Hadranellus anomalus n.gen. *et* n.sp. (Hymenoptera: Eulophidae): an example of extreme intraspecific variation in an endemic New Zealand insect

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ABSTRACT

Hadranellus anomalus, a new genus and species of tetrastichine Eulophidae, is described. This species shows considerable variation in characters normally expected to be fairly stable in tetrastichine morphology and is one example of such variation found in endemic New Zealand insects.

Keywords: Eulophidae, Tetrastichinae, *Hadranellus*, intraspecific variation, New Zealand

INTRODUCTION

The tetrastichine eulophids are one of the most biologically diverse groups of parasitic Hymenoptera. Tetrastichine species are known to be parasitoids or hyperparasitoids of hosts in over 100 families in 10 insect orders. The larvae of some species are predatory, consuming spider eggs, mites and nematodes (the latter two hosts in galls); still other species are phytophagous, being seed-infesters, gall-formers, or inquilines. Few other groups of parasitic Hymenoptera display such a range of host utilization.

Tetrastichines are equally diverse in other aspects of their biology, such that few characterizations can be made about the group as a whole. Species can be solitary or gregarious, primary or secondary parasitoids, and monophagous to polyphagous. Although species predominantly attack larvae or pupae, many egg parasitoids are known, and even a few parasitoids of adults. Further information on biology of Tetrastichinae is given by Graham (1987) and LaSalle (1994).

Tetrastichines are also a quite speciose and abundant group, and it is difficult to collect in almost any geographical realm without encountering numerous examples of this subfamily. Yet, despite their abundance and the variety of differences in their biology, the group is quite stable morphologically. Indeed, the relatively uniform morphology makes species identifications difficult, if not impossible, in most parts of the world, and it is only quite recently (Graham 1987, 1991; Bouček 1988; LaSalle 1994) that a stable generic classification has been introduced.

In this paper we describe a new genus and species of tetrastichine eulophid, *Hadranellus anomalus*, from New Zealand. It is particularly interesting because, like many other New Zealand insects, it displays a remarkable amount of morphological variation. Tetrastichines, like all other organisms, are known to display a certain level of intraspecific variation, but this is usually not too extreme. *H. anomalus* not only displays a high level of variation in species-level characters, but also in characters that are normally quite stable in tetrastichines and have been used at the generic level in other geographic realms. This species appears to represent another example of high intraspecific variation found in many endemic New Zealand insect species (see discussion below).

MORPHOLOGY AND ABBREVIATIONS

Keys which allow the recognition of Tetrastichinae from the other subfamilies of Eulophidae have been provided by Graham (1987), Bouček (1988) and Grissell & Schauff (1990). Morphological terminology follows LaSalle (1994). The following abbreviations are used for morphological terms in the text:

A1-A4, anelli 1-4
F1-F4, funicular segments 1-4
CC, costal cell
SMV, submarginal vein
PMV, postmarginal vein
MV, marginal vein
SV, stigmal vein

The following acronyms are used for museums and collections:

ANIC, Australian National Insect Collection, CSIRO, Canberra, Australia
BMNH, The Natural History Museum, London, UK
BPBM, Bernice P. Bishop Museum, Honolulu, Hawaii, USA
CNC, Canadian National Collection, Ottawa, Canada
LAS, Collection of the senior author
NZAC, New Zealand Arthropod Collection, Mt Albert Research Centre, Auckland,
    New Zealand
UCD, University of California, Davis, USA
UCR, University of California, Riverside, USA
USNM, United States National Museum (Natural History), Washington, D.C., USA

DESCRIPTIONS
Hadranellus, n.gen.
(Figs 1-18)

Type species: *Hadranellus anomalus*, n.sp. Gender masculine.

Diagnosis

A3 and A4 distinctly swollen, quadrate, and with many small setae; A1 transverse and without setae; A2 either transverse and asetose, or swollen to about half the size of A3 and with setae. Scutellum without submedian lines, with distinct sublateral lines which are laterally carinate; number of setae variable, from 4 (2 distinct pairs) to 13 (placed laterally but not distinctly paired). Midlobe of mesoscutum with many scattered setae, however at least a small median area is bare of setae; median line absent or present. PMV present and distinct, variable in length from 0.4-1.0 the length of SV. Propodeal spiracle with entire rim exposed.

Female

Head (Fig. 1). Slightly wider than thorax in dorsal view; in frontal view slightly wider than high. Scrobal cavities converging dorsally, frontofacial suture represented by a median line. Antennal toruli inserted at or slightly above level of ventral margin of eyes. Malar sulcus present, curved or angular; slight fovea may be present at the base of the eye. Clypeus truncate to weakly bilobed.

Antenna (Figs 7-12). Scape slightly swollen or ventrally expanded, apex generally extending at least slightly above the level of the vertex. Four anelli present, with A3 and A4 large, setose, and usually quadrate; sometimes A2 also large, setose and up to about half the length of A3. Funicle with three segments, varying in length, but all at least slightly longer than wide. Clava with three segments; terminal spine short to medium.

Mesosoma (Figs 2-6). Pronotum uniformly setose. Midlobe of mesoscutum with many scattered setae, however at least a small median area is bare of setae; median line absent or present; scapula regularly setose. Scutellum without submedian lines; with distinct sublateral lines which are laterally carinate; number of setae variable, from 4 (2 distinct pairs) to 13 (placed laterally but not distinctly paired). Dorsellum varying from roughly rectangular to more or less triangular or semicircular in shape. Propodeum lightly sclerotised with a more or less distinct median carina; hind corner of propodeum usually appearing acute due to a distinct, posteriorly directed, pointed protuberance, although this protuberance may be reduced or absent (Figs 4-6); spiracle with entire rim exposed; callus with 6-15 setae.
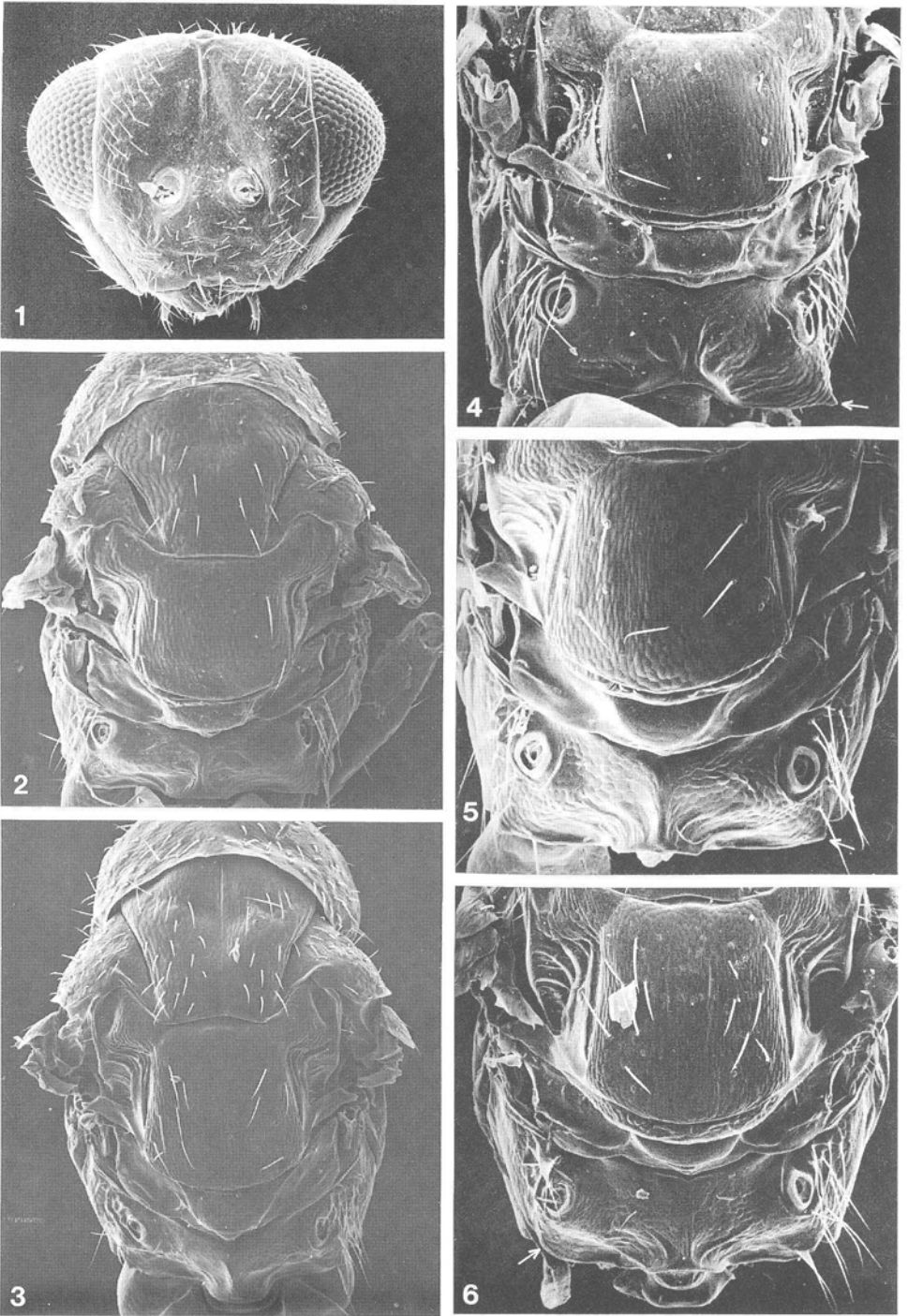
Figs 1-6: *Hadranellus anomatus* 9. 1, head (S, WD); 2, mesosoma (S, SD); 3, mesosoma (N, AK); 4, scutellum and propodeum (S, WD); 5, scutellum and propodeum (N, WI); 6, scutellum and propodeum (N, AK). Letters in parentheses indicate North Island (N) or South Island (S) plus geographic district (abbreviations from Crosby *et al. 1976*).
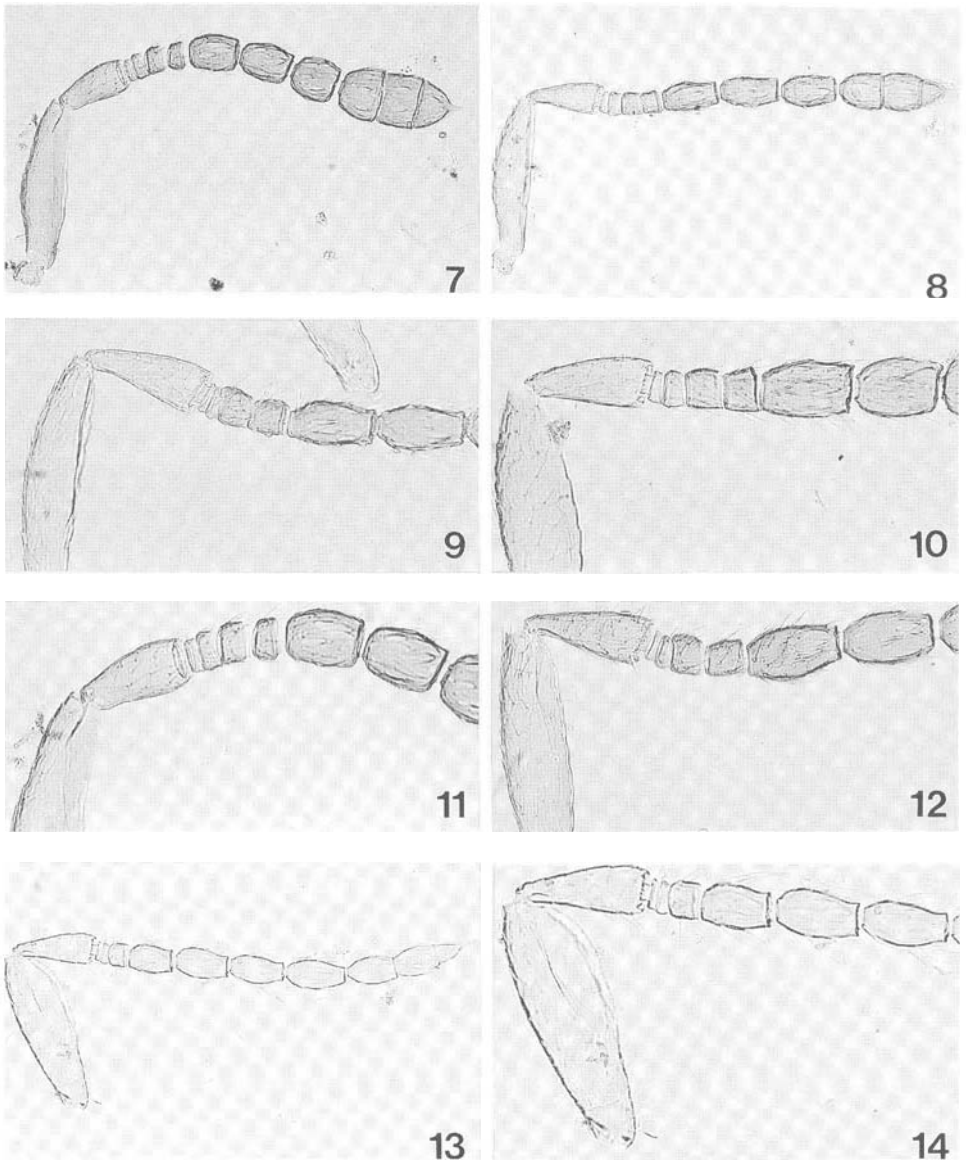
Figs 7-14: *Hadranellus anomalus.* 7, ♀ antenna (S, MC); 8, ♀ antenna (N, WI); 9, ♀ anelli (N, AK); **10,** ♀ anelli (S, NN); **11,** ♀ anelli (S, MC); **12,** ♀ anelli (N, AK); **13,** ♂ antenna (N, AK); 14, ♂ scape and anelli (N, AK). Letters in parentheses indicate North Island (N) or South Island (S) plus geographic district (abbreviations from Crosby *et al. 1976).*

Forewing (Figs 15-18). PMV present and distinct, variable in length from 0.4-1.0 the length of SV. Hyaline break usually present and distinct between parastigma and MV, sometimes weak or absent. Dorsal surface of SMV with 2-5 (usually 3 or 4) setae.

Gaster. Hypopygium extending from about half to slightly more than half the overall length of the gaster. Ovipositor sheaths slightly exserted. Cereal setae varying from having one of the cereal setae distinctly longer than the next longest and sinuate or curved, to having the two longest setae subequal in length and straight or only slightly curved.
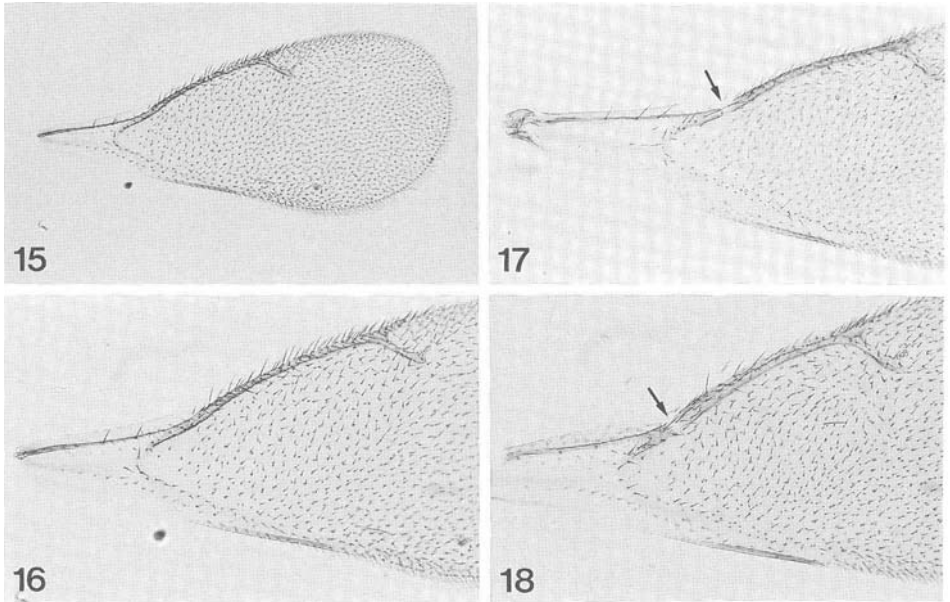
Figs 15-18: *Hadranellus anomalus,* ♀. 15, forewing (N, WI); 16, base of forewing (N, WI); 17, base of forewing (N, AK); 18, base of forewing (N, AK). Letters in parentheses indicate North Island (N) or South Island (S) plus geographic district (abbreviations from Crosby *et al. 1976).*

Male

Similar to female except in sexual characters. Antenna (Figs 13, 14) with 3 anelli and 4 funicular segments; scape slightly expanded; A1 and A2 anelliform, transverse; A3 quadrate, with several semi-erect setae. All funicular segments distinctly longer than wide, narrowed apically, and with numerous long, semi-erect setae; these setae not arranged in distinct basal whorls.

Etymology

The name *Hadranellus (hadros:* Greek - well-developed, stout; *anellus:* Latin - ring, circular) refers to the enlarged anelli in the female antenna.

Discussion

The characters given in the diagnosis will serve to distinguish *Hadranellus* from all other tetrastichine genera. In particular, the presence of four anelli, of which at least the last two are enlarged and bearing setae, immediately differentiate it. There are several other genera of Tetrastichinae which have four anelli, but in these genera the anelli are always transverse and without setae.

A few tetrastichine genera have antennae which bear a superficial resemblance to *Hadranellus.* The genus *Tetrastichomyia* (Holarctic, Africa) has three anelli, with A3 enlarged and setose; but this genus only has one large anellus (as opposed to two in *Hadranellus),* and differs in a number of other characters (see Graham 1987, 1991; LaSalle 1994). The genus *Quadrastichodella* (Australia, introduced elsewhere) has four distinct anelli, however these are all clearly transverse, and the scape and pedicel bear distinct rasp-like structures (see Boucek 1977, 1988; Graham 1987, 1991; LaSalle, 1994).

Relationships within the Tetrastichinae are as yet unresolved, and the relationship of *Hadranellus* to other tetrastichine genera is not clear. Graham (1987) provided a list of important characters in the Tetrastichinae, and hypothesized their primitive and derived conditions. *Hadranellus* appears to possess a combination of primitive and derived

characters. Unfortunately, many of the characters listed by Graham only serve to distinguish autapomorphic character states present in one or a few genera, or can be shown to have displayed reversals and/or convergences.

For example, *Hadranellus* possesses the following primitive characters: PMV at least half the length of SV; male antenna without distinct whorls of setae; propodeal spiracle with entire rim exposed; callus with three or more setae. It also has the following derived characters: scutellum without submedian lines; scutellum with deep sublateral lines which are laterally carinate. The precise relationships of *Hadranellus* will require an in-depth analysis of the Tetrastichinae.

Hadranellus anomalus, n.sp.
(Figs 1-18)

In addition to the characters given in the generic description:

Female

Length 1.25-2.0 mm. Head and body brown to dark brown or black, usually with at least a slight metallic shine. Coxae and legs light brown to yellow. Antenna with scape and pedicel yellow to light brown, flagellum brown. Sculpture as in photomicrographs.

Antenna (Figs 7-12). Length/width ratios of segments as follows: scape 3.5-4.4; pedicel 2.0-2.5; F1 1.4-2.1; F2 1.3-2.0; F3 1.0-1.65; club 2.0-3.0. Combined length of anelli at least slightly longer (1.05-1.3 times) than F1.

Forewing (Figs 15-18). Very slightly infuscated, veins brown to light brown; usually with a hyaline break in the parastigma. Wing vein ratios (length) as follows: CC/MV 0.9-1.4; MV/PMV 2.7-7.0; MV/SV 2.5-4.0; PMV/SV 0.4-1.0.

Male

Length 1.1-1.65 mm. Similar to female in colour and non-sexual characters. Antenna (Figs 13, 14) with length/width ratios of segments as follows: scape 2.8-3.5; pedicel 2.3-2.75; F1 1.4-1.5; F2 1.4-1.75; F3 1.75-2.1; F4 1.75-2.2; club 3.9-4.4. Combined length of anelli from 0.7-1.2 times the length of F1. Ventral sensory plaque (Fig. 14) about half the length of the scape and placed distally.

Material examined

Regional abbreviations are taken from Crosby *et al.* (1976).

Holotype ♀, New Zealand, North Island, Auckland, Lynfield, Wattle Bay, 5.iii.1977, G. Kuschel (NZAC).

104 ♀, 23 ♂ paratypes. All specimens from New Zealand. All specimens deposited in NZAC unless indicated otherwise.

North Island. ND, Waipoua Forest, 7.xii.1961, G. Kuschel, from leaf mould (2 ♀ 1 ♂ USNM); ND, Waipoua Forest, 7.xii.1961, ex. litter (7 ♀ 1 ♂); ND, Poor Knights Island, Tawhiti Rahi, xii.1980, malaise trap (1 ♀); ND, Omahuta SF, 6.x.1980, J. S. Noyes (1 ♀ BMNH); AK, Murphy's Bush, Flat Bush, 30.viii.1977, J. C. Watt, dead rachides (2 ♀ : ANIC, NZAC; 1 ♀ 1 ♂ LAS; 1 ♀ : BPBM, UCR, UCD); AK, Lynfield, 29.iii.1975, G. Kuschel, litter (1 ♀); AK, Lynfield, 10.x.1975, G. Kuschel (2 ♀ CNC); AK, Lynfield, 3.iv.1979, G. Kuschel, malaise trap (1 ♀ BMNH); AK, Lynfield, iv.1980, G. Kuschel (1 ♀); AK, Lynfield, x.1980, G. Kuschel, malaise trap (1 ♀ BMNH); AK, Lynfield, i.1981, G. Kuschel (2 ♀ 1 ♂ USNM); AK, Titirangi, 28.iv-6.v.1980, P. A. Maddison, malaise trap (1 ♀ 1 ♂ BMNH); AK, Titirangi, iv.1980, P. A. Maddison, malaise trap (1 ♀ 1 ♂); AK, Titirangi, xi.1980, G. W. Ramsay, malaise trap (1 ♀ : BMNH, NZAC); AK, Massey, 28.xii.1979, E. W. Valentine, malaise trap (1 ♀ : BMNH, NZAC); AK, Massey, 3.i.1981, E. W. Valentine (1 ♂ BMNH); AK, Huia, x.1980, B. M. May, malaise trap in bush (1 ♀ BMNH); AK, Huia, xi.1980, B. M. May, malaise trap in bush (1 ♀); AK, Huia, ii.1981, B. M. May, malaise trap in bush (1 ♀ LAS); AK, Birkenhead, x.1980, J.F. Longworth, Malaise trap in second growth bush (1 ♀ : BMNH, NZAC); AK, Waitakere Ra, xi.1980, J. S. Noyes (2 ♀ BMNH); AK, Pollock, 17.ix.1958, R. A. Cumber (1 ♀); BP, L. Rotoiti Res., N. Rotorua, 24-29.iii.1978, S. & J. Peck (1 ♀ : CNC, NZAC); TO, Tongariro NP, Upper Tongariro R., 28.xii.1970-3.i.1971, H. A. Oliver, malaise trap in *Nothofagus* forest (1 ♀); WN, Otaki, 6 km. SSE Otaki, 7.iii,1978, J. S. Dugdale, fungus on logs (1 ♀).

South Island. SD, Ship Cove, 27-30.xi.1972, J. McBurney, litter (11 ♀ NZAC; 6 ♀ BMNH; 2 ♀ ANIC; 1 ♀ : BPBM, UCD, UCR); NN, Whangamoa Saddle, 31.i.1978, A. K. Walker, sprayed rotten wood (1 ♀); NN, Whangamoa Saddle, 27.i-3.ii.1979, A. K. Walker & L. Mound, *Nothofagus* forest (1 ♀); NN, Motueka, Takaka Hills, Canaan Saddle, 1.ii.1978, S. & J. Peck (1 ♀ CNC); NN, Pelorus Bridge, 4.xii.1980, J. S. Noyes, E. Valentine, A. K. Walker, *Podocarpus* forest (1 ♂ BMNH); NN; Farewell Spit, 13.xii.1980, J.S. Noyes, E. Valentine, A.K. Walker, under *Leptospermum* (1 ♂); BR, Lower Buller Gorge, 16.xii.1970, H. A. Oliver, malaise trap (5 ♀ 1 ♂ NZAC; 4 ♀ BMNH); BR, Lake Rotoiti, 4-9.ii.1978, S. & J. Peck, malaise trap (2 ♀ 3 ♂ NZAC; 1 ♀ 2 ♂ BMNH; 1 ♀ 1 ♂ : CNC, LAS, USNM); BR, Lake Rotoiti, 24.iii.1977, A. K. Walker, sweeping seeding *Agrostis tenuis* (1 ♂); BR, Lake Rotoroa, 11.xii.1980, J. S. Noyes, E. Valentine, A. K. Walker (1 ♀ BMNH); BR, Punakaiki, 29.xii.83-3.i.1984, L. Masner, malaise trap (1 ♀ CNC); BR, 10 mi. E. Reefton, 5.ii.1979, L. A. Mound (1 ♀); MB or KA, Clarence Valley, 12.ii.1969. E. W. Valentine, swept grasses (1 ♀); WD, Hokitika, L. Mahinapua Res., 20 m, 26-30.i.1978, S. & J. Peck, *Podocarpus* bog, malaise trap (3 ♀ 2 ♂ NZAC; 2 ♀ 1 ♂ CNC); WD, Jackson Bay, 13-14.ii.1977, T. K. Crosby, malaise trap (1 ♀); MC, Birdlings Flat, 17.xi.1976, J. S. Dugdale, litter (8 ♀ NZAC; 2 ♀ LAS); OL, Makarora, 21-24.i.1978. S. & J. Peck, *Nothofagus* forest edge, malaise trap (1 ♀); FD, rd to L. Hauroko, 2.ii.1968, J. I. Townsend, moss (1 ♀).

Biology

Not known. Habitat associations include from dead rachides, leaf litter, leaf mould, native bush, second growth bush, *Nothofagus* [Fagaceae] forest, *Podocarpus* [Podocarpaceae] forest, *Podocarpus* bog, fungus on logs, sprayed rotten wood, under *Leptospermum* [Myrtaceae], sweeping seeding *Agrostis tenuis* [Poaceae], swept grasses and moss.

Variation

This species shows a great deal of intraspecific variation, and this variation does not appear to be linked to distribution or even always consistent with populations. Most characters (such as the number of setae on the SMV and the length of the postmarginal vein) display levels of variation which are fairly typical of species-level variation within Tetrastichinae. However, several characters show higher levels of variation. The most striking examples are: the anelli of the female antenna, setation of the scutellum, structure of the propodeum, presence or absence of a hyaline break in the parastigma, and length of the cercal setae.

Anelli. Two main forms of antenna were distinguished: A2 small, only slightly longer than A1, and clearly less than half the length of A3 (type A; Fig. 9); A2 enlarged, distinctly longer than A1, and about half the length of A3 (type B; Fig. 10). Variation did not clearly fall into only these two groups, and intermediate forms can be seen (Figs 11, 12).

The distribution of these antennae at first appeared to indicate a trend or cline from North Island (predominantly type A) to South Island (predominantly type B) populations. However, further examination showed exceptions to this trend. Examples of type A antenna were found on the North Island in the north (Northland, Auckland, Bay of Plenty) and in the south (Wellington), and on South Island in the northwest (Buller, Nelson) and the northeast (Marlborough, Kaikoura). Examples of type B antenna were found on North Island in the central regions (Taupo, Wanganui), and on South Island in the northeast (Marlborough Sounds) and central and southern regions (Westland, Mid Canterbury, Fiordland), giving a disjointed distribution. Populations from the South Island regions of Westland and Mid Canterbury in particular contained examples exhibiting grades of antennal form between the two types.

The preponderance of specimens with type B antenna in central North Island and in central and southern South Island initially suggested that the variation might be related to altitude, since these areas are predominantly mountainous. However, all the specimens from the lowland coastal promontory of Ship Cove in the Marlborough Sounds, South Island, also exhibited type B antenna.

The variation in A3 and A4 should also be noted (Figs 9-12). Although both A3 and A4 are usually more or less quadrate (Figs 9, 10, 12), in some cases they are both distinctly wider than long (Fig. 11). Also, A3 can be longer than A4 (Fig. 10), shorter than A4 (Fig. 12), or about equal in length (Fig. 9).

Setation of the scutellum. The number of setae on the scutellum varies from 4 setae which are placed in 2 distinct pairs (Figs 2, 4) to 13 setae which are placed laterally but not arranged in distinct pairs (Figs 3, 6); with a complete range of intermediate forms (Fig. 5). As with the previous character, initial examination suggested the presence of a geographical cline. Specimens from the North Island (Auckland, Bay of Plenty and Wellington) had high numbers of scutellar setae (range 4-13, average 9.1); specimens from the South Island (Marlborough Sounds, Nelson, Buller, Westland, Mid Canterbury, Otago Lakes, Fiordland) had low numbers of scutellar setae (range 4-8, average 4.6). However, there are specimens from the northern part of the North Island (Northland) which also had low numbers of scutellar setae (range 4-8, average 5.3), similar to those from the South Island.

Structure of propodeum. The hind corner of the propodeum (Figs 4-6, arrow) can vary from appearing acute due to having a distinct, posteriorly directed, pointed protuberance (Fig. 4) to appearing evenly rounded due to the absence of this protuberance (Fig. 6), although most specimens show at least a small protuberance (Fig. 5). This character showed no geographical tendencies, and variation existed in all samples assessed.

The shape of the dorsellum should also be noted (Figs 4-6), as it varies from almost rectangular (Fig. 4) to more or less triangular or semicircular (Figs 5, 6).

Hyaline break in parastigma. The parastigma of the forewing usually has a hyaline break of at least moderate strength in the venation between the submarginal vein and the marginal vein (Figs 17, 18, arrow), however this break is sometimes absent (Fig. 16). The absence of the break only occurs rarely.

Cercal setae. The cercal setae vary from having one of the cercal setae distinctly longer than the next longest and sinuate or curved, to having the two longest setae subequal in length and straight or only slightly curved. As with the previous two characters, this shows no geographical trends.

DISCUSSION OF VARIATION

The reason for this intraspecific variation in *H. anomalus* is not clear, but it appears that many insect species endemic to New Zealand may have exceptionally high levels of intraspecific variation. Mound & Walker (1986: 49) discussed their new genus *Deplorothrips* (Thysanoptera: Phlaeothripidae) and concluded that, "Unfortunately it is not possible at present to decide whether the available material represents only highly variable species or a series of intergrading species, each of which is itself variable."

Harris (1987) found considerable amounts of variation in New Zealand spider wasps (Pompilidae). In addition to extreme levels of what might be considered as "normal" variation, he also noted that "Teratological abnormalities affecting the body, appendages, and wing venation are surprisingly frequent, and occur in all species" (*loc. cit.*, p. 13).

Noyes (1988) also addressed this subject, discussed and illustrated several examples, and pointed out that within the Encyrtidae, "This variation is often so extreme that given small, isolated samples of a single species it is very easy to accept that several species may be present. However, with larger samples it becomes impossible to divide the material into discrete morphological segregates." (*loc. cit.*, p. 17).

This is indeed the case with *H. anomalus*. Initial examination led us to believe that two or possibly three species were present, but after studying a large number of specimens (n = 128), we found that we were unable to find any consistent means of separating this species into smaller units. In particular, there was no correlation between variation displayed by any single character with variation seen in other characters, and there was no consistent geographic correlation with character variation. Noyes (1988) also found that for the most part variation did not appear to be linked to geographical distribution or altitude.

What was particularly surprising to us was the extent of variation displayed. Characters such as number of scutellar setae, size and shape of the anellar segments, presence of a pointed protuberance on the hind corner of the propodeum, presence of a hyaline break in the parastigma, and length of cercal setae are variable in *H. anomalus*; however, these

are all characters which have been considered sufficiently constant to have been used at the generic level in other parts of the world (Bouček 1977; Graham 1987, 1991; LaSalle 1994). We do not feel that this variation negates the value of these characters in tetrastichine systematics for other geographical regions, rather that it emphasizes the amount of variation found in New Zealand.

Intraspecific variation within parasitic Hymenoptera is well-known and can be caused by a variety of reasons. Unruh & Messing (1993) reviewed this subject, and gave several examples of such variation in response to abiotic factors, host suitability and susceptibility to toxins. However, such genetic variation does not generally manifest itself as differences in external morphology, but rather as geographic or host races, or differences in physiological characteristics such as fecundity or insecticide resistance.

Relatively few papers have discussed either the occurrence or causes of intraspecific morphological variation in parasitic Hymenoptera. High levels of intraspecfic variation in both colour and morphology have been recorded in the aphidiine genus *Aphidius* (Pungerl 1986), and the eulophid genus *Pnigalio* (Barrett *et al.* 1988), and Janzon (1986) showed that allometry could be responsible for some degree of structural variation in *Pteromalus* species.

Other studies have related this variation to specific factors. Differences in hosts have been shown to result in antennal differences in the families Scelionidae (Johnson *et al.* 1987) and Mymaridae (Huber & Rajakulendran 1988), and Meyerdirk & Moratorio (1987) showed that host could influence antennal structure, ovipositor and tibia length, and wing length and width in the mymarid *Anagrus giraulti*. Pinto *et al.* (1989) subjected isofemale strains (cultures started from a single parthenogenetic female) of *Trichogramma* to differing environmental conditions and found that differences in temperature and host could cause distinct morphological differences in these genetically similar individuals.

Although host information is not known for *H. anomalus*, this species has been collected from a variety of different habitats, and it could be that some factor associated with its host or habitat plays a role in producing the high amounts of variation. On the other hand, it has been suggested that rapid speciation into a variety of relatively recently vacated ecological niches could also be partly responsible (Noyes 1988). Conclusive evidence as to factors which might be responsible for high levels of intraspecific morphological variation in New Zealand remains to be found.

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