 2005).

The caterpillars were hand-picked from the host plants *Poa cita* Edgar (silver tussock) and *Festuca novae-zelandiae* (Hack.) (Cockayne, fescue tussock), and subsequently reared to fate in the laboratory (i.e. death of caterpillar or emergence of either adult moth or parasitoid). The collected parasitoids were preserved in vials with 95% ethanol, and sent to the University of Wyoming Insect Museum (UWIM).

Eleven specimens were pin-mounted for taxonomic description, 21 remained in alcohol from which 2 legs were sent to Julia Stigenberg at Stockholm University for DNA analyses as a part of her project about the phylogeny of Euphorinae. Morphological terminology follows Sharkey and Wharton (1997) and Zitani et al. (1998). Explanatory illustrations are provided in Aguirre et al. (2011). Sculpture terminology is based on Harris (1979). Specimens were measured using a Leica M80 stereomicroscope with micrometer on a 10× ocular. Digital images were captured with a Leica M205 C stereomicroscope with digital Leica DFC295 camera kit and processed with Leica Application Suite Version 3.8.0 auto-montage software. Scanning Electron Microscopy (SEM) images were produced at the University of Wyoming, Robert A. Jenkins Microscopy Facility. Descriptions were made with the DELTA software (Dallwitz

1974, 1980). Holotypes and paratypes are deposited at the Museum of New Zealand Te Papa Tongarewa (MONZ). Voucher material is deposited at the University of Wyoming Insect Museum (UWIM).

Results

Meteorus orocrambivorus Aguirre & Shaw, sp. n.

<http://zoobank.org/F111A855-0E56-49EC-84E5-A5818175173C>

http://species-id.net/wiki/Meteorus_orocrambivorus

Diagnosis. Occipital carina complete; ocelli small (ocelli-ocular distance 2.0–2.3× ocellar diameter in females, 1.7× in males); mandible stout and twisted; notauli smooth and not distinct in females, but deeply impressed, narrow, distinct and rugose in males; female micropterous, male macropterous; propodeum smooth in females, but rugulose-lacunose in males; tarsal claw without lobe; dorsope and laterope absent; ventral borders of first tergite almost touching distally; ovipositor 1.9–2.3× longer than first tergite).

Description of holotype female. *Body color.* Dark brown-ferruginous

Body length. 3.5 mm.

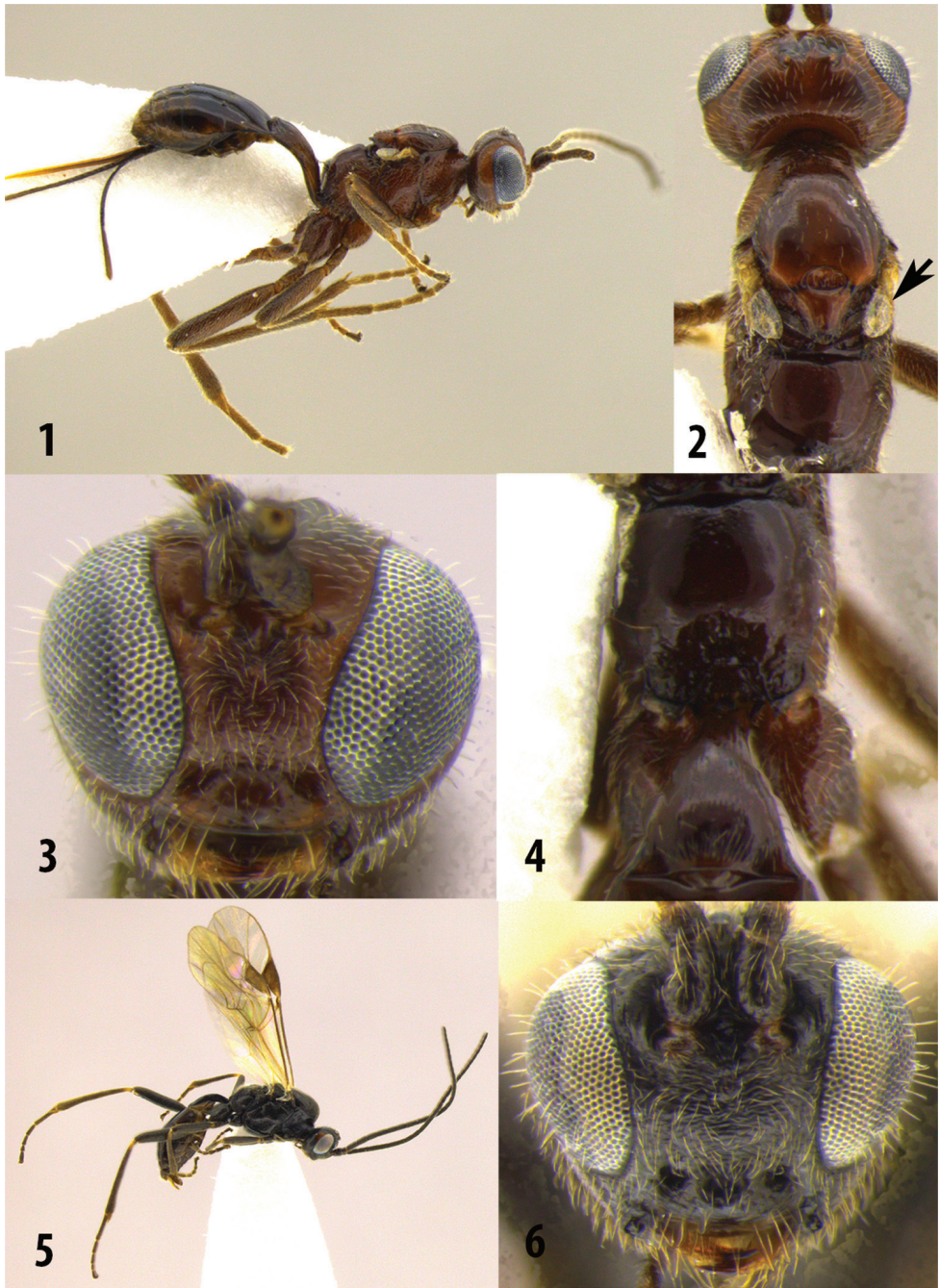
Head. (Fig. 3). Antenna with 16 flagellomeres; flagellar length/width ratios as follows: F1 = 2.6, F2 = 2.2, F3 = 1.9, F 14 = 1, F 15 = 0.9, F 16 = 2.0; head 1.1× wider than high; occipital carina complete; ocelli ocular distance 2.0× ocellar diameter; head height 1.4× eye height; temple length 0.7× eyes length in dorsal view; vertex in dorsal view not descending vertically behind the lateral ocelli; frons smooth and polished; maximum face width 1.4× minimum face width; face finely rugulose; minimum face width 0.7× clypeus width; clypeus punctate; malar space length 0.4× mandible width basally; mandible stout and twisted.

Mesosoma. (Figs 2, 4, 7 and 9). Pronotum in lateral view dorsally rugose; propleuron smooth and polished; notauli smooth and not distinct; mesonotal lobes not defined; mesoscutum smooth and polished; scutellar furrow with one carina; mesopleuron smooth but rugulose close to tegula; sternaulus long, wide and rugose; metapleuron mostly smooth, rugose close to the coxa; suture between propodeum and metapleuron foveate; propodeum smooth; absence of longitudinal and transversal carinae on propodeum; median depression on propodeum weakly present.

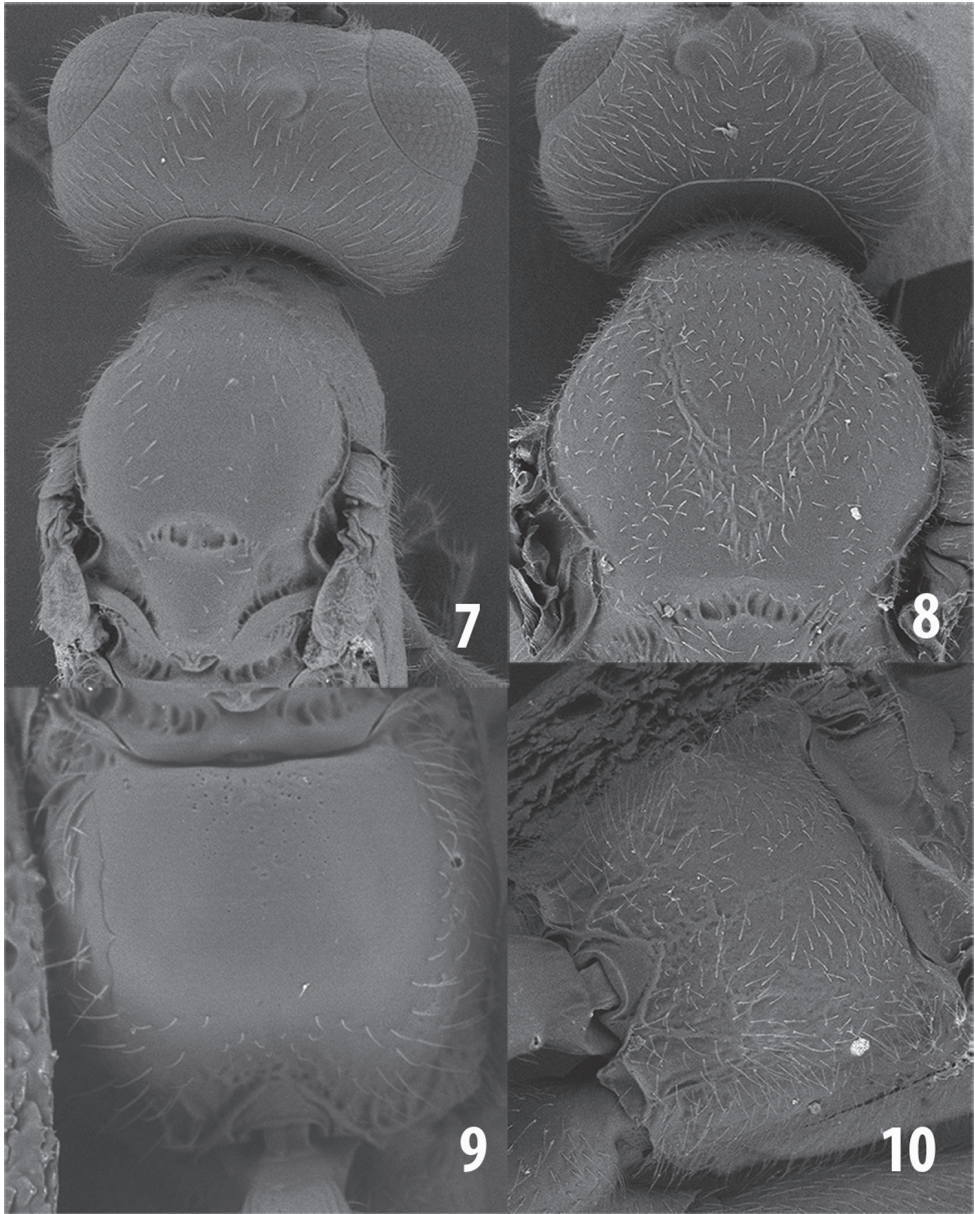
Wings. Very reduced, at most reaching the scutellum apex (Fig. 2).

Legs. Hind coxa slightly strigose dorsally; the remaining surface irregular and punctulate; hind femur 4.8× longer than it is wide; tarsal claw without lobe.

Metasoma. (Figs 1 and 4). Dorsope and laterope absent; ventral borders of first tergite almost touching distally; first tergite smooth and polished except the apical border with short and convergent costae; ovipositor 2.0× longer than first tergite; ovipositor both not thickened basally and straight.



Figures 1–6. *M. orocrambivorus* sp. n. **1** Female lateral habitus **2** Female head and mesonotum dorsal view. The arrow indicates the reduced wing **3** Female head frontal view **4** Female propodeum and first metasomal tergite dorsal view **5** Male lateral habitus **6** Male frontal view.



Figures 7–10. Contrasting differences between males and females. **7** female head and mesonotum dorsal view **8** male head and mesonotum dorsal view **9** female propodeum dorsal view **10** male propodeum dorsal view.

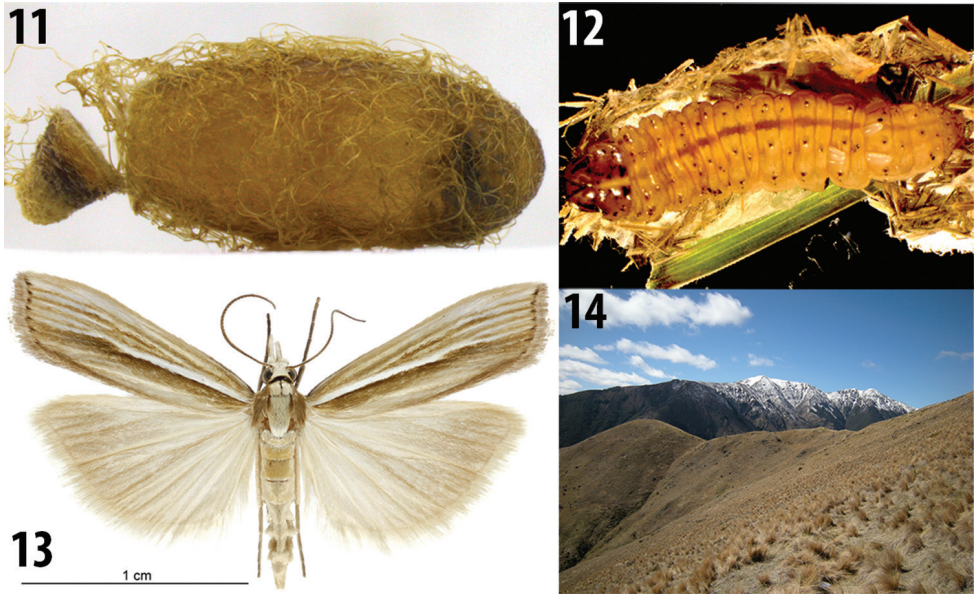
Female variation based on paratypes. Body length 3.0–3.1 mm; head with long and scattered setae; head 1.2× wider than high; ocelli ocular distance 2.3× ocellar diameter; head height 1.3× eye height; temples length 0.6× eyes length in dorsal view; maximum face width 1.3× minimum face width; face strigulate; minimum face width

0.8× clypeus width; malar space length 0.3–0.6× mandible width basally; pronotum in lateral view dorsally lacunose-foveate, faintly costate ventrally; sternaulus carinate-foveate; propodeum smooth except a small, punctate patch dorsally; hind coxa either strigate-punctate, strigate, or with very small and disperse punctures; hind femur 4.6–5.2× longer than it is wide; ventral borders of first tergite touching for a short distance; first tergite with costae convergent, faintly demarcated; T2 and T3 slightly coriaceous; ovipositor 1.9–2.3× longer than first tergite; ovipositor neither thickened basally nor curved.

Male variation based on paratypes. (Figs 5, 6, 8 and 10). Body black except the head with a small testaceous patch on the temple behind the eye; wings hyaline; body length 3.7 mm; antenna with 27 flagellomeres; ocelli ocular distance 1.7× ocellar diameter; head height 1.6× eye height; temples length 0.8–0.9× eyes length in dorsal view; vertex in dorsal view not descending vertically behind the lateral ocelli; maximum face width 1.2× minimum face width; minimum face width equal to clypeus width; malar space length 0.7–0.9× mandible width basally; propleuron punctulate and shiny; notauli deeply impressed, narrow, distinctive and rugose, with pronounced longitudinal carina; mesoscutal lobes well defined; central lobe of mesoscutum punctate; scutellar furrow with seven carinae; mesopleuron smooth and polished; sternaulus rugose; propodeum rugulose-lacunose; longitudinal and transversal carinae on propodeum absent; median depression on propodeum absent; hind coxa with very small and dispersed punctures; wing length 3.6–3.7 mm; second submarginal cell of fore wing not strongly narrowed anteriorly; vein r 0.5× length of 3Rsa (fore wing); vein 3Rsa 0.8× length of r-m (fore wing); vein m-cu of fore wing postfurcal; vein 1M 0.8–1× length of cu-a (HW); vein 1M 0.8× length of 1r-m (hind wing); dorsope and laterope absent; apparent dorsopes as deep grooves in the common dorsopes location; first tergite with faintly demarcated and parallel costae, which become more obvious on the apical border.

Comments. The micropterous condition of *M. orocrambivorus* females is unique among all known *Meteorus*. However if the males are compared with the rest of the New Zealand fauna, *M. orocrambivorus* seems closest to *M. cobbis* Huddleston (Huddleston 1986; p. 256, numeral 6 in the key). Males of both species share the following character states: body mostly black except a small, lighter patch (yellow or testaceous) on the temple behind the eyes; small ocelli (ocelli ocular distance $\geq 1.5\times$ ocellar diameter); eyes almost parallel (maximum face width $\leq 1.2\times$ minimum face width); mandibles stout and twisted; propodeum rugulose; dorsopes and lateropes absent, and ventral borders of first tergite touching for a short distance. *M. orocrambivorus* can be separated from *M. cobbis* by having antennae with 27 flagellomeres (30–33 in *M. cobbis*), notauli narrow, carinate and distinct (broad and reticulated in *M. cobbis*), and first tergite costate (strigose in *M. cobbis*).

Holotype. Female (point-mounted). NEW ZEALAND, South Island, Lewis Pass, Hope River Valley, Glynn Wye Station, 42°36.73'S, 172°27.78'E, 650 m; host plant *Poa cita* Edgar (silver tussock), host caterpillar *Orocrambus ramosellus* Doubleday (Crambidae); collected as solitary parasitoid during the period November 2008 to January 2009; Claudio de Sassi, collector.



Figures 11–14. 11 *M. orocrambivorus* sp. n. cocoon 12 *O. ramosellus* caterpillar 13 *O. ramosellus* adult 14 Lewis Pass, the type-locality.

Paratypes. Two females and seven males same data as the holotype; one female same data as holotype except collected at 42°36.88'S, 172°27.62'E, 800 m; two females and two males same data as holotype except collected at 42°36.72'S, 172°26.58'E; three females and two males same data as holotype except the host caterpillar collected feeding on *Festuca novae-zelandiae* (Hack.) Cockayne at 1000 m; one female same data as holotype except the host caterpillar collected feeding on *F. novae-zelandiae* at 42°36.88'S, 172°26.58'E; one female same data as holotype except the host caterpillar collected feeding on *F. novae-zelandiae* at 42°36.88'S, 172°26.58'E, 650 m; six females and four males same data as holotype except the host caterpillar collected feeding on *F. novae-zelandiae* at 42°36.88'S, 172°26.58'E, 1000 m; one female and one male same data as holotype except the host caterpillar collected feeding on *F. novae-zelandiae* at 42°38.83'S, 172°22.17'E, 650 m.

Distribution. NEW ZEALAND, South Island, Lewis Pass, Hope River Valley, Glynn Wye Station.

Cocoon. (Fig. 11). Length 4.4 mm; width 1.6 mm; honey-brown translucent except apex cap golden, posteriorly bordered by a dark ring; oval-shaped, densely wrapped by silk, irregular cap border, anterior end (cap) nipple-like. The cocoon was found unattached inside a structure built by the caterpillar using grass leaves and silk (Fig. 12). No trace of a suspending thread was detected.

Biology. (Figs 12 and 13). The information gathered from the type series and additional rearings indicates that *M. orocrambivorus* is a solitary parasitoid of larval *O. ramosellus*, *O. simplex* and *M. leucaniana*. Parasitized *Orocrambus* have been collected feeding on *F. novae-zelandiae*, *P. cita*, *Holcus lanatum* L., *Anthoxantum odoratum* L.,

Agrotis capillaris L., *Festuca rubra* L. and *Rytidosperma setifolium* (Hook. f.) Connor & Edgar. *M. leucaniana* was collected on *F. novae-zelandiae*.

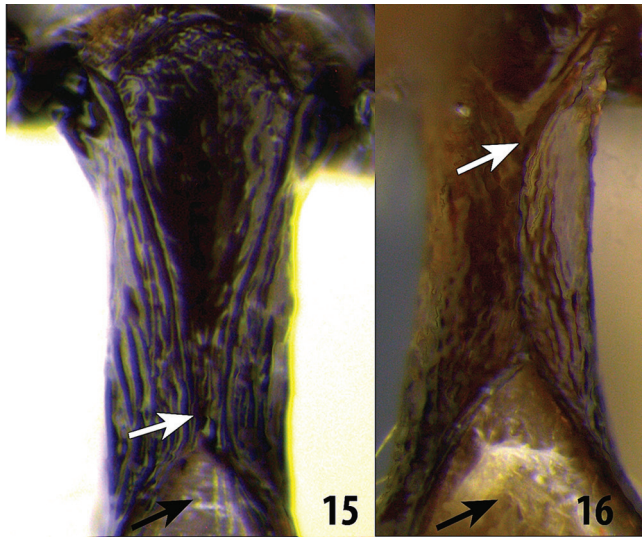
Etymology. The species name *orocrambivorus* is a reference to its feeding habit. The stem of the specific epithet refers to the genus name of the host caterpillar, *Orocrambus*, and the suffix comes from the Latin *-vorare* meaning “devour.”

Discussion

The results of a molecular-based phylogenetic analysis carried out by Julia Stigenberg (unpublished data) placed *M. orocrambivorus* close to *Meteorus versicolor* Wesmael. *Meteorus versicolor* belongs to clade IIB proposed by Stigenberg and Ronquist (2011); their phylogenetic analysis partly agrees with Maeto's work (1990), which was based on morphology. Clade IIB corresponds with Maeto's *pulchricornis* (excluding the *colon* subgroup) and *rubens* groups (Stigenberg and Ronquist 2011). Their members are characterized by having a narrow face, strongly twisted mandibles, absence of a tubercle on the frons, and short ovipositor (length less than 2× the length of the first tergite; Stigenberg and Ronquist 2011). *Meteorus orocrambivorus* and *M. versicolor* share a complete occipital carina, slender and twisted mandibles, and no dorsope. However, *M. orocrambivorus* has the tarsal claw without a lobe (tarsal claw with a distinct basal lobe in *M. versicolor*) and ventral borders of first tergite almost touching distally (ventral borders of first tergite completely joined along its basal half in *M. versicolor*, Figs 15–16). *Meteorus versicolor* is a widely distributed species known from the Eastern and Western Palaearctic Region and introduced to North America for biological control of *Euproctis chrysorrhoea* L. (Lymantriidae) (Muesebeck 1923); its host range comprises about 80 lepidopteran species in fifteen families, mostly macrolepidoptera (Yu et al. 2012, Stigenberg and Shaw 2013). Despite the phylogenetic position of *M. orocrambivorus* in the aforementioned analysis, it is difficult to track the origin of the wingless condition in *Meteorus* since *M. orocrambivorus* was the only Australasian species included.

Wing reduction as an adaptation to live in concealed, small and close-fitting niches is a compelling hypothesis to explain wing reduction in several species of Doryctinae (Seltmann and Sharkey 2007, Belokobylskij and Kula 2012, Belokobylskij and Austin 2013). The frequent sampling of wasps with remarkable wing-reduction under the leaf-litter of forested habitats suggests that the necessity of chasing hosts in cryptic habitats has shaped the reduction (Iqbal et al. 2003, Seltmann and Sharkey 2007, Belokobylskij and Kula 2012, Belokobylskij and Austin 2013). The Costa Rican species *Oroceguera andersoni* Seltmann & Sharkey (Braconidae: Doryctinae) is a good example of a wingless parasitoid associated with forest leaf-litter (Seltmann and Sharkey 2007). Since *Orocrambus* caterpillars spin their cocoons at the base of tussock grasses and *M. leucaniana* constructs tunnels in the detritus layer surrounding tussocks, *M. orocrambivorus* female wasps are pressed to succeed in tight spaces.

But a possible adaptation to live in cryptic environments does not fully explain the remarkable sexual dimorphism. The common pattern of sexual dimorphism in *Meteorus*



Figures 15–16. 15 *M. orocrambivorus*, ventral borders of first tergite almost touching distally 16 *M. versicolor*, ventral borders of first tergite completely joined along its basal half. White arrows on both pictures indicate the apical section of the structure. Black arrows indicate the most apical point where the ventral borders converge.

species is: body size and relative eyes size smaller in males than females, relative ocelli size larger in males than females, antennae longer in males than females, in some cases darker body color in males than females, and the obvious absence of ovipositor in males. The morphological deviation in *M. orocrambivorus* females is so extreme that the initial assignment of females to the genus *Meteorus* was dependent on the examination of males. A fleeting glimpse of a *M. orocrambivorus* female in the field could lead to confusion because of its ant-like appearance. The close morphological and behavioral resemblance to ants is called myrmecomorphy, and it is outlined by a set of departures from the common bauplan in those arthropods having it (McIver and Stonedahl 1993): abdominal constriction, well developed mandibles, elbowed or clubbed antennae, color change, loss or reduction of wings, head enlargement and microstructural modifications (changes in surface sculpture and pubescence). Compared with males, *M. orocrambivorus* females display notable differences in color body (Figs 1–6), wing reduction (Fig 2), reduction in number of flagellomeres, relative head size (Fig 7–8) and texture of body surface (Figs 2, 4 and 7–10). Smooth surfaces on the mesoscutum and propodeum are extremely rare in *Meteorus*, and such surfaces displayed by *M. orocrambivorus* may be unique in the genus. Patterns of myrmecomorphy reflected by modifications on body shape and surface texture may be explained by the Wasmannian mimicry, a special case of Batesian mimicry: when ants antennate each other, one feature they are looking for to recognize conspecifics is the texture of the body surface (Rettenmeyer 1970). This behavior matches with changes in sculpture present in *M. orocrambivorus* females, but additional field observations are necessary to

corroborate an ant-mimicry model: 1) possible model ants sharing the same habitat with *M. orocrambivorus*, 2) model ants showing a denser distribution than *M. orocrambivorus*, and 3) model ants displaying an aggressive behavior or unpalatable to predators (Mappes and Alatalo 1997).

Acknowledgements

We thank Julia Stigenberg for providing results of the DNA analysis. Dr. Zhaojie Zhang of the University of Wyoming Microscopy Core Facility is thanked for his kind assistance and advice with scanning electron microscopy. We are also grateful to the Museum of New Zealand Te Papa Tongarewa and especially to Mr Ricardo Palma for his kindness in allowing access to the museum's Hymenoptera collection. The auto-montage imaging system was provided by National Science Foundation grant DEB-10-20751. Any opinions, findings, and conclusions expressed are those of the author and do not necessarily reflect the views of the National Science Foundation. CdS was supported by a University of Canterbury Doctoral Scholarship and a Hellaby Trust Fellowship. The research was funded by the Marsden Fund (UOC-0705, grantholder Jason M. Tylianakis) and the Miss E. L. Hellaby Indigenous Grassland Research Trust.

References

- Aguirre H, Sarmiento CE, Shaw SR (2011) Taxonomic revision and morphometric analyses of *Meteorus* Haliday, 1835 (Hymenoptera: Braconidae: Meteorinae) from Colombia. *Zootaxa* 2938: 1–68.
- Austin DA, Jennings JT (2009) A new highly aberrant doryctine wasp *Spathius lubomiri* sp. n. (Hymenoptera: Braconidae: Doryctinae), from Lord Howe Island. *Zookeys* 20: 275–284. doi: 10.3897/zookeys.20.120
- Barratt B, Ferguson C, Logan R, Barton D, Bell N, Sarathchandra S, Townsend R (2005) Biodiversity of indigenous tussock grassland sites in Otago Canterbury and the central North Island of New Zealand. I. The macro-invertebrate fauna. *Journal of the Royal Society of New Zealand* 35: 287–301. doi: 10.1080/03014223.2005.9517786
- Belokobylskij SA, Austin DA (2013) New species of flightless doryctine parasitoid wasp (Hymenoptera: Braconidae: Doryctinae) from Australia and New Zealand. *Australian Journal of Entomology* 4(52): 338–355. doi: 10.1111/aen.12042
- Belokobylskij SA, Kula RR (2012) Review of the brachypterous, micropterous, and apterous Braconidae of the cyclostome lineage (Hymenoptera: Ichneumonoidea) from the Palearctic Region. *Zootaxa* 3240: 1–62.
- Belshaw R, Quicke DLJ (2002) The robustness of ancestral state estimates: evolution of life history strategy in ichneumonoid parasitoids. *Systematic Biology* 51: 450–477. doi: 10.1080/10635150290069896

- Berry JA, Walker GP (2004) *Meteorus pulchricornis* (Wesmael) (Hymenoptera: Braconidae Euphorinae): An exotic polyphagous parasitoid in New Zealand. *New Zealand Journal of Zoology* 31: 33–44. doi: 10.1080/03014223.2004.9518357
- Dallwitz MJ (1974) A flexible computer program for generating identification keys. *Systematic Zoology* 23: 50–57. doi: 10.2307/2412239, <http://delta-intkey.com>
- Dallwitz MJ (1980) A general system for coding taxonomic descriptions. *Taxon* 29: 41–46. doi: 10.2307/1219595, <http://delta-intkey.com>
- Harris AH (1979) A glossary of surface sculpturing. *Occasional papers in Entomology* (28): 1–31.
- Huddleston T (1986) The braconid genus *Meteorus* in New Zealand (Insecta: Hymenoptera). *Journal of Natural History* 20: 255–265. doi: 10.1080/00222938600770201
- Iqbal M, Austin AD, Belokobylskij SA (2003) Diversity and Biogeography of reduced-winged doryctine wasps (Hymenoptera: Braconidae) in Australasia. *Records of the South Australian Museum. Monograph Series* 7: 243–247.
- Maeto K (1990) Phylogenetic relationships and host associations of the subfamily Meteorinae Cresson (Hymenoptera: Braconidae). *Japanese Journal of Entomology* 58: 383–396.
- Mappes J, Alatalo RV (1997) Batesian mimicry and signal accuracy. *Evolution* 51(6): 2050–2053. doi: 10.2307/2411028, <http://www.jstor.org/stable/2411028>
- McIver JD, Stonedahl G (1993) Myrmecomorphy: morphological and behavioral mimicry of ants. *Annual Review of Entomology* 38: 351–379. doi: 10.1146/annurev.en.38.010193.002031
- Muesebeck CFW (1923) A revision of the North American species of ichneumon-flies belonging to the genus *Meteorus* Haliday. *Proceedings of the United States National Museum* 63: 1–44. doi: 10.5479/si.00963801.63-2470.1
- Rettenmeyer CW (1970) Insect mimicry. *Annual Review of Entomology* 15: 43–74. doi: 10.1146/annurev.en.15.010170.000355
- Roff DA (1990) The evolution of flightlessness in insects. *Ecological Monographs* 60(4): 389–421. doi: 10.2307/1943013, <http://www.jstor.org/stable/1943013>
- Seltmann K, Sharkey M (2007) A new genus and species of apterous Doryctinae (Hymenoptera: Braconidae) from Costa Rica. *Zootaxa* 1415: 17–24. <http://www.mapress.com/zootaxa/2007f/zt01415p021.pdf>
- Sharkey MJ, Wharton RA (1997) Morphology and terminology. In: Wharton RA, Marsh PM, Sharkey MJ (Eds) *Manual of the New World genera of the family Braconidae* (Hymenoptera). Special Publication of the International Society of Hymenopterists, No. 1 (Washington DC): 19–37.
- Shaw MR (2009) A new, highly sexually dimorphic species of *Cosmophorus* Ratzeburg (Hymenoptera: Braconidae: Euphorinae) reared from Corsica. *British Journal of Entomology and Natural History* 22: 151–157.
- Shaw SR (1997) Subfamily Meteorinae. In: Wharton RA, Marsh PM, Sharkey MJ (Eds) *Manual of the New World genera of the family Braconidae* (Hymenoptera). Special Publication of the International Society of Hymenopterist, No. 1 (Washington DC): 123–136.
- Stigenberg J, Ronquist F (2011) Revision of the Western Palaearctic Meteorini (Hymenoptera: Braconidae), with a molecular characterization of hidden fennoscandian species diversity. *Zootaxa* 3084: 1–95.

- Stigenberg J, Shaw MR (2013) Western Palaearctic Meteorinae (Hymenoptera: Braconidae) in the National Museums of Scotland, with rearing, phenological and distributional data, including six species new to Britain, and a discussion of a potential route of speciation. *Entomologist's Gazette* 64: 251–268.
- Yu DSK, Achterberg C van, Horstmann K (2012) Taxapad 2012, Ichneumonoidea 2011. Database on flash-drive. Ottawa, Ontario, Canada. www.taxapad.com
- Zitani NM, Shaw SR, Janzen DH (1998) Systematics of Costa Rica *Meteorus* (Hymenoptera: Braconidae: Meteorinae) species lacking a dorsope. *Journal of Hymenoptera Research* 7(2): 182–208. <http://biostor.org/reference/490>