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Larval Characteristics and Generic Placement of Endemic Hawaiian Hemerobiids (Neuroptera)[1]

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ABSTRACT: The brown lacewings (Neuroptera: Hemerobiidae) have undergone a spectacular radiation on the Hawaiian Archipelago; currently 23 endemic micromine species are recognized, 19 of which were described by Perkins and four by Zimmerman. Recent systematics studies, using adult morphological characteristics, placed these lacewings in the cosmopolitan genus *Micromus.* Two of the Hawaiian species (*Micromus vagus* [from Hawai'i and Maui] and *M. rubrinervis* [from Hawai'i]) exhibit larval characteristics indicating a close relationship with *Micromus.* Both species have more larval traits in common with *Micromus* than with other hemerobiid genera. However, until larvae from the three other genera in Microminae become available, it is not possible to designate whether any of these larval traits are synapomorphic for *Micromus.* The results also indicate that phylogenetic analyses of the Hemerobiidae should include all instars and that interspecific comparisons should be made on equivalent semaphoronts.

OUR STUDY FOCUSES on one of Hawai'i's most diverse and fascinating groups of predatory insects, the endemic micromine brown lacewings (Neuroptera: Hemerobiidae). R. C. L. Perkins pioneered in the collection and systematic study of Hawaiian hemerobiids. He described 23 species, which were grouped into three new genera (Perkins 1899, 1910). Nineteen of these species remain recognized, and they include some with heavily scalloped wings, as well as flightless species with coriaceous forewings and rudimentary or no hind wings. Subsequent to Perkins' work, E. C. Zimmerman added four new species and compiled a comprehensive review of the group (Zimmerman 1957). Both Perkins and Zimmerman recognized numerous similarities between the endemic Hawaiian micromine species and the cosmopolitan genus *Micromus* (Perkins 1899, Zimmerman 1957), but they allocated the species among three genera, *Nesomicromus, Pseudopsectra,* and *Nesothauma.* More recently, all 23 species of micromine hemerobiids endemic to Hawai'i were included in *Micromus* (Monserrat 1990, Oswald 1993). No study has examined whether the Hawaiian micromine lineage is monophyletic.

Almost all previous systematic work on hemerobiids is based exclusively on the adult stage, and knowledge of hemerobiid larvae is generally poorly developed. Nevertheless, some detailed descriptions of hemerobiid larvae exist (e.g., Killington 1936, 1937, 1946, MacLeod 1960), and syntheses of the scattered larval descriptions are beginning to emerge (MacLeod 1960, Veenstra et al. 1990, Krakauer and Tauber 1996). These investigations indicate that the comparative morphology of the larvae will contribute substantially to the overall systematic analysis of the group (e.g., see MacLeod 1960, Krakauer and Tauber 1996).

Krakauer and Tauber (1996) described a suite of traits that distinguishes *Micromus* larvae from those of seven genera representing six subfamilies other than Microminae. Larvae in these seven genera share many of the traits expressed

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by *Micromus;* moreover, there are no studies of larvae from the three other micromine genera. Consequently, it is not possible to delineate whether any of the traits are synapomorphic for *Micromus* or to assign polarity to the character transformations. Despite these limitations, the suite of traits consistently separated *Micromus* larvae from the other genera. And, until hemerobiid larvae are subject to a general systematic study, a modified version of the previous comparison forms a useful basis for examining whether the larval morphology of the Hawaiian hemerobiids is consistent with their current placement in *Micromus.* Here we focus on two endemic species of Hawaiian hemerobiids, *Micromus rubrinervis* (Perkins) and *M. vagus* (Perkins).

Previously, the larva of only one endemic Hawaiian hemerobiid (*M. vagus*) was described (Terry 1908); unfortunately, that description is not sufficiently detailed to aid in generic comparisons. A subsequent reference to an endemic hemerobiid larva (Williams 1931) is questionable because the associated figure depicts a green lacewing larva (Neuroptera: Chrysopidae). Therefore, it is not surprising that the inclusion of the endemic Hawaiian brown lacewings within *Micromus* was based exclusively on adult characters.

Several Hawaiian insect taxa show single-island endemism (Howarth and Mull 1992); *M. rubrinervis* follows this pattern. This species is known only from mid- to high-elevation forests on the island of Hawai'i (Zimmerman 1957). In contrast, *M. vagus* has been recorded from all six of the main islands and an array of habitats, including, during the first half of the century, lowland agricultural fields (Terry 1908, Williams 1931, Zimmerman 1957). Adults of the two species are superficially similar, but differ in wing venation and terminalic structures.

MATERIALS AND METHODS

We examined larvae (F_1 offspring) of *M. vagus* that were reared from adults collected in Kīpuka Puaulu, Hawai'i Volcanoes National Park, on the island of Hawai'i (1993) and in the Waikamoi Forest Reserve, Ko'olau State Forest (north slope of Haleakalā, 1050–1300 m), on Maui (1989). Our larval specimens of *M. rubrinervis* originated from females collected at two sites on Hawai'i: Kīpuka Puaulu, Hawai'i Volcanoes National Park (1993), and Volcano, a small town east of the national park (1993). Voucher specimens are in the Cornell University Insect Collection (Lot no. 1205), the Bishop Museum (adults and larvae), and the Research Collection of Hawai'i Volcanoes National Park.

Field-collected adults were maintained in glass vials under a photoperiod of 16:8 (L:D); the temperature was 21 ± 1°C during the photophase and 18 ± 1°C during the scotophase. Humidity was kept high in the vials by enclosing them in a plastic bag containing moist paper towels. Adults were provided green peach aphids, *Myzus persicae* (Sulzer), every 1–3 days. Cotton plugs in the vials, which usually served as the substrate for oviposition, were removed daily when eggs were observed. Larvae were reared individually under the same photoperiod, temperature, and humidity as the adults. The diet consisted of green peach aphids and occasionally pea aphids, *Acyrthosiphon pisum* (Harris). Although psocids (but not aphids) are endemic to Hawai'i and presumably compose the usual prey of most Hawaiian hemerobiids, several *Micromus* species (including *M. vagus*) consume nonnative aphids in the field (Zimmerman 1957). All individuals were examined daily for molting or cocoon spinning.

Larvae were killed in KAAD solution (a mixture of kerosene, alcohol, glacial acetic acid, and dioxane [see Stehr 1987]) and stored in 95% ethanol. Specimens of each instar were cleared in a solution of 10% KOH for 2 days. Lateral incisions were made in large specimens to facilitate the removal of internal structures that did not clear adequately. Subsequently, larvae were moved to clearing fluid (lactic acid, phenol, and glacial acetic acid) mixed with double stain (lignin pink and acid fuchsin), where they remained for 1 day at 50°C. Larvae were then passed through a series of ethanol solutions (70%, 85%, 95%, at least 2 hr in each solution), followed by a 1:1 or 1:2 mixture of 95% ethanol and glycerin for 1 day. Finally, they were mounted in glycerin on depression slides.

The following structures were measured before specimens were cleared (Figure 1): width of head (greatest head width, including the eyes);

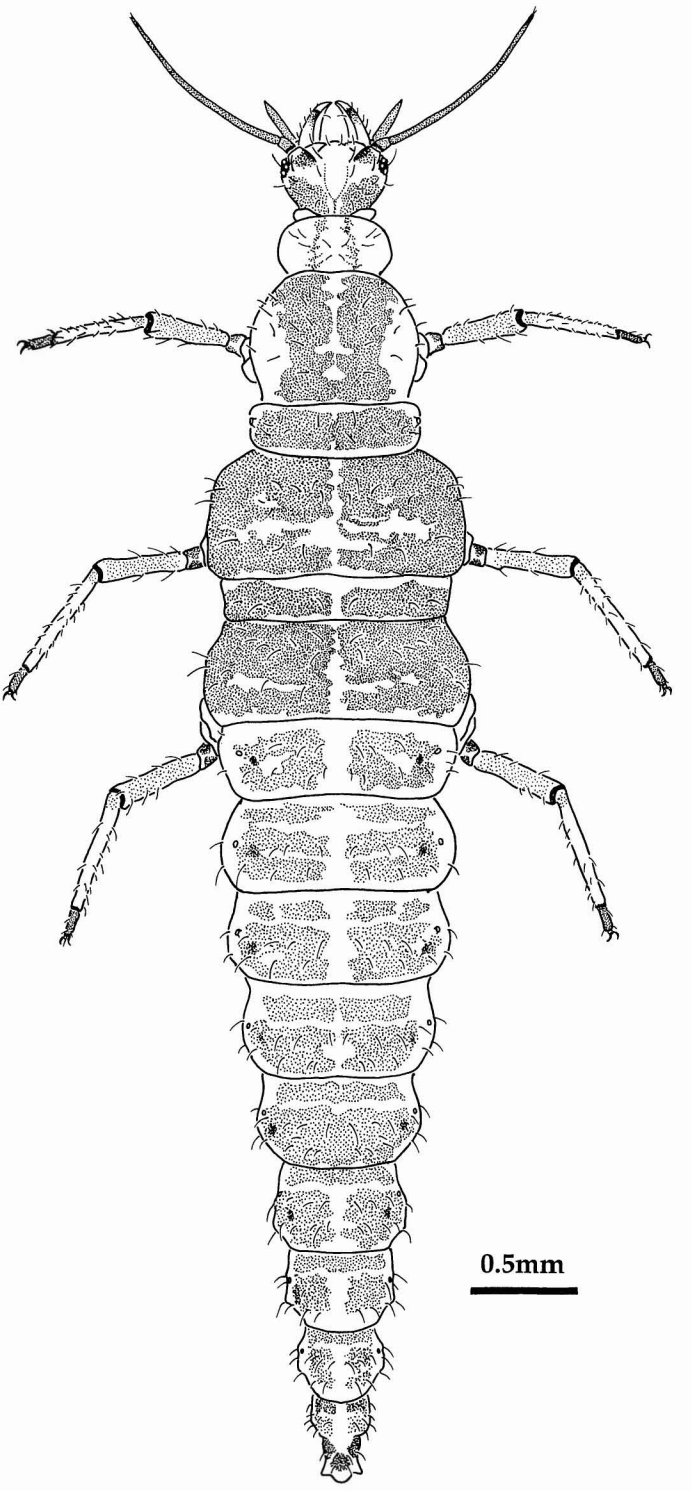

FIGURE 1. *Micromus vagus* third instar, dorsum.

length of head (medial, excluding jaws); length of jaws (straight-line distance from distal tip to medial margin of the base); length of flagellum; length of pedicel; length of scape (medial); length of labial palpi (excluding mentum); length of distal segment of labial palps; body length (tip of mandibles to tip of abdomen); length of cervix; width of cervix; widths of prothorax, mesothorax, and metathorax (maximum values); length of prothoracic, mesothoracic, and metathoracic tibiae; length of prothoracic, mesothoracic, and metathoracic tarsi (including tarsal claw, but not including pulvillus in first instars); length of the tinted portion (proximal) of the prothoracic, mesothoracic, and metathoracic tibiae. Cleared specimens were used to examine morphological detail and setal patterns. Comparisons between *M. rubrinervis* and *M. vagus* were made with a *t*-test of the differences between two means.

Character States of Hawaiian Species

Below we analyze the two Hawaiian species relative to 18 characters that previously were shown to differ among the larvae of hemerobiid genera (*Hemerobius:* Killington 1937, Nakahara 1954, Miller and Lambdin 1984, Krakauer and Tauber 1996; *Wesmaelius:* Killington 1937; *Sympherobius:* Killington 1937; *Psectra:* Killington 1946; *Drepanacra:* New 1975; *Megalomus:* Killington 1937, MacLeod 1960; *Drepanepteryx:* Fulmek 1941; *Micromus:* Killington 1936, Kawashima 1958, Miller and Cave 1987, Krakauer and Tauber 1996). Three traits (nos. 1, 2, and 5 below) separate *Hemerobius, Wesmaelius, Drepanepteryx,* and *Micromus* from *Sympherobius, Psectra, Drepanacra,* and *Megalomus.* Additional traits distinguish *Micromus* from *Wesmaelius* (nos. 4 and 5), and a suite of five traits delineates *Micromus* from *Hemerobius* (nos. 6–10). Only one trait (no. 3, the fused pedicel and flagellum) distinguishes *Micromus* from *Drepanepteryx,* the genus that in our comparison is most closely related to *Micromus* (see Oswald 1993).

(1) HEAD CAPSULE–CERVIX RELATIONSHIP (second and third instars): (a) protracted, (b) retracted. In *Sympherobius, Psectra, Drepanacra,* and *Megalomus* the head capsule is greatly recessed into the cervix; whereas in *Hemerobius, Wesmaelius, Drepanepteryx,* and *Micromus,* it extends beyond the cervix. The head capsules of most of our specimens of *M. rubrinervis* and *M. vagus* are protruding (Figure 1); any variability in this character is an artifact of preservation; the head capsules of the living larvae were not retracted.

(2) ANTENNA: JAW RATIO (third instars): (a) >1.2, (b) <1.2. Unlike those in *Sympherobius, Psectra, Drepanacra,* and *Megalomus,* the antennae of *Hemerobius, Wesmaelius, Drepanepteryx,* and *Micromus* extend well beyond the jaws. Although the antennal lengths of *M. rubrinervis* and *M. vagus* differ (Appendix 1), in both species the antennae are at least 1.6 times longer than the jaws (Table 1). Veenstra et al. (1990) proposed a second measure of relative antennal length (i.e., in proportion to the width of the head). In third instars of *Sympherobius, Psectra, Drepanacra,* and *Megalomus,* the antennae are shorter than the width of the head capsule. In *Hemerobius, Wesmaelius, Drepanepteryx,* and *Micromus,* including *M. vagus,* the antennae are longer than the width of the head (Table 1). In *M. rubrinervis* they are subequal to the width of the head.

Relative antennal length may also distinguish *Micromus* from *Hemerobius* (see trait 11 below).

(3) PEDICEL AND FLAGELLUM: (a) fused, (b) articulated. In the six genera for which data are clear (Table 2), the two distal antennal segments are separate and articulated, whereas in *Micromus* they appear united. The antennal segments appear fused in *M. rubrinervis* and *M. vagus.*

(4) FLAGELLAR LENGTH: (a) > terminal seta, (b) < terminal seta. An extremely shortened flagellum is unique to *Megalomus* (MacLeod 1960). The two Hawaiian species have flagella that are much longer than the terminal setae (Figure 1).

(5) TERMINAL SEGMENT OF LABIAL PALP: (a) not swollen, (b) bulbous. Swollen or bulbous palps characterize *Sympherobius, Psectra, Drepanacra,* and *Megalomus* larvae. With one exception (*Micromus tasmaniae* Walker [New and Boros 1983]), *Micromus* species, including the two from Hawai'i, share unmodified (elongate and fusiform) palps (Figure 1).

(6) JAW LENGTH: HEAD WIDTH RATIO (second and third instars): (a) <1.5, (b) ≥ 1.5. Exceptionally long larval jaws (ratio of jaws: width of

TABLE 1

MORPHOMETRICS OF *M. vagus* AND *M. rubrinervis* LARVAE

COMPARISON	INSTAR	RATIO (range)	
		M. rubrinervis[a]	*M. vagus*[b]
Antennal length/jaw length	3rd	1.6–1.9	3.0–3.7
	2nd	1.5–1.7	2.6–3.4
	1st	1.5–3.3	2.2–4.2
Antennal length/head width	3rd	1.0–1.1	1.8–2.4
	2nd	1.0–1.3	1.7–2.2
	1st	1.1–1.9	1.8–2.2
Cervical length/width	3rd	0.7–1.0	0.4–0.7
	2nd	0.6–0.9	0.3–0.7
	1st	0.5–0.7	0.3–0.6
Prothoracic tarsal length/tibial length	3rd	0.3–0.4	0.2–0.3
	2nd	0.3–0.5	0.3–0.4
	1st	0.4–0.5	0.4–0.5
Length of tibial marking/total tibial length	3rd	1.0	0.2–0.3
	2nd	1.0	0.2–0.5
	1st	0.1–1.0	0.1–0.5
Pedicelar length/flagellar length	3rd	1.2–1.9	1.7–2.3
	2nd	1.1–1.4	1.4–1.7
	1st	0.7–1.3	1.0–1.2
Distal palpal segment length/total palpal length	3rd	0.8–0.9	0.7–0.8
	2nd	0.8–0.9	0.7–0.8
	1st	0.7–0.8	0.7–0.8

[a] Sample size: $n = 10$ (five individuals of each instar from each of two field-collected females).
[b] Sample size: $n = 15$ (five individuals of each instar from each of three field-collected females).

head capsule ≥ 1.5) distinguish *Wesmaelius* larvae from those of other genera (e.g., Veenstra et al. 1990). Neither Hawaiian species has particularly long jaws (ratio of jaw length: width of head capsule <1.0) (Appendix 1).

(7) CORONAL SUTURE: (a) present, (b) absent. In *Hemerobius* and perhaps *Wesmaelius* larvae the coronal suture is absent, and the genae are separated by the frons, which extends to the posterior margin of the head capsule (Killington 1937, Krakauer and Tauber 1996). In all other genera, the coronal suture is present and the right and left genae meet medially on the dorsum of the head capsule. Among *Micromus* species, the length of the coronal suture varies (compare *M. posticus* [Miller and Cave 1987] with *M. paganus* L. [Veenstra et al. 1990]). In the two Hawaiian species, the suture is readily apparent (Figure 1).

(8) PLEUROSTOMAL SUTURE (second and third instars): (a) unbifurcated, (b) bifurcated. In *Hemerobius* and perhaps *Wesmaelius* larvae a branch of the pleurostomal suture extends below the eyes (see figure 2 in Krakauer and Tauber [1996], also Killington [1937]). *Micromus* species, including the Hawaiian species, lack such a branch. The character state of the other genera is unknown. *M. rubrinervis* larvae occasionally show stemmatal pigmentation that superficially resembles the subocular arm of the pleurostomal suture, but the suture itself does not extend below the eye.

(9) GENAL COLORATION: (a) genae darker than frons, (b) genae lighter than frons. *Hemerobius* larvae generally possess a dark frons and light genae; in *Psectra, Megalomus,* and *Micromus* the genae are as dark as or darker than the frons. The state of this character is unclear for the other genera. Although head coloration differs between *M. rubrinervis* and *M. vagus,* the genae are at least as dark as the frons in both species.

(10) PROTHORACIC SCLERITE: (a) present, (b) absent. Extreme reduction or loss of the prothoracic sclerites apparently is unique to *Megalomus* (MacLeod 1960). Prothoracic sclerites are prominent on both of the Hawaiian species.

(11) MESO- AND METATHORACIC SCLERITES: (a) prominent, (b) reduced. Reduced meso and/

TABLE 2

DISTRIBUTION OF CHARACTER STATES AMONG LARVAE OF EIGHT HEMEROBIID GENERA AND TWO HAWAIIAN SPECIES

NO.	CHARACTER STATE	DISTRIBUTION[a]								
		Hem	*Wes*	*Sym*	*Pse*	*Dra*	*Meg*	*Drx*	*Mic*	*Haw*
1.	Head capsule–cervix									
	(a) protracted, (b) retracted	a	a	b	b	b	b	a?	a	aa
2.	Antenna: jaw ratio									
	(a) > 1.2, (b) < 1.2	a?	a?	b	b	b	b	a	a	ab
3.	Pedicel and flagellum									
	(a) fused, (b) articulated	b	b	b	b	?	b	b	a	aa
4.	Flagellar length									
	(a) > terminal seta, (b) < terminal seta	a	a	a	a	a	b	a	a	aa
5.	Terminal segment labial palps									
	(a) fusiform, (b) bulbous	a	a	b	b	b	b	a?	a	aa
6.	Jaw length: head width									
	(a) < 1.5, (b) > 1.5	a	b	a	a	a	a	a	a	aa
7.	Coronal suture									
	(a) present, (b) absent	b	b?	a	a	?	a	a	a	aa
8.	Frontal suture, posterior margin									
	(a) curved, (b) acute	b	b?	a	?	?	b	a	a	aa
9.	Pleurostomal suture									
	(a) unbifurcated, (b) bifurcated	b	?	?	?	?	?	?	a	aa
10.	Prothoracic sclerite									
	(a) present, (b) absent	a	a	a	a	a	b	a?	a	aa
11.	Meso- and metathoracic sclerites									
	(a) present, (b) absent	a	?	b	b	?	a	b	a	aa

NOTE: *Hemerobius* and *Wesmaelius* represent Hemerobiinae; the other genera each represent a single subfamily (see Oswald 1993). See text for descriptions of characters.

[a] *Hem, Hemerobius:* Killington 1937, Nakahara 1954, Miller and Lambdin 1984, Krakauer and Tauber 1996; *Wes, Wesmaelius;* Killington 1937; *Sym, Sympherobius:* Killington 1937; *Pse, Psectra:* Killington 1946; *Dra, Drepanacra:* New 1975; *Meg, Megalomus:* Killington 1937, MacLeod 1960; *Drx, Drepanepteryx:* Fulmek 1941; *Mic, Micromus:* Killington 1936, Kawashima 1958, Miller and Cave 1987, Krakauer and Tauber 1996; *Haw, Macromus vagus* and *M. rubrinervis,* respectively.

or metathoracic sclerites characterize some genera whose larvae have heads that are retracted into the prothorax (e.g., *Sympherobius* and *Psectra*) (Killington 1937, 1946, MacLeod 1960). Meso- and metathoracic sclerites are prominent on both Hawaiian species.

Seven additional characters distinguish the *Hemerobius* spp. from the *Micromus* spp. that Krakauer and Tauber (1996) studied. Information on the character states of other taxa is not available, but we include the traits in this comparison because of the proposed close relationship between the Hawaiian species and *Micromus. M. vagus* and *M. rubrinervis* vary in the expression of some of these traits; both have the *Micromus* pattern in four of them.

(12) ANTENNAL LENGTH: JAW LENGTH RATIO: (a) >2.0, (b) <2.0. *Hemerobius* larvae usually have antennal: jaw ratios between 1.0 and 2.0, whereas in *Micromus* larvae, the antennae are at least twice the length of the jaws. In each instar of *M. vagus,* the antennae are almost three times the length of the jaws (Table 1). Most first instars of *M. rubrinervis* also have long antennae; however, in second and third instars, the antennal length is slightly less than twice the length of the jaws (Table 1). We suggest that the antennae of the second and third instars are secondarily reduced in *M. rubrinervis.*

(13) FRONTAL SUTURE, POSTERIOR MARGIN: (a) curved, (b) acute. In *Hemerobius,* the right and left arms of the frontal suture meet posteriorly in an acute angle (Killington 1937, Krakauer and Tauber 1996). Although the slope of the arms of the frontal suture may vary within *Micromus,* the posterior margin of the frontal suture is curved (U-shaped), not angular, in all species studied to date, including the two Hawaiian species (Figure 1).

(14) TRIANGULAR GENAL MARKING AT BASE

OF MANDIBLES (second and third instars): (a) dark, (b) light. In *Micromus,* the triangular area at the lateral base of the mandibles is much darker than the surrounding genal region. In *Hemerobius,* the area is pale. Of the two Hawaiian species, *M. rubrinervis* larvae have the dark *Micromus*-like triangular marking, whereas in *M. vagus* the area is not much darker than the surrounding genae.

(15) CERVICAL LENGTH: CERVICAL WIDTH RATIO: (a) ~1: 1, (b) <1: 1. Although cervical dimensions may vary among *Micromus* species, in general, a cervical length: width ratio of ~1: 1 distinguishes *Micromus* larvae from *Hemerobius* larvae (which usually have a shorter and wider cervix). The two Hawaiian species deviate from the *Micromus* pattern by having short, wide cervices. Some of this variation may result from differences in the degree of distention during preservation.

(16) LONGITUDINAL BANDING OF MESO- AND METATHORACES: (a) absent, (b) present. The dorsa of most *Hemerobius* species are banded longitudinally. By contrast, the meso- and metathoraces of most *Micromus* species have broad transverse bands anteriorly or are dark throughout (Killington 1936, Kawashima 1958, Miller and Cave 1987, Krakauer and Tauber 1996). *M. vagus* has the typical *Micromus*-like pattern (Figure 1 [also see Terry 1908]); whereas the thoracic segments of *M. rubrinervis* larvae lack dark markings.

(17) PROTHORACIC TARSAL: TIBIAL LENGTH RATIO: (second and third instars): (a) <0.33, (b) >0.33; (first instars): (a) <0.5, (b) >0.5. In contrast to *Hemerobius* larvae, *Micromus* larvae have relatively short tarsi. Although the first instars of both species and the second instars of *M. vagus* approach the *Micromus*-like pattern, second instars of *M. rubrinervis* and third instars of both species have relatively long tarsi (Table 1).

(18) PROTHORACIC SCLERITES, ORIENTATION OF ANTERIOR MARGIN (second and third instars): (a) curved medially or parallel to longitudinal body axis, (b) curved laterally. In the Nearctic *Micromus* larvae that we studied previously (Krakauer and Tauber 1996), the prothoracic sclerites are either sigmoid or crescentic, with anterior ends running parallel to the longitudinal body axis or curving medially; in *Hemerobius* they arch laterally. In *M. vagus* the sclerites are wedge-shaped; those in *M. rubrinervis* are either wedge-shaped or their anterior ends curve laterally. Thus the prothoracic sclerites of neither Hawaiian species fit the *Micromus* pattern.

Comparison of M. rubrinervis *and* M. vagus

Unlike the North American species of *Micromus* previously studied (Krakauer and Tauber 1996), *M. rubrinervis* and *M. vagus* differ in a large number of structural characters (Table 1), as well as in their coloration, chaetotaxy (Table 3), and morphometrics (Appendix 1). Several of these differences are discussed above (traits nos. 12–18). Below, we list additional traits that are useful in separating the two species; full descriptions of the larvae will be published elsewhere. Unless indicated otherwise, the traits apply to all three instars, and quantitative differences are significant ($P < 0.05$).

COLORATION OF HEAD CAPSULE (second and third instars). Genae and frons: *M. rubrinervis,* medium or dark brown; *M. vagus,* light or medium brown, except genae medium or dark brown posteriorly. First instars of both species generally have little pigmentation.

METATHORACIC SPIRACLES. *M. rubrinervis,* present; *M. vagus,* absent. The metathoracic spiracles in *M. rubrinervis* are much smaller than

TABLE 3

SETATION OF *M. vagus* AND *M. rubrinervis* LARVAE

SEGMENT	INSTAR	NO. OF SETAE (range) *M. rubrinervis*[a]	NO. OF SETAE (range) *M. vagus*[a]
Head (dorsum)	3rd	14–20	16
	1st	12–14	12
Head (venter)	3rd	16–18	12–14
	1st	8–12	8–12
Cervix	3rd	81–112	18–26
	1st	0	0
Prothorax	3rd	118–152	42–54
	1st	14	14
Abdominal segment 1	3rd	54–72	18–22
	1st	8–20	12–16
Abdominal segment 2	3rd	76–106	24–30
	1st	10–20	16–18

[a] Sample size: $n = 4$ (two individuals of each instar from each of two field-collected females).

the prothoracic spiracles. Only one other species of hemerobiid, *M. tasmaniae* Walker, is reported to have metathoracic spiracles (New and Boros 1983). The evolutionary implications of this presumably major morphological transition are currently unknown.

DORSAL SETATION. *M. rubrinervis,* dense; *M. vagus,* sparse (Table 3). The setation on *M. rubrinervis* second and third instars is remarkable among hemerobiid larvae. Both the number and the length of the setae resemble those of some chrysopid larvae (Tauber 1974, Tauber et al. 1992).

DISCUSSION

With one minor exception, *M. rubrinervis* and *M. vagus* larvae exhibit the suite of traits that characterizes *Micromus.* Thus, the morphological traits of the larvae as well as of the adults (see Oswald 1993) of the known endemic Hawaiian species are consistent with the inclusion of the Hawaiian micromine lineage in *Micromus.* At this point, several of these traits may be autapomorphic for *Micromus* (e.g., no. 3, the fused pedical and flagellum; no. 9, the unbifurcated pleurostomal suture; no. 14, the dark genal marking). However, because the larvae of the other three genera in Microminae are unstudied, these character states may indicate either generic or subfamilial relationships. Thus, support from larval morphology for placing the Hawaiian species in *Micromus* remains tentative until the larval characteristics of the other three micromine genera are examined.

We explain the contradictory (non-*Micromus*-like) characteristics of the two species (e.g., prothoracic sclerite shape, color of the genal marking, ratios of tarsal to tibial length, antennal length in *M. rubrinervis*) in two ways. First, the nonconforming traits may be generally variable within the genus, in which case our concept of what constitutes a *Micromus* larva may require modification when more larval material becomes available. Because the previous diagnosis was based on limited material (predominantly north-temperate species), it would not be surprising if the *Micromus* larval diagnosis were to change. The only Southern-Hemisphere species whose larvae are described (*M. tasmaniae* [see New and Boros 1983]) exhibits traits not found in other members of the genus (e.g., modified setae and palps). Larval specimens of additional micromine species from the Southern Hemisphere could provide valuable insight into the origin and relationships of the Hawaiian lineage.

Second, in some cases, taxa on isolated islands show more spectacular differentiation than do continental lineages. In many Hawaiian taxa, evolution has resulted in reversals, parallelisms, and convergences, as well as bizarre and unusual forms that are not evident in continental forms (e.g., Carlquist 1974, Williamson 1981). Any of these possibilities could have occurred during the radiation of the endemic Hawaiian hemerobiids.

The first instars of *M. vagus* and *M. rubrinervis* generally express the *Micromus* traits more consistently than do later instars. Moreover, the first instars of the two species resemble each other more closely than do the later instars. Such an ontogenetic pattern implies that first instars are evolutionarily more conservative than later instars (see Wheeler 1990*a,b* for a similar ontogenetic pattern in beetle larvae). Among the Hawaiian hemerobiids, this trend is evident in traits of the thorax and abdomen (e.g., setation, ratios of tarsal: tibial length, coloration), as well as the head (ratios of antennal: jaw length); and it highlights the value of including all instars in phylogenetic studies. It also supports the contention that for phylogenetic studies, comparisons should be made among individuals in comparable semaphoronts (Hennig 1966, Wheeler 1990*a*); comparisons across semaphoronts may be misleading.

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APPENDIX 1

MEASUREMENTS OF *M. rubrinervis* AND *M. vagus* LARVAE

STRUCTURE	INSTAR	(mean ± S.D., mm) *M. rubrinervis*[a]	*M. vagus*[b]
Body length	3rd	6.90 ± 0.49	6.39 ± 0.74
	2nd	4.59 ± 0.49	4.41 ± 0.40
	1st	3.02 ± 0.23	2.61 ± 0.24
Width of head	3rd	0.55 ± 0.03	0.54 ± 0.04
	2nd	0.43 ± 0.02	0.39 ± 0.03
	1st	0.31 ± 0.03	0.27 ± 0.01
Length of head	3rd	0.53 ± 0.04	0.48 ± 0.02
	2nd	0.41 ± 0.03	0.34 ± 0.03
	1st	0.28 ± 0.05	0.24 ± 0.02
Length of jaws	3rd	0.34 ± 0.03	0.32 ± 0.02
	2nd	0.29 ± 0.01	0.25 ± 0.01
	1st	0.22 ± 0.03	0.18 ± 0.03
Length of pedicel	3rd	0.34 ± 0.02	0.70 ± 0.04
	2nd	0.24 ± 0.08	0.44 ± 0.04
	1st	0.21 ± 0.05	0.27 ± 0.01
Length of flagellum	3rd	0.24 ± 0.02	0.36 ± 0.02
	2nd	0.20 ± 0.07	0.31 ± 0.02
	1st	0.23 ± 0.02	0.25 ± 0.02
Length of antenna (excluding scape)	3rd	0.59 ± 0.03	1.06 ± 0.05
	2nd	0.48 ± 0.02	0.75 ± 0.05
	1st	0.43 ± 0.06	0.52 ± 0.02
Length of scape	3rd	0.07 ± 0.01	0.09 ± 0.01
	2nd	0.05 ± 0.00	0.07 ± 0.01
	1st	0.04 ± 0.01	0.05 ± 0.01
Palpal length (total)	3rd	0.41 ± 0.02	0.48 ± 0.03
	2nd	0.34 ± 0.02	0.32 ± 0.09
	1st	0.27 ± 0.02	0.26 ± 0.02
Palpal length (distal segment only)	3rd	0.34 ± 0.02	0.35 ± 0.03
	2nd	0.27 ± 0.02	0.24 ± 0.06
	1st	0.22 ± 0.02	0.20 ± 0.01
Cervical length	3rd	0.46 ± 0.08	0.29 ± 0.05
	2nd	0.29 ± 0.04	0.19 ± 0.03
	1st	0.16 ± 0.02	0.12 ± 0.02

(continued)

APPENDIX 1

MEASUREMENTS OF *M. rubrinervis* AND *M. vagus* LARVAE

STRUCTURE	INSTAR	(mean ± S.D., mm)	
		M. rubrinervis[a]	*M. vagus*[b]
Cervical width	3rd	0.52 ± 0.03	0.53 ± 0.04
	2nd	0.38 ± 0.03	0.37 ± 0.03
	1st	0.27 ± 0.02	0.26 ± 0.03
Prothoracic width	3rd	0.73 ± 0.05	0.83 ± 0.06
	2nd	0.50 ± 0.03	0.53 ± 0.05
	1st	0.34 ± 0.03	0.33 ± 0.04
Mesothoracic width	3rd	1.00 ± 0.09	1.19 ± 0.11
	2nd	0.68 ± 0.04	0.76 ± 0.07
	1st	0 45 ± 0.05	0.47 ± 0.09
Metathoracic width	3rd	1.04 ± 0.09	1.21 ± 0.11
	2nd	0.70 ± 0.06	0.76 ± 0.08
	1st	0.45 ± 0.06	0.48 ± 0.09
Prothoracic tibial length	3rd	0.37 ± 0.02	0.63 ± 0.04
	2nd	0.29 ± 0.01	0.39 ± 0.03
	1st	0.22 ± 0.02	0.25 ± 0.01
Prothoracic tibial marking (length)	3rd	0.37 ± 0.02	0.12 ± 0.03
	2nd	0.29 ± 0.01	0.10 ± 0.05
	1st	0.15 ± 0.08	0.05 ± 0.01
Prothoracic tarsal length	3rd	0.12 ± 0.02	0.17 ± 0.02
	2nd	0.12 ± 0.02	0.13 ± 0.01
	1st	0.10 ± 0.00	0.12 ± 0.04
Mesothoracic tibial length	3rd	0.42 ± 0.03	0.66 ± 0.05
	2nd	0.30 ± 0.02	0.40 ± 0.03
	1st	0.23 ± 0.02	0.23 ± 0.08
Mesothoracic tibial marking (length)	3rd	0.42 ± 0.03	0.12 ± 0.03
	2nd	0.30 ± 0.02	0.09 ± 0.05
	1st	0.17 ± 0.08	0.06 ± 0.02
Mesothoracic tarsal length	3rd	0.14 ± 0.02	0.17 ± 0.02
	2nd	0.12 ± 0.02	0.14 ± 0.02
	1st	0.11 ± 0.02	0.12 ± 0.04
Metathoracic tibial length	3rd	0.49 ± 0.04	0.75 ± 0.05
	2nd	0.36 ± 0.03	0.44 ± 0.03
	1st	0.25 ± 0.02	0.25 ± 0.09
Metathoracic tibial marking (length)	3rd	0.47 ± 0.10	0.14 ± 0.05
	2nd	0.36 ± 0.03	0.11 ± 0.04
	1st	0.18 ± 0.09	0.06 ± 0.03
Metathoracic tarsal length	3rd	0.16 ± 0.02	0.18 ± 0.03
	2nd	0.13 ± 0.02	0.14 ± 0.02
	1st	0.12 ± 0.02	0.12 ± 0.02

[a] Sample size: $n = 10$ (five individuals of each instar from each of two field-collected females).
[b] Sample size: $n = 15$ (five individuals of each instar from each of three field-collected females).