INSECTS OF HAWAI'I

VOLUME 16
HAWAIIAN CARABIDAE (COLEOPTERA), PART 1:
INTRODUCTION AND TRIBE PLATYNINI

JAMES K. LIEBHERR
and
ELWOOD C. ZIMMERMAN

University of Hawai'i Press, Honolulu
2000
THE INSECTS OF HAWAII

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Department of Entomology
Comstock Hall
Cornell University
Ithaca, NY 14853-0901

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Front cover: Blackburnia polhemusui Liebherr
Back cover: Blackburnia fractistriata (Perkins)
INSECTS OF HAWAI'I

A Manual of the Insects of the Hawaiian Islands, including an Enumeration of the Species and Notes on Their Origin, Distribution, Hosts, Parasites, etc.

VOLUME 16
HAWAIIAN CARABIDAE (COLEOPTERA), PART 1:
INTRODUCTION AND TRIBE PLATYNINI

by JAMES K. LIEBHERR
Professor and Curator of Entomology
Cornell University
Research Associate in Natural Sciences, Bernice P. Bishop Museum

and ELWOOD C. ZIMMERMAN
Curator Emeritus
Australian National Insect Collection, C.S.I.R.O.

Line drawings by
Curtis P. Ewing

University of Hawai‘i Press
Honolulu
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ABSTRACT

The carabid beetle species of the tribe Platynini are revised for the Hawaiian Islands based on information from the adult stage. The 129 known species are considered member taxa of the genus Blackburnia Sharp, NEW STATUS. Twenty-two generic names previously used to classify the Hawaiian Platynini are placed in synonymy with Blackburnia. Primary types representing all available species and varietal names were examined, and lectotypes designated. Native species are arrayed in four subgenera: Protocaccus, NEW SUBGENUS, comprising one species, B. (P.) mandibularis, NEW SPECIES, of Kauai; Colpocaccus Sharp, NEW STATUS, with four species; Blackburnia, sensu stricto, with 51 species, of which 13 are newly described; and Metromenus Sharp, NEW STATUS, with 73 species, of which 19 are newly described. NEW SPECIES of the subgenus Blackburnia include B. atra, B. bryophila, and B. waialeale of Kauai; B. hihia of Oahu; B. polhemusi of Molokai; B. viridis, B. pukalaina, B. pilikua, B. polipoli, B. medeirosi, and B. kipahulu of Maui; and B. kukui and B. ewingi of Hawaii Island. NEW SPECIES of the subgenus Metromenus include B. kahili, B. asquithi, and B. pauma of Kauai; B. huhula, B. paludicola, B. paloloensis, and B. fordi of Oahu; B. platyophthalmica and B. hakeakapa of Molokai; B. ulaula, B. liliu, B. ipu, B. kuiki, B. abaxoides, B. auana, B. boveolata, B. bartletti, B. kauwa, and B. fulgida of Maui. NEW NAMES required to replace homonyms resulting from generic synonymization include: Blackburnia (Blackburnia) kamehameha = Anchoteffius gracilis Sharp, 1903; Blackburnia (Metromenus) komohana = Mecomenus koebelei Sharp, 1903; Blackburnia (Metromenus) haleakala = Mecostomus perkinsi Sharp, 1903; Blackburnia (Metromenus) kilauea = Atelothrus hawaiiensis Sharp, 1903; Blackburnia (Metromenus) lanaihalensis = Mesothriscus lanaiensis Sharp, 1903. The following NEW SYNONYMIES are proposed (senior synonyms first): Blackburnia (Colpocaccus) posticata (Sharp) = Colpocaccus marginatus Sharp; Blackburnia (Colpocaccus) hawaiensis (Sharp) = Colpocaccus apicalis Sharp; Blackburnia (Blackburnia) lucipetens (Blackburn) = Colpodiscus lahainensis Sharp; Blackburnia (Blackburnia) micans (Sharp) = Derobroscus politus Sharp and Derobroscus solitarius Sharp; Blackburnia (Blackburnia) brevipes (Sharp) = Disenochus flavitarsis Sharp; Blackburnia (Metromenus) muscicola (Blackburn) = Mesothriscus prognathus Sharp; Blackburnia (Metromenus) protorta (Blackburn) = Metromenus angustifrons Sharp; Blackburnia (Metromenus) kilauea = Mesothriscus hawaiiensis Sharp (junior homonym of Colpocaccus hawaiiensis Sharp) and Metromenus lentus Sharp (junior homonym of Pseudobroscus lentus Sharp); Blackburnia (Metromenus) fraterna Blackburn = Anchomenus scrupulosus Blackburn, Metromenus aequalis Sharp, and Metromenus velox Sharp; Blackburnia (Metromenus) pavidha Sharp = Mesothriscus truncatus Sharp; Blackburnia (Metromenus) sphodriiformis (Sharp) = Atelothrus limbatus Sharp, Atelothrus longicollis Sharp, Mesothriscus collaris Sharp, and Metromenus cinctus Sharp; Blackburnia (Metromenus) erro (Blackburn) = Atelothrus politus Sharp; Blackburnia (Metromenus) insociabilis (Blackburn) = Atelothrus stenopus Sharp.

Identification keys are provided to the tribes of Carabidae known from Hawaii, subgenera and species of native Hawaiian Platynini, and platynine species introduced to Hawaii. Native species treatments include diagnosis and description for newly recognized species or diagnostic combination for previously proposed species, line illustrations and habitus photo, distributional map, and natural history and phylogenetic information.
Taxonomic classification of the Hawaiian Platynini is based on cladistic analysis. The evolution of brachyptery has proceeded four times independently during the course of the platynine radiation. Two species are known cave troglobites, exhibiting reduced eyes and reduced cuticular melanization. These species are most closely related to moss-inhabiting taxa, suggesting that colonization of moss-covered voids in the forest floor was the means to enter lava tube caves. Phylogenetic relationships among the native species indicate that Kauai is the root of the current extant radiation, with progressive colonization of the Hawaiian Islands continuing throughout time since the origin of Kauai. Within-island vicariance has facilitated speciation on all of the islands. On the older island of Oahu, this has been followed by secondary dispersal, resulting in many broadly sympatric species within the Waianae and Koolau Ranges. This secondary mixing has been largely restricted to present rain forest habitats, as 22 of the 32 Oahu species remain restricted to either the Waianae or the Koolau. Vicariant barriers are especially evident on the sunken and fragmented island of Maui Nui, where endemic relatives can often be found on Molokai, West Maui, and Haleakala. Haleakala is the site of the most loss of biodiversity, through the loss or disturbance of mesic forests of koa (Acacia koa A. Gray) that housed numerous species collected in the 1870s to 1890s. On all the islands, evident losses of species are concentrated in the drier, leeward communities. The most dramatic reduction in populations has been the loss of B. (Colpocaccus) tantalus from Oahu. Though this species was distributed across the island, and constituted 40% of specimens in the nineteenth century, it has not been seen since 1940.

Three adventive platynine species are also treated taxonomically: Laemostenus complanatus (Dejean), Calathus ruficollis (Dejean), and Metacolpodes buchanani (Hope). The first colonized Hawaii Island about 1950 and has expanded its range throughout much of the drier forests of Mauna Kea and Mauna Loa. Calathus ruficollis, a native of the Pacific coast of North America, is found on Oahu, and was probably introduced from San Diego. Metacolpodes buchanani, native to Asia but also introduced to Oregon, was introduced to Oahu in or before 1991, and by 1999 had expanded its range to include Kauai, Molokai, Maui, and the island of Hawaii.
The mountain rises by itself out of the turning night
out of the floor of the sea and is the whole of an island
alone in the one horizon alone in the entire day
as a word is alone in the moment it is spoken . . . (Merwin 1998)

HAWAIIAN NATURAL HISTORY

The occurrence of a linear array of isolated islands, situated in a tropical region of persistent trade winds, provides ideal conditions for evolution of a diverse array of life forms. Isolation ensures that colonization of the island chain is a rare event. Indeed, the Hawaiian Islands were first found by human colonists, most likely voyaging from the Marquesas Islands, some time between 300 and 750 A.D. (Kirch 1998). The developing Hawaiian culture became totally isolated for centuries before the Islands were rediscovered by Captain James Cook in 1778. Islands arising from the action of a deep-mantle thermal plume have existed in the mid-Pacific near the position of the present-day Hawaiian Islands for upwards of 70 Ma (Clague & Dalrymple 1989). These islands have resulted from sequential activity of at least 129 volcanoes (Clague 1998) over the course of the Pacific Plate’s northwestward movement above the Hawaiian thermal plume. Hawaiian volcanoes occur along two parallel tracks, resulting in islands that often represent the fusion of one or more pairs of individual volcanoes. This topographic diversity within islands, coupled with moderate isolation of one island from the next along this linear array, has created opportunities for continual within-archipelago colonization that has built upon the much rarer colonization events from outside the archipelago. Though changes in climate resulted in vertical shifts in vegetation zones during the Quaternary, available evidence supports the persistence of northeasterly trade winds as well as greater precipitation during glacial periods over that period (Loope 1995). Only in those rare times when there were no subaerial lands, due to faster erosion than island building, has this tropical moisture been allowed to continue untapped across the Pacific. Whenever high Hawaiian Islands have been in existence—and it is estimated that some have been present for the past 29 Ma (Carson & Clague 1995)—subtropical storms from the northeast or tropical air masses from the south would have bathed these mountains in torrential rainfall, allowing development of dense rain forests. Rainfall occurs consistently season to season in most of the windward montane regions, with more than 40 cm of rain—sometimes over 200 cm—falling each month on windward sides of the high islands (Price 1983). This high rainfall leads to rapid erosion. This is accompanied by cataclysmic landslides that have sundered huge portions of each island (Moore et al. 1989). The growing weight of new islands depresses the Pacific Plate, and this causes subsidence of both those islands and others near them (Moore 1987, Moore et al. 1990). These combined forces eventually submerge each island. Soil development proceeds in this system through two distinct periods: an initial geologically short period when weathering makes primary minerals available to colonizing plants (Vitousek et al. 1997), followed by a long period during which only allochthonous input of nutrients—sea foam dissolved in fog drip and desert dust blown from Asia—provides minerals to support luxuriant forest growth (Kennedy et al. 1998). This combination of climatic stability over the short term, habitat persistence over the long term, and habitat isolation within the archipelago optimally sets the stage for the development of
specialization (Southwood 1977) in those taxa able to exploit Hawaiian habitats. Species-level radiations of Hawaiian insects, like those of few other places, are characterized by an immense diversity of geographically restricted species displaying amazingly specialized life histories (Zimmerman 1970, Howarth 1990).

**HAWAIIAN CARABID BEETLES**

Carabid beetles are the numerically dominant terrestrial predatory insects in native Hawaiian wet forests. They occupy forests from 400 m elevation to timberline. Several species live in more leeward situations, in open savannah and scrub formations dominated by plants such as hairgrass (*Deschampsia nubigena* Hillebrand) and mamane (*Sophora chrysophylla* Salisbury). Others are found along streams, or on isolated woody plants living in bogs. Only a few species live in more extreme environments, such as open talus and aeolian habitats above timberline, or in caves. Given this pattern of occurrence, most native Hawaiian carabid taxa appear to be moisture limited, and are not found in dry grasslands or sclerophyllous scrub, especially those dominated by introduced plant species.

The native Carabidae belong to three tribes, with each tribal assemblage having a unique pattern of distribution and diversity. The earliest ancestor to arrive in the evolution of the island chain was evidently the ancestor of the monophyletic radiation in the Platynini. The native Platynini live on all the high islands from Kauai to Hawaii Island. Their ancestral taxon may have colonized Kauai or an older island now eroded or submerged to the northwest. Their present-day diversity mirrors the complexity and ages of the various islands (Table 1).

Kauai exhibits a moderate level of diversity relative to the other islands, but is not as diverse as Oahu because it constitutes only the eroded aspects of a single volcano, Waialeale. Within Kauai, species are restricted to isolated ridges emanating from the main massif of Waialeale, indicating that allopatric speciation and isolation by distance has operated on this island, but not to the same degree as on those islands composed of more than one large volcano. Of course, were Kauai's sister island Niihau larger and taller, it could still support native rain forest, and we would find native Platynini there.

Oahu is made up of two major volcanoes, Koolau and Waianae. The current topography of Oahu represents the more stable, adjoining, and overlapping portions of these two volcanoes. Their outer portions have been lost to the sea through erosion and prodigious landslides (Moore et al. 1989). Most beetles that happened to remain land bound after cataclysmic landslips have retained absolute fidelity to their volcanic homes; 22 of the 32 species are restricted to one or the other volcano—8 to Waianae, 14 to Koolau—whereas only 10 species are more widely distributed across the island.

The islands of Molokai, Lanai, Kahoolawe, and Maui are the submerged fragments of Maui Nui, the previous "Big Island" before the present island of Hawaii broke the surface of the ocean about 430,000 years ago (Carson & Clague 1995). Each windward fragment—i.e., Molokai, West Maui, and Haleakala—has been home to extensive windward forests, and they support an extensive diversity of species. The 78 extant species of Maui Nui represent 60% of the entire species diversity of Hawaiian Platynini, thus illustrating the importance of topographic complexity in generating species in this group. The current stature of Haleakala, the most recent and therefore least eroded of the Maui Nui
Table 1. Species-level diversity of native Hawaiian Platynini, the number of species endemic to each island, and the percentage endemism on each island; maximum island age from Clague & Dalrymple (1989). Maui Nui totals indicated in bold; Molokai, Lanai, West and East Maui were united as Maui Nui during the Pleistocene.

<table>
<thead>
<tr>
<th>Island</th>
<th>Island age (Ma)</th>
<th>No. species</th>
<th>No. endemic</th>
<th>% endemism</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kauai</td>
<td>5.1</td>
<td>24</td>
<td>24</td>
<td>100</td>
</tr>
<tr>
<td>Oahu</td>
<td>3.7</td>
<td>32</td>
<td>32</td>
<td>100</td>
</tr>
<tr>
<td>Maui Nui</td>
<td>1.9</td>
<td>68</td>
<td>64</td>
<td>94</td>
</tr>
<tr>
<td>Molokai</td>
<td>1.9</td>
<td>22</td>
<td>18</td>
<td>82</td>
</tr>
<tr>
<td>Lanai</td>
<td>1.3</td>
<td>5</td>
<td>3</td>
<td>60</td>
</tr>
<tr>
<td>West Maui</td>
<td>1.3</td>
<td>17</td>
<td>13</td>
<td>76</td>
</tr>
<tr>
<td>East Maui</td>
<td>0.8</td>
<td>34</td>
<td>30</td>
<td>88</td>
</tr>
<tr>
<td>Hawaii</td>
<td>0.4</td>
<td>7</td>
<td>5</td>
<td>71</td>
</tr>
<tr>
<td>Total</td>
<td>—</td>
<td>129</td>
<td>125</td>
<td>97</td>
</tr>
</tbody>
</table>

volcanoes, has extensive habitats above timberline, from approximately 2000 to 3000 m elevation. Two species of Platynini, *Blackburnia frigida* (Blackburn) and *B. lenta* (Sharp), live only in this treeless zone, though *B. frigida* was historically found below timberline elevations out of the forest on the leeward side of Haleakala. The Molokai and West Maui fragments of Maui Nui presumably also supported open habitats from likely timberlines near 2000 m to their summits at 3000 m and above (Carson & Clague 1995). *Blackburnia munroi* of Molokai and *B. viridis* of West Maui are most closely related to *B. frigida*. Like *B. frigida*, both species live along water’s edge in rocky situations, although unlike *B. frigida* on Haleakala, these situations are interspersed among forest habitats on Molokai and West Maui.

Though the island of Hawaii is as topographically complex as Maui Nui, with the five volcanoes of Kohala, Mauna Kea, Hualalai, Mauna Loa, and Kilauea constituting its mass, time has not yet advanced sufficiently for Hawaiian Platynini to diversify in Hawaii’s broadly continuous windward forests. Of the seven platynine species on Hawaii Island, only *Blackburnia ewingi* is restricted to a single volcano.

The tribe Psydrini, represented in Hawaii by the genus *Mecyclothorax* Sharp, exhibits a substantially different pattern and history of diversification in Hawaii. Like Platynini, Psydrini comprises many endemic species; however, this monophyletic radiation (Britton 1948a) does not include any species on Kauai. Perkins (1896d) remarked on this absence, and specifically collected for these beetles on Kauai. Subsequent collectors have also not found them there, making it an almost absolute certainty that psydrines do not now occur on Kauai (Table 2).
Table 2. Species-level diversity of native Hawaiian Psydrini, the number of species endemic to each island, and the percentage endemism on each island (data from Britton 1948a). Maui Nui totals indicated in bold; Molokai, Lanai, West and East Maui were previously united as Maui Nui.

<table>
<thead>
<tr>
<th>Island</th>
<th>No. species</th>
<th>No. endemic</th>
<th>% endemism</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kauai</td>
<td>0</td>
<td>0</td>
<td>—</td>
</tr>
<tr>
<td>Oahu</td>
<td>6</td>
<td>6</td>
<td>100</td>
</tr>
<tr>
<td><strong>Maui Nui</strong></td>
<td><strong>64</strong></td>
<td><strong>63</strong></td>
<td><strong>99</strong></td>
</tr>
<tr>
<td>Molokai</td>
<td>20</td>
<td>20</td>
<td>100</td>
</tr>
<tr>
<td>Lanai</td>
<td>2</td>
<td>2</td>
<td>100</td>
</tr>
<tr>
<td>West Maui</td>
<td>5</td>
<td>4</td>
<td>80</td>
</tr>
<tr>
<td>East Maui</td>
<td>38</td>
<td>37</td>
<td>97</td>
</tr>
<tr>
<td>Hawaii</td>
<td>17</td>
<td>17</td>
<td>100</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>87</strong></td>
<td><strong>86</strong></td>
<td><strong>99</strong></td>
</tr>
</tbody>
</table>

Britton (1948a) also determined that those species possessing the more generalized elytral striation within the psydrine radiation of *Mecyclothorax* are most prevalent on Molokai. The *Mecyclothorax* species on Oahu, conversely, appear the most highly specialized morphologically. These findings, taken in concert with absence of this group on Kauai, strongly suggest that the Hawaiian Psydrini are descended from an ancestor that colonized Maui Nui, probably Molokai, and have spread to include Oahu and Hawaii in their aggregate distribution. Thus, this radiation of 87 described species, plus an almost equal number of undescribed forms we are currently studying, has been in residence in Hawaii no longer than the age of Molokai (i.e., 1.9 Ma, Carson & Clague 1995). As in the Platynini, the complexity of Maui Nui coupled with perhaps two million years of evolutionary change has resulted in most of the species production of *Mecyclothorax*. In contrast to Platynini, 17 described species are known from Hawaii, suggesting a higher rate of speciation or earlier colonization of Hawaii for psydrines versus platynines.

The third higher taxon to include endemic Hawaiian carabid beetles—Bembidiini (Table 3)—has been built up by repeated colonization, with more limited speciational radiation after several founding events. Worldwide, the Bembidiini constitute riparian species, with the Hawaiian taxa similar in that regard. Five bembidiine genera are represented in Hawaii, though only three of these have colonized the islands naturally: *Gnatholymnaeum* Sharp, *Tachys* Stephens, and *Bembidion* Latreille (Table 3). *Gnatholymnaeum*, represented by two species, is thought to be most closely related to either the North American genus *Amerizus* or the Palearctic *Lymnaeum* (Britton 1948b). The Hawaiian *Tachys* represent a mixture of adventively introduced and native species (Britton 1948b), at least one of which has been
Table 3. Diversity of species in the genera of Hawaiian Bembidiini (Britton 1948b).

<table>
<thead>
<tr>
<th>Genus</th>
<th>No. species</th>
<th>No. endemic</th>
<th>% endemism</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gnatholymnaeum</td>
<td>2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Lymnastis</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Typhlonesiotes</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Tachys</td>
<td>4</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Bembidion</td>
<td>18</td>
<td>14</td>
<td>78</td>
</tr>
</tbody>
</table>

recorded in caves (Howarth 1973). Similarly, the Hawaiian Bembidion include species such as B. niloticum Dejean, which are widespread across Asia to Egypt, and a variety of species known only from Hawaii, several with reduced flight wings. Hawaiian Bembidion are most taxonomically diverse in Kauai, the one island lacking Mecyclothorax species.

PROSPECTUS FOR REVISION OF HAWAIIAN CARABIDAE

Given the extremely high levels of endemism among the Hawaiian carabid fauna, adequate taxonomic treatment of the more speciose groups requires extensive field survey. This must be followed by intensive laboratory analysis, including dissection of specimens, scoring of characters for diagnosis and cladistic analysis, and comprehensive examination of type specimens to permit proper assignment of names. We have chosen to start revision of the Hawaiian Carabidae with the tribe Platynini, just as Sharp did 100 years ago. The reasons for first focusing on this group include their broad distribution across all of the high Hawaiian Islands, and their extreme differentiation, comparatively larger body size, and relatively lower levels of diversity compared to the Hawaiian Psydrini. We believe we have made a comprehensive survey of the islands, thus permitting revision at this time, although exploration of mountain ranges so far inaccessible will no doubt result in discovery of new species. The Hawaiian psydrines of the genus Mecyclothorax are no less interesting a group, but the large number of undescribed species discovered since Sharp’s (1903) and Britton’s (1948a) treatments suggests a greater attention to geographic sampling is required to permit an understanding of species limits in that radiation. We treat Mecyclothorax as the second part of this revision. Bembidiini, the third tribe containing native Hawaiian carabids, has comparatively few species that have resulted from multiple introductions, and it is less significant evolutionarily than either the Platynini or Psydrini. Therefore we treat it third. Accompanying treatment of Bembidiini will be coverage of all non-native carabid species, including those reported as adventives, those known to have become established in Hawaii, and those purposefully introduced in early biological control efforts.

Until completion of treatments for the Psydrini, Bembidiini, and the adventive species, the key below should be accompanied by the following publications as the best means to determine specimens in the various groups:
• Carabini (Swezey 1931, Pemberton 1949, Weber 1955, Gidaspow 1959);
• Bembidiini (Britton 1948b);
• Psydrini, *Mecyclothorax* Sharp (Britton 1948a);
• Harpalini (Britton 1948b, Zimmerman 1972, Samuelson et al. 1997);
• Panagaeini (Davis & Butler 1964);
• Anthiini (Davis & Butler 1964);
• Dryptini (Williams 1920);
• Chlaeniini (Williams 1920);
• Perigonini (Fullaway 1922, Swezey 1931);
• Masoreini (Zimmerman 1972);
• Lebiini (Britton 1948b, Zimmerman 1972).

Intentional introductions of species in the Scaritini, Cicindelini, Cychrini, and Pterostichini are assumed to have failed (Swezey 1931).

**KEY TO THE TRIBES OF CARABIDAE KNOWN FROM OR POSSIBLY OCCURRING IN HAWAII**

This key will allow tribal identification of any native, adventive, or intentionally introduced Hawaiian carabid beetle, with generic- and species-level identification then possible under individual tribal treatments. Because species identities were not consistently established before introduction, nor monitoring consistently undertaken after release during the past 100 years of biological control efforts, it is not possible to determine exactly what constitutes the purposefully introduced fauna (e.g., Swezey 1931). Therefore this key includes tribes for which species identities were known at introduction, even though many of the species known to have been released in Hawaii may have failed to establish.

1. Mesosternum and metasternum not completely surrounding each mesocoxal cavity laterally, the mesepimeron therefore adjoining the mesocoxa (Fig. 1A) ..... 2
   - Mesosternum and metasternum completely surrounding each mesocoxal cavity, thus separating mesepimeron from mesocoxa (Fig. 1B) ......................... 5

2(1). Procoxal cavities open caudally (prosternum does not completely surround them, and they are thus open to the mesosternum, Fig. 1C) ......................... 3
   - Procoxal cavities closed caudally (separated from the mesosternum by the prosternum, which completely encloses their posterior margins, Fig. 1D) ...... ........................................................................................................ Scaritini (Part 3)

3 (2). Antennae inserted on lateral portions of head between mandibular bases and front margin of eye, the mouthparts prognathous (held out in front when head is in relaxed position) ................................................................. 4
   - Antennae inserted on frons between compound eyes, the mouthparts hypognathous (held downward when head is in relaxed position) .......... Cicindelini (Part 3)
Fig. 1. Thoracic structures used to diagnose tribes of Carabidae found in Hawaii. A-B. Thoracic ventrites, ventral view: A, *Calosoma blaptoides* with disjunct mesocoxal condition, in which mesepimeron adjoins mesocoxa; B, *Metaco/podes buchanani* with conjunct mesocoxal condition, mesosternum and metasternum enclose mesocoxa. C-D. Prothorax, lateral view: C, *Calosoma blaptoides* (anterior margin to right) exhibiting posteriorly open procoxal cavities; D, *Scarites subterraneus* exhibiting posteriorly closed procoxal cavities. E. Pterothorax of *Scaphinotus ventricosus*, ventral view, showing both disjunct mesocoxal cavities, and metacoxae separated by medioposterior region of metasternum. eep, elytral epipleuron; msem, mesepimeron; mses, mesepisternum; mss, mesosternum; mtcx, metacoxa; mtem, metepimeron; mtes, metepisternum; mtf, metafemur; mts, metasternum; pcx, procoxa; pcxc, procoxal cavity; pepm, proepimeron; pepp, proepipleuron; peps, proepisternum; pn, pronotum; ps, prosternum; t, metatrochanter.
Fig. 2. Mouthpart and abdominal structures used to diagnose tribes of Carabidae found in Hawaii. A. Mentum, ventral view, showing subulate labial and maxillary palps, *Bembidion munroi*. B. Mentum, ventral view showing fusiform labial and maxillary palps, *Mecyclothorax montivagus*. C. Lateral margin of elytron and abdomen, *Blackburnia posticata*, dorsolateral view, showing smooth lateral margin at subapical situation; elytral plica internal and not visible. D. Lateral margin of elytron and abdomen, *Pterostichus californicus*, dorsolateral view, showing externally visible elytral plica or fold (at arrow of detail) that engages lateral portions of abdominal segment VII. E. Rounded elytral apex, *Blackburnia posticata*; tergum VIII covered. F. Truncate elytral apex, *Plocionus imidus*; tergum VIII uncovered. el, elytra; lp3, labial palpomere 3; m, mentum; mp4, maxillary palpomere 4; o, orifice of pygidial defensive gland; SVII, sternite VII; TVIII, tergite VIII.
4(3). Metacoxae contiguous (Fig. 1A) ......................................................... Carabini (Part 3)
— Metacoxae not contiguous, separated by metasternum (Fig. 1E) ...................
....................................................................................................................... Cychrini (Part 3)

5(1). Mandibles with a scrobal seta situated in the dorsolateral concavity .......... 6
— Mandibles asetose, the scrobal surface smooth ............................................. 7

6(5). Apical labial and maxillary palpomeres subulate (i.e., much more slender,
styliform compared to breadth of penultimate palpomeres, Fig. 2A) .............
....................................................................................................................... Bembidiini (Part 3)
— Apical labial and maxillary palpomeres fusiform, at their broadest point of greater
diameter than penultimate palpomeres (Fig. 2B) ............................... Psydrini (Part 2)

7(5). Extraordinarily large carabids (for Hawaii), > 30 mm total body length ...... 8
— Smaller beetles, <20 mm total body length .................................................. 9

8(7). Elytra deeply and coarsely striate, but without coalescent patches of white setae;
terminal segments of labial and maxillary palpi enlarged, arcuate-lanceolate,
and conspicuously canalicate ventrally from base to apex; antennae densely
setose from 4th antennomere ............................................................... Panagaeini (Part 3)
— Elytra coarsely striate, with numerous black setae and conspicuous maculae
composed of coalescent white setae; terminal segments of labial and maxillary
palpi fusiform; antennae densely setose over all segments ... Anthiini (Part 3)

9(7). Elytral lateral margin lacking an external plica apicad subapical sinuation (Fig.
2C), the lateral margin of elytra continuous from base to apex (in this configu-
ration, the abdomen is free to move ventrally away from the elytra) ............ 10
— Elyral lateral margin broken by an external plica, or elytral locking device,
whereby a carinate ridge emerges from the elytral inner surface to cause a
break along the smooth lateral margin of the elytra just apicad the subapical
sinuation (Fig. 2D) ................................................................. Pterostichini (Part 3)

10(9). Elytral apex truncate, tergite 8 broadly exposed (Fig. 2F) ....................... 11
— Elytral apex broadly rounded beyond the subapical sinuation (which may be
obsolete), largely covering tergite 8 (Fig. 2E) ............................................. 12

11(10). Entire body including elongate antennal scape conspicuously hirsute, pronotum
collarlike, without lateral marginal depression ......................... Dryptini (Part 3)
— Body surface and antennal scape glabrous except for longer sensory setae in
standard positions, pronotum flatter, with lateral marginal depression inside
lateral bead .............................................................................................. Lebiini (Part 3)

12(10). Pronotum and elytral disc glabrous except for longer sensory setae at consistent
(fixed) positions on the various sclerites .................................................. 13
— Pronotum and elytral disc covered with pelage of fine, short setae in addition to
longer sensory setae ........................................................................... Chlaeniini (Part 3)
13(12). Head usually with two supraorbital setae each side (if only one, it is situated at or caudad posterior margin of eye); abdominal sternite III glabrous medially

— Head with only one supraorbital seta each side situated between caudal margin and middle of eye; abdominal sternite III with fine setae covering median process between metacoxae ................................................................. Harpalini (Part 3)

14(13). Elytra with outer intervals glabrous except for large fixed setae in interval 8; discal striae present in various configurations ................................................................. 15

— Elytra finely setose near lateral and caudal margins in addition to larger fixed setae in interval 8; only eighth stria distinct, joining elytral margin caudad base and therefore obsolete basally, apically curving around apex almost to suture .......... ................................................................. Perigonini (Part 3)

15(14). Trochanters of hind legs very long, more than half length of metafemora; parascutellar striole absent (in adventive Hawaiian species) .... Masoreini (Part 3)

— Trochanters of hind legs only about 1/3 length of metafemora; parascutellar striole present ........................................................................................................... Platynini (Part 1)

### Historical Collections

The first carabid beetle collections in Hawaii were made in summer of 1830 by Franz Julius Ferdinand Meyen in the vicinity of Honolulu (Table 4). He was a 26-year-old seaman and botanist aboard the trading ship *Princess Louise* when his ship called on the port during a voyage around the world (Ratzeburg 1843). His four specimens—to be named *Anchomenus corruscus* by Wilfred Erichson (1834)—were given to Alexander von Humboldt upon Meyen’s return to Berlin. Meyen went on to become a professor of phytogeography at the University of Berlin (Meyen 1836, 1843), but died in 1840 from dysentery. The second expedition to bring back Hawaiian carabids also started in Berlin. Dr. Otto Finsch was sent out in 1872 by the Berlin Zoological Museum to collect insects across the Pacific, in Hawaii, the Marshall Islands, and the Gilbert Islands (Karsch 1881). Finsch spent time at Olinda, East Maui, where he collected 10 specimens representing five different species. Of these five species, two—*Blackburnia octoocellata* and *B. sharpi*—have not been observed in nature since the 1890s.

The preliminary German efforts were soon followed by survey activities sponsored by a considerably different agency. In 1876, the Anglican Church sent Thomas Blackburn to Hawaii to serve as Senior Priest and Chaplain to the Bishop of Honolulu. Blackburn had a long career in entomology before he became a cleric (Lea 1912), and during his time in Hawaii he collected extensively on Oahu, and made collecting trips to Kauai, Lanai, Maui, and Hawaii (Blackburn & Sharp 1885). He estimated that his Oahu collecting activities amounted to from one to 12 hours per fortnight spent in the Koolau Mountains during his
Table 4. Historical sequence of survey activities resulting in collection of native Hawaiian platynine carabids. Years, period of active collecting in Hawaii discernible from specimens examined; No. species, species attributable to collector based on label data; No. exx., total number of specimens collected by individual; Discoveries, number of times individual was first to collect a species; lsts/exx., Discoveries/No. exx.

<table>
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<tr>
<th>Investigator</th>
<th>Years</th>
<th>No. species</th>
<th>No. exx.</th>
<th>Discoveries</th>
<th>lsts/exx.</th>
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<td>F.J.F. Meyen</td>
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<td>1</td>
<td>4</td>
<td>1</td>
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<tr>
<td>O. Finsch</td>
<td>1872</td>
<td>5</td>
<td>10</td>
<td>5</td>
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<td>T. Blackburn</td>
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<td>147</td>
<td>23</td>
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<td>R.C.L. Perkins</td>
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<td>91</td>
<td>4515</td>
<td>64</td>
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<td>A. Koebbele</td>
<td>1890s</td>
<td>23</td>
<td>336</td>
<td>2</td>
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<tr>
<td>W.M. Giffard</td>
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<td>41</td>
<td>1026</td>
<td>1</td>
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<tr>
<td>G.C. Munro</td>
<td>1906-1940</td>
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<td>42</td>
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<tr>
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<td>671</td>
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<tr>
<td>J.C. Bridwell</td>
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<td>21</td>
<td>347</td>
<td>2</td>
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<td>J.A. Kusche</td>
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<td>F.X. Williams</td>
<td>1918-1946</td>
<td>21</td>
<td>182</td>
<td>—</td>
<td>—</td>
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<tr>
<td>E.H. Bryan, Jr.</td>
<td>1919-1940</td>
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<td>152</td>
<td>1</td>
<td>0.007</td>
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<tr>
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<td>31</td>
<td>427</td>
<td>1</td>
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<td>1935-1960</td>
<td>34</td>
<td>996</td>
<td>—</td>
<td>—</td>
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<td>1955-1972</td>
<td>17</td>
<td>79</td>
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<td>1959-1976</td>
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<td>139</td>
<td>2</td>
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<tr>
<td>W.C. Gagné</td>
<td>1968-1984</td>
<td>32</td>
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<tr>
<td>F.G. Howarth</td>
<td>1972-1991</td>
<td>25</td>
<td>98</td>
<td>3</td>
<td>0.031</td>
</tr>
<tr>
<td>A.C. Medeiros</td>
<td>1984-1993</td>
<td>17</td>
<td>1296</td>
<td>2</td>
<td>0.002</td>
</tr>
<tr>
<td>J.K. Liebher</td>
<td>1991-1998</td>
<td>89</td>
<td>9900</td>
<td>10</td>
<td>0.001</td>
</tr>
<tr>
<td>D.A. Polhemus</td>
<td>1991-1998</td>
<td>59</td>
<td>2164</td>
<td>2</td>
<td>0.001</td>
</tr>
</tbody>
</table>
six years on the island, plus four trips to the Waianae Mountains that totaled seven days. His off-Oahu forays were considerably more limited, including four days on Kauai, 42 on Maui, and 23 days on Hawaii. Blackburn was most impressed with Haleakala: "The eastern end of Maui is, in my opinion, the head-quarters of the insect fauna of the archipelago" (Blackburn & Sharp 1885, 205). He worked various elevations on Haleakala from the isthmus up to about 5000 ft., "but not exploring much above 5000 feet of elevation, as the supply of insects evidently fell off above that region" (Blackburn & Sharp 1885, 206).

Blackburn collected a total of 29 species of Hawaiian Platynini, 23 of them novel discoveries (Table 4). He described many of these (Blackburn 1877, 1878a, 1878b, 1881, 1884), and sent specimens to Dr. David Sharp, then a medical doctor in Dumfries, Scotland (Walker 1922). Their collaboration was summarized in Memoirs on the Coleoptera of the Hawaiian Islands (Blackburn & Sharp 1885), in which 6 genera and 30 species of Hawaiian Platyninini were listed. The various names proposed by Karsch (1881) were synonymized with senior Blackburn names in the systematic catalogue portion of the Memoirs. Sharp was greatly impressed by the diversity within Platyninini (which he called Anchomeninini):

This brings out a striking endemicity in the Hawaiian Anchomeninini, which is much increased by a more detailed study of their peculiarities; and, in illustration of this, I may mention that Mr. H.W. Bates—undoubtedly at present the first of our authorities on this important family of beetles—when I had the pleasure of submitting to him a series of about half the species of Hawaiian Anchomeninini, pronounced them, after a brief inspection, to be very peculiar and highly endemic. Indeed, so peculiar are some of these Anchomeninini that they have been referred by authorities to other subfamilies, Mr. Blackburn and Herr Karsch having considered one of the genera —Atrachycnemis—as a member of the Harpalini, and Karsch having treated another genus—Disenochus—as a member of the Broscini, while Mr. Blackburn thought it rather to belong to Pterostichini. Although I have been able to examine each of these genera in a very imperfect manner, I believe, however, that both will prove to be aberrant Anchomeninini. (Sharp 1885, 264)

No doubt his experience with the Hawaiian Carabidae—as well as other highly endemic groups such as Nitidulidae, Anobiidae, Cerambycidae, and Curculionidae—fueled Sharp's curiosity concerning Hawaiian insects. When he was invited to the curatorship of insects at the Cambridge Natural History Museum in 1890, he became the colleague of Professor Alfred Newton. Both were members of the executive subcommittee of the Royal Society and British Association Joint Committee for the Zoology of the Sandwich Islands, formed to support zoological exploration in the islands (Manning 1986). The committee searched for a suitable collector to be sent to Hawaii, and with the support of E.B. Poulton of Oxford University, R.C.L. Perkins was invited to apply. He was found suitable, and in January 1892 Perkins was chosen for the job. He left London in February and arrived in Honolulu on 10 March 1892.

Perkins spent three periods of time in Hawaii during his tenure as specimen procurer for the Joint Committee; III-1892—IX-1894, III-1895—III-1897, and V-1900—XII-1901 (Manning 1986). He spent portions of 92 months in the field throughout the islands (Liebherr & Polhemus 1997b), indefatigably collecting insects, birds, and molluscs. What we know of Hawaiian insects as they occurred in the nineteenth century is due almost
completely to the efforts of R.C.L. Perkins (see Scott 1956, Manning 1986, Liebherr & Polhemus 1997b). Perkins collected fully 70% of the so-far-known Hawaiian Platynini, and was the first to see half of the known fauna (Table 4). He noted microhabitat situations for many species, and when he recopied his notes many years after he left the islands—he burned the originals—his keen memory permitted him to associate subsequently described species names (e.g., Sharp 1903) with the actual collection events during his survey work of the 1890s. We have added biological information from these notes to the species treatments herein.

Perkins completed his survey activities for the Joint Committee in 1901, and then worked for the Territorial Board of Agriculture from 1902 to 1904. The Hawaiian Sugar Planters’ Association (H.S.P.A.) hired him as Director of the Division of Entomology when that unit was formed, where he worked until ill health forced him to leave the islands in 1912 and return to England. Starting during the surveys of the Joint Committee and continuing throughout this time as an economic entomologist, Perkins collaborated with a circle of entomologists, some of whom collected for him, or followed in his footsteps collecting insects across the islands. The first was Albert Koebele, who worked as an economic entomologist in the islands from 1893 to 1905. Koebele’s material is notoriously inadequately labeled—his standard label for all Hawaiian insects was “Hawaii/A. Koebele”—however he made important discoveries of two rare taxa—Blackburnia koebelei and B. komohana—from West Maui (Sharp 1903):

His success in the field was due to his acute perception of the habits of insects, and unsurpassed perseverance, and he was naturally a very quick worker, so that with insects that are rare and difficult to obtain, he could collect a greater number in a given time than most of the best field workers we have known. (Perkins 1925, 362)

Otto H. Swezey was another prominent H.S.P.A. colleague of Perkins. More than any other entomologist since Perkins, Swezey traveled throughout Hawaii collecting a wide variety of insects. In addition, he made important contributions to biological control of sugarcane pests, and participated in the pioneering biological weed control program for lantana (Usinger & Zimmerman 1960). Walter M. Giffard, the third contributing colleague of Perkins associated with H.S.P.A., was not a professional entomologist, but made his living with W.G. Irwin & Co. from 1877 to 1909. It was only in retirement that he took up entomology full time (Swezey & Fullaway 1931). He collected on all the islands, contributing particularly to our knowledge of the distribution of species in the eastern reaches of Waimea Canyon, Kauai, and the drier western reaches of Haleakala. On Haleakala, his collections are from areas now extensively modified by introduction of pasture grasses or exotic forest trees. He collected the sole specimen of one species we describe—Blackburnia polipoli—at the spring of that name on the southwest flank of Haleakala. J.A. Kusche collected with Giffard on Kauai, accompanying him to the Waialae River, and adding records from Olokele Canyon, Kokee State Park, and the high Alakai.

George C. Munro is the last of Perkins’ contemporaries who added material to the basis for this revision. A native New Zealander, he first served as assistant to H.C. Palmer, collector for the Rothschild ornithological expedition that served as the spur to the Joint Committee (Manning 1986), and then cooperated extensively with Perkins over many years. He became ranch manager for Lanai in 1911 (Hobdy 1993), but continued to explore
the islands’ bird life (Munro 1960). Even after Perkins left the islands, Munro sent specimens to England that Perkins named. He did not collect many specimens, but he had a keen eye for novelties, attributable by his discovery of one new species of *Blackburnia*—appropriately given the species appellation *munroi* by Perkins (1936)—as well as a giant *Mecyclothorax* species from the Upper Hamakua Ditch, Hawaii, so far known only from the holotype (Perkins 1937).

The post-Perkins era comprises three periods: (1) between the World Wars; (2) post-War to pre-helicopter; and (3) a modern helicopter-assisted period. The H.S.P.A. continued as the chief institution responsible for entomological support during the first period, with F.X. Williams and Elwood C. Zimmerman collecting under its auspices. During the 1950s, Everett J. Ford, then with the United States Department of Agriculture, collected extensively on Oahu, and made one collecting trip to Molokai. Following the Viet Nam War, availability of helicopter transport and pilots capable of flying under Hawaiian conditions made accessible previously isolated regions, such as Waiaelale (Kauai), Puu Kukui, Lihau (West Maui), and the region from Keanae to Kipahulu Valleys (East Maui), to entomological survey. Robin Rice added significantly to our knowledge of Kauai species by surveying areas inaccessible to Perkins, and Wayne Gagné and Frank Howarth of Bishop Museum did the same for eastern Haleakala.

As expected, the probability that any collector will encounter an undescribed Hawaiian platynine carabid beetle has plummeted since the time of Blackburn’s activities (Table 4, lists/exx.). Perkins’ surveys in the 1890s encompassed a much broader geographic extent than Blackburn’s. Moreover he collected long series, and discovered 64 species, though only at a rate of one to two beetles per hundred collected. For much of the twentieth century, only a few undescribed species were found, due mainly to the necessary restriction of collectors’ activities to areas also accessible to Perkins during the 1890s. Opening of lands to scientific study by the State of Hawaii, The Nature Conservancy of Hawaii, and other cooperating organizations, coupled with the availability of helicopter support, has changed this situation. Now essentially any isolated massif is potentially accessible to scientists. The novel discoveries of Rice, Howarth, Gagné, Medeiros, Liebherr, and Polhemus are the result of this conjunction of opportunities. Howarth’s (1972) discovery of the endemic lava tube fauna marks the other recent survey opportunity, resulting in his discovery/effort ratio being the highest since Blackburn (Table 4).

**Taxonomic Material**

This revision is based on examination of 25,287 specimens held in 16 different collections (Table 5, Appendix). We thank the following curators and scientists for access to their material, many specimens of which they personally collected: G. A. Samuelson, Bernice P. Bishop Museum, Honolulu (BPBM); S. J. Hine, The Natural History Museum, London (BMNH); D. A. Polhemus and T. L. Erwin, United States National Museum of Natural History, Smithsonian Institution, Washington, D.C. (NMNH); M. L. Goff, University of Hawaii, Manoa (UHEM); D. H. Kavanaugh, California Academy of Sciences, San Francisco (CASC); B. R. Kumashiro, Hawaii Department of Agriculture, Honolulu (HDAC); T. L. Deuve, Museum National d’Histoire Naturelle, Paris (MNHP); A. F. Newton, Jr., Field Museum of Natural History (FMNH); P. D. Perkins, Museum of Comparative Zoology (MCZC); Y. Bousquet, Canadian National Collection, Ottawa.
Table 5. Numbers of specimens and species held in collections used as the basis for revision of the Hawaiian Platynini. Collection codes as in the text.

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<th>No. species</th>
<th>Collection</th>
<th>No. specimens</th>
<th>No. species</th>
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(CNCI); R. L. Takumi, Haleakala National Park, Makawao, Maui (HALE); F. Hieke and M. Uhlig, Museum für Naturkunde der Humboldt-Universität zu Berlin (MNHU); M. A. Ivie, Montana State University (MTSU); R. T. Bell, University of Vermont, Burlington (UVCC); D. Foote, Hawaii Volcanoes National Park, Volcano, Hawaii (HAVO).

Survey Techniques

**Historical collecting techniques.** When Perkins arrived in Hawaii in spring of 1892, he had little idea how to collect native carabids. Sharp soon instructed him, “Don’t forget my sifting dodge, also try under big stones in semi-shady places, also sunset sweeping + beating, and don’t forget to try light in suitable places especially if you can set it on a white sheet in a nice open place out of doors. From what H. H. Smith said he finds evening sweeping + beating very productive” (Sharp 1892a). Clearly this advice from England did not prove immediately useful, for Sharp wrote a month later, “I am very glad to hear of your fresh insect captures. Of course I am very sorry you have not got Carabidae yet; I am inclined to think one reason may be your working so much in the forest, but of course this is only a guess. However you must correspond with Mr. Blackburn on the subject for it certainly looks very blank that you should in five months have only got 2 species out of the 60 Blackburn discovered. It seems clear that it must be owing partly at any rate to the difficult ways of collecting. I don’t hear you say anything about sifting, but I think it is a very good way of getting things . . .” (Sharp 1892b). Perkins may have tried sifting, but in our experience, this works in only limited terrestrial situations with periods of sunshine, and so he may have abandoned it. At any rate, this technique is not mentioned in any field notes or lot descriptions. Perkins must have beaten vegetation for insects, as he would lie on his stomach in the lee of an upended beating sheet while field-pinning microlepidopterans
(Perkins, pers. comm. to ECZ, 1950). However, again this technique is not mentioned in notes attributable to carabid collections. That weather influenced his choice of collecting methods is attested to by another letter from Sharp: “At Puna you had been very much annoyed by heavy rain + no doubt the difficulty on the wet sides of the islands must be to find fine weather to collect in. Blackburn I think tried evening sweeping, about sundown with more success than other methods in these localities, but of course doing that depended on getting some fine weather” (Sharp 1895).

Based on notes accompanying his lots (Anonymous n.d.), and his field collecting notes (reviewed in Manning 1986), Perkins did much carabid collecting by looking under bark of dead and dying *Acacia koa* A. Gray, as well as under downed koa logs. He also found beetles under stones. He described a technique, or dodge, he called grubbing (Manning 1986, 12), whereby he would clear a circle of leaf litter on mesic, sandy soil and watch for carabids darting across this open arena. We have found this technique to be very useful in mesic closed-canopy forests near the rain shadow boundary, as in these situations the soil is well developed, leaves evenly cover the ground as they are not concentrated in large mats due to excessive rain, and carabids are active in the leaf litter-soil boundary. In wetter forests, the soil may be more saturated with water, leaves tend to clump in mats in depressions or near tree roots and logs, and carabids tend to occupy more arboreal situations, such as the moss covering trunks and roots and in the crotches of trees, particularly ohia lehua (*Metrosideros polymorpha* Gaudichaud-Beaupré). Perkins also collected at light, and records many moths from such activities, but given the high preponderance of brachypterous carabid species in Hawaii, such activity would result in collecting relatively few species.

Perkins never missed an opportunity to look for specimens. When out in the field he would sleep in his clothes upon a bed made up of successive layers of ohia lehua branches, *Styphelia* boughs, and then ferns. After his bed had decayed a bit, he would collect the carabids that accumulated under the mattress (Perkins, pers. comm. to ECZ, 1950).

**Current collecting techniques.** The recent survey period from 1991 to the present has included geographically extensive sampling across all the Hawaiian Islands, with an attempt to maintain consistent sampling techniques. We have continued to make improvements in our collecting protocols, so that at the present time we feel we have the ability to adequately sample a site for carabids, and other taxa, while maintaining the integrity of fragile Hawaiian ecosystems. Future work at new sites, and repeated sampling at sites we have visited should incorporate the following set of activities.

1. Beating vegetation at dusk and during nighttime, during rain or dry periods, will result in discovery of a wide variety of carabid beetle taxa. Beetles actively forage and mate on plant surfaces at night, and they may be knocked onto a beating sheet by tapping standing vegetation. For larger trees, such as olapa (*Cheirodendron*) or ohia lehua (*Metrosideros*), an axe handle may be needed to provide enough impact to dislodge insects active in the canopy. Carabid beetles are also active on ferns, both low soft ferns and *Cibotium* tree ferns, and these should be beaten as well. Some species, such as *Blackburnia dyscolea* of Maui, *B. palmae* of Oahu, and their relatives are almost always found in the leaf axils of ieie (*Freycinetia*), so this species should be particularly inspected if present. We know little of the host preferences for carabid beetles, and as they are presumed to be generalist predators, specific attachment to a particular host species seems unlikely. Nonetheless, carabid beetles are almost always much more numerous on ohia lehua than
olapa on any particular night. Therefore, attention to the host plant substrate, and separation of individuals collected off various host plants is called for.

(2) Sifting arboreal moss mats, or preferably spraying such mats with an outdoor pyrethrin insecticide allows discovery of the many individuals that inhabit such microhabitats. We initially started our survey using destructive sifting of moss mats, using Reitter sifters, and examination and sorting of the siftate on beating sheets, either in sunshine or rain. However, it is clear that the moss mats require the lifetime of the tree on which they occur to reach the well-developed condition observed in Hawaiian rain forests. Therefore, we advocate setting 3 m × 3 m sheets under aerial roots and trunks covered with mosses, applying the insecticide using small hand-held commercially available spray containers, and then collecting the insects off of the sheet as they flee the moss. This technique can result in vast numbers of specimens—e.g., carabids, damsel bugs (Hemiptera: Nabidae), seed bugs (Hemiptera: Lygaeidae), bristletails (Archeognatha), and spiders (Araneae)—that may be collected from moss adhering to a single ohia lehua tree. Therefore it is incumbent on the collector to prepare all this material or make it available to specialists so that all valuable taxonomic data are preserved. We have found that once the insecticide is applied, the sheet should be left for 1-1.5 h to ensure retrieval of all exiting specimens. This constraint has led us to adopt a standardized protocol whereby four trees are sprayed per locality per day by any one collector. Working in teams, a survey group could simultaneously run several sheets, though insects such as carabids and nabids remain capable of running off the sheet even after they have been sprayed, so sheets should not be left unattended.

(3) On large koa and ohia lehua trees, small cavities under bark flaps or exfoliating bark layers can serve as daytime refuges for carabid beetles. These can be collected alternatively by scraping the bark with a 3-tined hand cultivator, or more preferably by applying a pyrethrin spray above a sheet cut to surround the trunk. Use of the pyrethrin spray preserves the irregular bark layers, allowing other beetles to colonize these cavities within days of spray application.

(4) Sifting ground-level leaf litter and grubbing, as described above, permit examination of terrestrial species found on the soil boundary.

(5) Walking trails and examining tree trunks at night can be used to find active insects. Many of the carabid species on Kauai and Oahu tend to be mostly active on the ground, and night searching with a headlamp is the best means to find them. Other species—e.g., *Blackburnia aterrima* and *B. asquithi* of Kauai and *B. agilis*, *B. fracta*, and *B. sphodriformis* of Haleakala—are extremely agile climbers, and can be found running on tree trunks or tree fern fronds at night. In savannah and upland situations, for example on Haleakala, species such as *B. frigida* can be found on the ground feeding and mating during nighttime hours. *Blackburnia rupicola* rests in the leaf litter under *Sophora* plants during day, and then becomes active on top of the leaf litter during nighttime.

(6) Some species favor very wet situations, and they may be found along watercourses, either in gravelly streambeds, or on exposed wet rock covered with moss. Species with such preferences include the clade of *B. costata* of Kauai, *B. corrusca* of Oahu, and *B. molokaiensis* of Maui Nui, as well as the species pair *B. munroi* of Molokai, and *B. viridis* of West Maui. Recent discoveries of rarely encountered species have come from variants on this wet, terrestrial habitat. Lava tube caves have been shown to support a highly distinctive fauna, with species restricted to various zones in the cave environment (Howarth
1993). Continued exploration of such situations will no doubt result in discovery of more
cave specialists. Occupation of near-surface voids—Howarth’s twilight zone to transition
zone—seems to fit recent discoveries of *B. polhemusi* and *B. platyophthalmaica*, both
described herein. These species have only been found by pyrethrin fogging ground-level
moss along a small stream and escarpment in Molokai. Future attention to such hidden
microhabitats is warranted.

**Geographic localities.** Recent survey activities (Table 4) have expanded the range of
localities from which carabid beetles have been sampled. The latitude/longitude coordinates
of these field sites have been recorded using GPS position finders in the field, with those
readings corroborated by U.S. Geological Survey topographic maps. Pre-GPS localities
have been given latitude/longitude coordinates by several means. If the locality is present
within the U.S.G.S. Geographic Names Information System (GNIS), those coordinates were
adopted. For streams and valleys, elevation was used in conjunction with topographic maps
to assign a single latitude and longitude to a particular collecting position. If the place name
was not in the GNIS, earlier gazetteers were used, including Coulter (1935), Pukui et al.
(see Manning 1986) were reviewed for the particular dates found on specimen labels, with
coordinates assigned based on Perkins’ description of his movements, known base camps,
etc. Blackburn’s localities were in part assignable based on his written itinerary in
Blackburn & Sharp (1885).

Throughout this revision we treat Hawaiian place names using English spelling rules
(i.e., we omit the glottal stops that give the Hawaiian language its characteristic cadence
[the only exception is the island names included with the Otte base maps used for depicting
geographic distributions]). We have adopted this convention for two reasons: (1) locality
names as we present them are consistent with those on U.S.G.S. maps, the standard
geographic reference for the islands; and (2) locality names are consistent with species
epithets derived from Hawaiian words or localities, which based on the zoological code
(I.C.Z.N. 1999) cannot contain diacritical marks. Transliteration from Hawaiian to English
requires only the removal of glottal stops and concatenation of letters, permitting easy
conversion from one language to the other. Conversely, using the names we present to
search for information in the gazetteers is trouble free, as those references are arranged only
by the sequence of English letters used to portray the Hawaiian word.

The historical period of collecting to the present has seen the replacement of English
units of measure with the metric system. For modern records, all textual information is
presented in metric units. However, we have retained English units when discussing
localities of Perkins and Blackburn, as they used these measures in their notes, which we
quote heavily. The specimen date-locality database (Appendix) presents elevation data in
both metric and English units.

Based on our examination of specimen labels, gazetteers, field notes, and U.S.G.S.
resources, we have been able to assign geographic coordinates to 90% of all collection
records for Hawaiian Platynini (Appendix). Examination of the extent of survey activities
in the first half of collections to date (1870-1929) versus the second half (1930-1998)
illustrates several points. These points are, in part, specific to each island, so we comment
on each in turn.

**Kauai.** The early period of exploration on Kauai focused on regions accessible via river
valleys of the Waimea, Waialae, Makaweli, and Olokele (Fig. 3). Perkins entered the high
plateau of the Alakai Swamp via the Waialae River, following cow trails from Kaholuamano where he had access to a mountain house owned by the Gay family. He also gained access to the headwaters of the Waimea in creeks in what is now Kokee State Park. He had the support and friendship of Valdemar Knudsen (Knudsen 1895), and so could work out of Knudsen’s mountain house at Halemanu (Merwin 1998). He also stayed with George C. Munro and the Francis Gay family, gaining valuable information on the local flora and conditions (Manning 1986). Perkins climbed the ridge between the Makaweli and Hanapepe, finding *B. transiens*, endemic to that ridge, in the process.

Present-day surveys have resampled many of these areas covered by Perkins, with the exception of Kaholuamano and the Makaweli-Hanapepe region. We have made preliminary samples from Mt. Waialeale summit bog, Mt. Kahili (the ridge extended directly south from Waialeale summit), as well as the Makaleha Mountains to the northeast of Waialeale. The patterns of endemism on Kauai are shaped like a wheel with Waialeale at the hub. Species are uniquely distributed at the high, wet hub of Waialeale, as well as on at least some of the spokes such as Mt. Kahili and Makaweli, though no species endemic to the Makalehas has yet been found. The most promising sites for discovery of undescribed Kauai Platynini are
to the north of Waialeale, on Namolokama Mountain. Even 100 years after Perkins began surveying the fauna of Kauai, no entomologist has had the opportunity to stand at the summit of this mountain, much less spend the time to adequately sample the insect fauna.

Oahu. Because of its comparatively more gentle climate, lower elevations, and proximity to metropolitan staging areas, Oahu has been the most consistently sampled of all the Hawaiian Islands over all periods of exploration. Both Blackburn and Perkins spent much time in the southern Koolau Range. Similarly, they explored both windward and leeward sides of the Waianae Range, especially the slopes of Mt. Kaala, at a time spanning the destruction of many of the forests on that range due to tapping of underground water sources. Comparing recent geographic coverage to that before 1929 (Fig. 4) indicates that early records were generally of broader distributional extent. In most cases this more extensive sampling took place in leeward areas of the Koolaus as well as lowland areas surrounding the northern Waianaeas. These areas are unproductive today due to the extensive coverage by adventive weeds, as well as, no doubt, to destruction of the lowland native fauna by invasive ants (Perkins 1913, Gagné 1979). On the whole, however, present-day Oahu samples can be compared to those of a century ago without the confounding
influence of different collecting points, as most sites have either been collected in both early and recent periods of sampling, or early sites are adjacent to recently sampled sites.

**Molokai.** The windward forests of Kamakou volcano in East Molokai have attracted collectors from Perkins’ time to the present day. The core of the sampled areas is within Molokai Ranch, now managed by The Nature Conservancy. As on Oahu, Perkins’ localities include leeward areas that are now heavily disturbed (Fig. 5). On Molokai this disturbance has taken the form of dense stands of non-native coniferous forest trees choking out the native vegetation. In Perkins’ time, this leeward native forest was already highly disturbed due to exploitation and elimination of sandalwood (*Santalum* spp.) for trade in the early 1800s (Cuddihy & Stone 1990). Nonetheless, the comparatively drier area of Makakupaia served well as a mountain base camp. These successive disturbances notwithstanding, the challenge on Molokai remains the resampling of any pockets of native vegetation remaining along the leeward edges of the original forest distribution, as these sites are the lone known localities of species such as *B. debilis* and *B. perkinsi*.

The transition from leeward dry forest to extremely wet forest occurs across a very narrow geographic expanse on Molokai. Forests along the Pelekunu Rim east of Mt. Kamakou are extremely wet with standing water occurring in depressions on the uneven forest floor. No more than 2 km leeward the forest is being opened to a savannah formation, where windward, mauka showers compete with pleasant drying sunshine for the collector’s attentions.

**Maui.** The early period of collecting on Maui witnessed survey of the leeward edges of Haleakala’s rain forest, and only limited incursions into the bastions of the West Maui Mountains (Fig. 6). In West Maui, Brother Mathias Newell collected in Iao Valley, and Albert Koebele worked the leeward ridges above Lahaina up to about 1200 m. Perkins also visited Iao and the ridge to the south, Kapilau. Exceedingly rainy weather prevented further collecting in this range.

On Haleakala, Perkins followed Blackburn’s path up the leeward edge of the forest to near Olinda. Perkins established base camps at 4000 ft. (1210 m) and 5000 ft. (1515 m) along the forest edge during his trips to the mountain in 1894 and 1896. The lower site was the mountain house of a Mr. Pogue (Perkins 1894a), whereas the higher site was near the
Fig. 6. Distribution of collection samples from Maui containing Hawaiian Platynini for the early survey period (1870-1929) (●), recent survey period (1930-1998) (■), or both periods (□).

Ukulele Camp site. From these he walked into the forest at various elevations, as well as along the road from Olinda to the summit. In 1894 he notes “A lovely morning. Went out about two miles, but saw nothing worth shooting - i.e. no rare species. Returned disgusted at 2” (Perkins 1894a, April 2). Such a hike would have taken him east to the proximity of Haipuena Gulch. In all of Perkins’ extant notes, this is the greatest distance he mentions walking into the forest toward the east. On several occasions he walked to the summit at Red Hill, noting a stay at “Blackburn’s cave at about 9000 feet” (Perkins 1894a, April 9). He returned to the summit several days later, collecting the only known specimens of \( B. lenta \) “from 9500 to the top” (Perkins 1894a, April 11).

Perkins sought to re-collect species found by Blackburn, working downward in elevation from his camp at 1210 m toward Olinda. Our other knowledge of species distributions at lower elevations is based on early twentieth century collections made by Otto Swezey and E.H. Bryan. They gained access to the Koolau Ditch service roads eastward from Kailua to the Keanae Valley from 1918 to 1929. Swezey also entered the lower reaches of Kipahulu Valley, collecting upward to 455 m elevation.

Recent surveys of Maui have greatly expanded geographic coverage of the island. The West Maui peaks of Hanaula, Lihau, Puu Kukui, and Mt. Eke have become available for comprehensive sampling through the availability of helicopter transport for personnel and supplies, plus administrative support from governmental and private landowners. These sites were not accessed by nineteenth-century collectors, resulting in discovery of numerous undescribed species by recent expeditions. Helicopter transport has also made
 sampling possible on the broad, windward expanse of Haleakala. Localities within Hawaii Natural Area Reserves have been visited in Heleleikeoha, Kopiliula, and Kuhiwa Valleys, as well as middle elevations in the Keanae Valley, above the regions sampled by Swezey and Bryan. Kipahulu Valley Scientific Reserve was first comprehensively investigated entomologically in the 1980s by W. C. Gagné and F. G. Howarth in collaboration with A. C. Medeiros. Continued surveys in the 1990s, both in the valley and in the surrounding highlands have given us a first look at the entomological diversity of the southeastern flank of Haleakala. In the Waikamoi Block, many of the western rain forest sites of Blackburn and Perkins, such as Olinda, and Haleakala from 4000 ft. (1500 m) to the summit, have been repeatedly visited in recent surveys, though several species found in the last century—e.g., *B. agonoides*, *B. anomala*, *B. lenta*, *B. octoocellata*, and *B. terebrata*—have not been rediscovered.

**Lanai.** Being exceedingly small and having experienced a cavalcade of ecological disasters associated with succeeding waves of introduced, then feral ungulates (Hobdy 1993), it is a wonder that Lanai supports any native fauna or flora. Nonetheless, the Lanaihale summit and adjacent backbone of the island are home to several native carabid species. These highland sites have been sampled both by Perkins and recent collectors (Fig. 7). Perkins also found suitable habitat in Kaibohena Gulch, now bordered downstream by a golf course and the Koele Lodge. This gulch remains the only known site for *B. lanaihalensis*, a species known only from two specimens collected by Perkins in 1894.

**Hawaii.** Blackburn made two trips to the island of Hawaii, on the first landing at Kailua (Kona), then traveling to Waimea and on to the slopes of Mauna Kea, which he climbed with the botanist J.R. Watson. Blackburn “procured very few insects; but I attribute it chiefly to ‘bad luck,’ as I am satisfied that the fine forest clothing this mountain must be home to many fine things” (Blackburn & Sharp 1885, 207). He then traveled to Hilo, making his way to the active crater of Kilauea—observed and described a dozen years before by Mark Twain (1872)—and then collected upward about 1000 ft. (300 m) in elevation on Mauna Loa. A second trip several years later started at Kealakekua Bay, with
the Reverend ascending to 6000 ft. (1820 m) elevation on the western flank of Mauna Loa. Unfortunately, the minimal labeling of Blackburn's specimens precludes assignment of most of his specimens to specific localities.

Perkins concentrated his survey activities on the transect from Hilo to Kilauea, collecting in the Olaa rain forest and in forests around Kilauea. He also traveled to the Kau District southwest of Kilauea, and to the forests above Kailua-Kona (Fig. 8).

Fig. 8. Distribution of collection samples from Hawaii Island containing Hawaiian Platynini for the early survey period (1870-1929) (○), recent survey period (1930-1998) (■), or both periods (□).
Starting the recent survey period, Swezey and Williams collected on Mauna Kea at Nauhi Gulch in 1931. Building the Upper Hamakua Ditch in the Kohala Mountains north of Waimea also opened that region, first to the likes of George Munro, and leading to present-day entomologists. Recent discoveries of *B. ewingi* in the Kohala Mountains and *B. kukui* in the much better sampled vicinity of Kilauea suggest that continuing survey will produce significant findings. Clearly, the Big Island of Hawaii is just that, and our knowledge of platynine species distributions on this island remains among the most fragmentary in the chain.

**A Few Words about Larvae**

This revision is based solely on information inherent in the adult stage. Nonetheless, many larvae of these species are encountered in the field, many of them living in the same situations as the adults. The larval stages of *B. (Blackburnia) fracta* have been described (Liebherr 1995), and we have made a concerted effort to rear larvae of other species. To date, this has resulted in knowledge of at least the first instar larval stage for 25 species (Liebherr in press), and complete representation of the three larval instars for 19 species. Phylogenetic and taxonomic information on these stages will be presented later.

In general, larvae live with adults during the months of May and June, to October. For predominantly arboreal species, the larvae live within moss mats on trees, or among leaf bases on monocots, and presumably forage within these microhabitats. Arboreal larval habitation was observed and reported by Timberlake (1918), the only other instance of a report on Hawaiian platynine larvae. We have not seen larvae foraging in exposed situations even during dark conditions, consistent with their lack of protection via defensive secretions used by the adults. Larval prey would presumably include lepidopterous larvae feeding on or seeking shelter in the moss (Bridwell 1918) or other hidden locations, though this has not been observed, and the larval feeding habit of ingesting liquefied food after preoral maceration and predigestion precludes presence of identifiable food particles in the larval gut.

Larval identification is accomplished to the tribal level using a variety of keys (Emden 1942, Thompson 1979), though the larger adult body size of platynine species versus members of the Bembidiini or Psydrini results in most observable larvae being immature platynines of the genus *Blackburnia*.

**PHYLOGENY AND BIOGEOGRAPHY**

**Cladistic Analysis**

We have previously analyzed the Hawaiian Platynini using cladistic principles (Liebherr & Zimmerman 1998). We base the classification of Hawaiian Platynini advanced in this revision on the 206 unit-coded characters of that analysis; however, recent findings have allowed us to refine both the taxonomic and character-based information from that analysis. Through added field survey, we have discovered three more undescribed species—*Blackburnia platyophthalmica* of Molokai, *B. ipu* of Maui, and *B. ewingi* of Hawaii—as well as the male of *B. polhemusi* (Appendix). In addition, a trip to windward
Haleakala permitted us to survey a variety of sites at different elevations. This intensive sampling resulted in specimens that connected the previously diagnosable forms called “nsp. kuewa” and “nsp. kolukala” (Liebherr & Zimmerman 1998) to *B. abaxoides*. The present species diagnosis for *B. abaxoides*, presented herein, incorporates variation in pronotal shape and dorsal body microsculpture, with that variation represented as polymorphic character states in the cladistic analysis (Appendix). The provisional taxon names “kuewa” and “kolukala” should be discarded, as they have no claim to validity.

Cladistic analysis was performed on the 129 Hawaiian species-level taxa included in this matrix modified from Liebherr & Zimmerman (1998) using the computer program NONA (Goloboff 1995). Outgroup taxa from outside Hawaii used in our prior analysis to root the Hawaiian radiation were excluded from this analysis to economize the tree search. Pertinent NONA parameters used in the analysis were: hold* 100,000; hold/20; mult*200; max*. Such a strategy found more than 65,000 trees of length 1081 over the course of 5 days. The results of this brute force approach were confirmed using the parsimony ratchet (Nixon 1999). Most of the ambiguity in the character data results from character conflict among taxa of Division 2 (see extensive discussion in Liebherr & Zimmerman 1998).

In an added effort to reduce the numbers of equally parsimonious trees to allow more complete visual assessment of the results, the original data matrix was modified. Character codes were added to the matrix for 11 of the 12 taxa with missing data due to lack of male or female specimens (Appendix). The added character codes were determined using Farris (1970) optimization on the character states of known terminals and their hypothetical ancestors. We did not optimize male characters for *B. atra*, because its relatively basal cladistic position and the structure of relationships surrounding it made optimizations ambiguous.

We made one change in tree topology in the course of coding the missing data. Just as in Liebherr & Zimmerman (1998), the shortest cladograms place a clade of five species—*B. curtipes* of Kauai, *B. polipoli* and *B. sharp* of East Maui, *B. perkinsi* of Molokai, and *B. koebelei* of West Maui—as the sister taxon to *B. aaae*, a species found in the dark zone of a cave in Kipahulu Valley, East Maui (Fig. 9). That a five-species clade rooted on Late Miocene- to Pliocene-aged Kauai would be sister group to a single Maui cave species living in lava tubes of the Holocene- and Pleistocene-aged Hana Volcanics (Langenheim & Clague 1987) is unacceptable to us based on temporal and zoogeographic data. The relationship becomes more suspect when the characters used as its basis are examined: character 69, eyes reduced in convexity; character 80, third antennomere sparsely setose; character 143 reversed to elytral striae evenly punctured throughout length. The first occurs in parallel in the two Hawaiian cave platynines, and the second involves increased setosity, a trait associated with many cave-inhabiting carabids (Casale 1988). In addition to including a suspicious hypothesis of relationship in the shortest cladograms, the clades subtended by *B. aaae* and *B. curtipes* include 4 of the 12 species for which specimens of one or the other sex are lacking. Thus, at least part of the support for the pattern of relationship we find unacceptable is based on optimization of nodes surrounded by taxa lacking data. In our revised hypothesis, we remove the *curtipes* clade to sister-taxon status with the species triplet of *B. aaae + B. polhemusi + B. pilikua*, and code missing data with that topology in mind.

The completed matrix was analyzed using the hold*1000 option (other options as above), finding shortest trees of 1083 steps, with the first 1000 cladograms visualized using
CLADOS (Nixon 1995). Therefore, our predictions about possible future findings of male and female characters in the *B. aanae* + *B. curtipes* clade add two steps to the overall cladistic hypothesis.

In addition, we added a geographic character—a 4-state character with states Kauai = 0, Oahu = 1, Maui Nui = 2, and Hawaii = 3—to the matrix and mapped this character onto the resulting 1000 trees both as an unordered and ordered character. This character was not used in any tree searching calculations, but was used to choose among equally parsimonious cladograms using a biogeographic optimality criterion.

We chose one tree of the first 1000 based on the following four criteria.

1. *Blackburnia kahili*, the only species with tarsal dorsolateral sulci typical of Division 2 species but crinate bursal microtrichia typical of Division 1 is placed at the base of Division 2. This interpretation is discussed below under character evolution.

2. *Blackburnia longula* and *B. erro*, exceedingly difficult to diagnose species from West Maui and Haleakalā, respectively, are placed as sister species, with *B. constricta* of Molokaʻi, their sister taxon.

3. *Blackburnia tricolor* and *B. concolor*, also two very similar species from Molokaʻi and West Maui, respectively, are placed as sister species. *Blackburnia concolor* was treated as a variety of *B. tricolor* by Sharp (1903), though added material available today permits diagnosis of the two species.

4. The tree minimizes state changes in the geographic character—i.e., it requires the fewest transformations between the present four oceanic Hawaiian Island complexes. In this hypothesis the minimum unordered geographic transformation length is 27 steps, and the minimum ordered length is 34 steps. These geographic state transformations can be thought of as required dispersal events, so our preferred cladogram is one of those that minimizes such assumptions.

**Character Evolution**

The pattern of character state transformations is the basis for hypothesized phylogenetic relationships. As such, analysis of character evolution is simply the description of character state changes in the context of global parsimony analysis using all characters. Based on this pattern, one can hypothesize the evolutionary context within which the character originated, and if the functional attributes associated with the proposed origin of the character can be tested, some level of confidence in the interpretation of origin may be obtained. The pattern of evolutionary change for any one character is dependent on the cladogram topology, so care must be taken to include alternate interpretations due to alternate topologies or different equally parsimonious ways to optimize state changes on the cladogram. Given the very many equally parsimonious cladograms for the Hawaiian Platynini, we do not discuss evolutionary patterns of all of the characters. We focus on those characters that we feel are most important ecologically or taxonomically. We discuss independent evolutionary derivation of several characters we considered homologous in our matrix, but which in the context of this analysis must be interpreted as parallelisms. Though we discuss all of these in the context of the preferred cladogram (Fig. 9), we present information only for those characters that would exhibit the same or similar transformation patterns in any of the equally parsimonious cladograms. First mention of each character cites the character number assigned in the cladistic analysis (Liebherr & Zimmerman 1998) that formed the
Fig. 9. Preferred cladogram for Hawaiian ingroup Platynini based on matrix of Liebherr & Zimmerman (1998) modified as mentioned in text; step length 1083, CI=0.17, RI=0.72. Shortest multiple equally parsimonious trees found are 1081 steps. Cladogram branch lengths proportional to number of character state changes. Geographic distribution of species given in parentheses; these provide geographical information in taxon-area cladogram (TAC). Pronotal setation indicated by plus/minus formula following species name; first symbol for lateral setae, second for basal. If setal presence is polymorphic, seta for which polymorphism is observed set off from the other by "II." Characters discussed in text noted by Greek letters: loss of flight wings, i.e., brachyptery (ε); change in body form via reduction of humeri (β); change in body form due to development of abacoid humeri (α); development of elytral costae (Δ); configuration of tarsal dorsolateral sulci (Τ); dense ventral vestiture on tarsi (υ); long lobes on fourth tarsomere (λ); ventral excavation on male aedeagus (X); cristate microtrichia in bursal lumen (Ε); and glands on bursa copulatrix (Ω).
CARABIDAE PART I: PLATYNINI

Division I

kahili (Kauai) +/-
asquithi (Kauai) +/
pauma (Kauai) +/-
ulaula (Haleakala) +/
kauaeiensiis (Kauai) +/
optima (Kauai) +/-
transiens (Kauai) -/
opaca (Kauai) +/
alternans (Kauai) +/-
huhula (Oahu) +/
muscicola (Oahu) +/+/+
paludicola (Oahu) +/-
fossilpennis (Oahu) +/-
pratervis (Oahu) +/
audax (Oahu) -/
paloloensis (Oahu) -/
barda (Oahu) -/
oceania (Oahu) -/
lihau (West Maui) +/-
calathoides (Haleakala) +/-
cheloniceps (Molokai) +/+
platycephalica (Molokai) -/
psi (Haleakala) +/
latifrons (Molokai) -/
calathiformis (Haleakala) +/-
howarthi (Haleakala) +/-
debris (Molokai) +/
lut (Haleakala) +/-
microps (West Maui) +/-
tricolor (Molokai) +/-
concolor (West Maui) +/-
abaxoides (Haleakala) +/-
kahua (West Maui) +/-
haleakala (Haleakala) +/-
kilauea (Hawaii) +/-
lanaiahiensis (Lanai) +/-
vagans (Molokai) +/-
auna (West Maui) +/-
epicurus (Oahu) -/
hilaris (Oahu) -/
metromenoides (Oahu) +/
caliginosa (Oahu) -/
mutabilis (Oahu) -/
metlicella (Oahu) -/
fractistriata (Oahu) +/
fordi (Oahu) +/-
foveolata (Haleakala) +/-
fraternal (Oahu) +/-
fraternal "aequalis" form (Oahu) +/-
limbata (Kauai) +/-
pavida (Kauai) +/-
cuneipennis (Oahu) +/-
perpolita (Oahu) +/-
hakeakapa (Molokai) +/
moerens (Molokai) +/
spodriformis (Mau Nui) +/-
constricta (Molokai) +/
longula (West Maui) +/-
erra (Haleakala) +/-
bartlettii (West Maui) +/-
gracilis (West Maui) +/
dyscolea (Haleakala) +/-
platynoides (Molokai) +/-
depressa (Lanai) +/-
kauwa (West Maui) +/-
fulgidia (Haleakala) +/-
insociabilis (Haleakala) +/-
larator (Molokai) +/-
flipes (Lanai) +/-
basis for the analysis summarized in Fig. 9. To simplify visualization of state distributions for this particular discussion, characters of note are indicated by Greek letters both in the text and in Fig. 9.

**Brachyptery.** The colonist of the Hawaiian platynine radiation was fully winged and capable of flight. This primitive configuration is shared by *B. (Protocaccus) mandibularis* and all four species of the subgenus *Colpocaccus*. Wing loss (Fig. 9, o) was coded via four states of successive diminution of flight-wing size: character 200 = flight wings with wing ratio of 1.4-2.3; character 201 = wing ratio 0.4-1.1; character 203 = wings vestigial, extending beyond metanotum; and character 204 = wings very short, the vestige not extending beyond metanotum. The wing ratio represents the alar length (measured from costal vein base to wing apex) × maximum alar width, divided by elytrallength (defined as distance from scutellar apex to elytral sutural apex × maximum elytral width (Liebherr & Zimmerman 1998). The ancestor of Division 2 species (subgenus *Metromenus*) underwent the first three steps of this brachypterous development before the initial divergence in this lineage now preserved by extant species. The vestigial stubs of the metathoracic flight wings are extremely short in several species from Kauai, though this change occurs in the context of strictly flightless taxa.

Within Division 1 (subgenus *Blackburnia*), the clade subtended by *B. octoocellata* and *B. lucipetens* originated with species characterized by fully developed wings, but there were two independent transformations to brachyptery in descendant taxa. In *Blackburnia ewingi* and its sister taxon, the flight wings were all reduced to straps about ½ the length of the elytron. In the other clade, *B. maculata* of Kauai exhibits similar brachypterous wing stubs; however, its sister taxon—the two species on Oahu—retains fully developed wings. Whether one relies on cladistic character optimization, or assumes that an ancestor of *B. mystica* and *B. tibialis* must have colonized Oahu by flight, the undeniable conclusion obtains that *B. maculata* has autapomorphically lost its flight wings after producing the propagule that resulted in colonization of Oahu by the ancestor of the two Oahu species.

The remainder of Division 1 exhibits progressive evolution of brachyptery, first with the reduction of wings to a ratio of 1.4-2.3 in the clade of *B. costata*, *B. corrusca*, and *B. molokaiensis*, then to reduction of the flight wings to vestigial stubs in the rest of the species: the clade subtended by *B. sulcipennis*. The former three species previously constituted Sharp's genus *Chalcomenus*, and all are found along streamside habitats. There are no flight records of any individuals of these three species, and it is unlikely that wings this short could sustain long flights. Nonetheless, as beetles of these species live along streams they are subjected to periodic floods. In this situation even short distance or hopping flight upward away from the water's edge could provide the ability to maintain a population's presence along a particular watercourse.

**Evolution of body form.** The evolution of brachyptery eliminates all selection pressures associated with maintaining aerodynamic competence. As such, the beetle body may become specialized as a vehicle for terrestrial and arboreal movement through threedimensional substrates such as leaf litter, moss, loose soil or soil particles, or layers of bark and cambium. All volant species of Hawaiian Platynini have flattened bodies and dorsally flattened elytra. The elytral humeri are expanded laterally so that the elytral lateral margins are subparallel to parallel throughout the basal half to 2/3 of the elytral length. Reduction of the wings is highly associated with reduction of the humeri in lateral extent (character 154, Liebherr & Zimmerman 1998), so that in most brachypterous species the elytral lateral
margins converge anteriorly, and the humeral angle—the junction of the basal elytral groove with the lateral groove outside the eighth elytral interval—becomes rounded, not angulate. This humeral reduction occurs twice in parallel in Division 1 (Fig. 9, β), once in the common ancestor of *B. ewingi*, *B. rupicola*, and *B. incendiaria*, and a second time in the clade subtended by *B. sulcipennis*. This co-occurrence of brachyptery and humeral reduction is no doubt related to the reduction of the entire thoracic flight apparatus. The three species mentioned above with shortened but possibly functional flight wings—*B. costata*, *B. corrusca*, and *B. molokaiensis*—retain broad humeri even though the flight wings are moderately foreshortened. Conversely, the following species that have vestigial flight wings exhibit broad humeri, a reversal from the narrowed condition (Fig. 9, β-): *B. aterrima*, *B. polhemusi*, *B. perkinsi*, *B.  kaobelei*, *B. micantipennis*, and *B. blaptoides* (Figs. 69D, 108A, 116B-C, 135C, 154A). The first two of these species are composed of large beetles, whereas the next two include among the smallest beetles of the platynine radiation. The last species exhibits peculiarly inflated elytra coupled with markedly reduced eyes. All these variations point to the disconnection of elytral configuration from other aspects of body size and shape in flightless species.

Division 2 also exhibits a basal co-occurrence of humeral reduction and wing vestigialization (Fig. 9, βωωω). The most striking subsequent modification to body form in this clade involves the development of broad, angulate humeri reminiscent of the Palearctic pterostichine genus *Abax* Bonelli. This transformation occurs on Oahu and defines the clade subtended by *B. paludicola* (Fig. 9, α). These broad species diversified on Oahu, and also colonized Maui Nui, though not the island of Hawaii. Based on our preferred cladogram topology, this body form evolved once, with a single reversal to the narrow body shape seen in taxa at the base of Division 2 occurring in the ancestor of *B. howarthi*, *B. debilis*, and *B. kuiki* (Fig. 9, α-). It seems unlikely that this reversal to a narrow body was required for the evolution of the cave habitation by *B. howarthi*, as both the more cladistically basal abacoid species such as *B. lihau*, *B. platyophthalmica*, and *B. calathiformis*, and the narrow more apical species *B. kuiki* have been found exclusively in moss mats. As in Division 1, species in Division 2 exhibit broad humeri while exhibiting vestigial wings. In this instance this reversal is observed twice: once in a clade of three species including *B. pavida*, *B. cuneipennis*, and *B. perpolita*, and once in *B. moerens*.

**Elytral costae.** The development of medially angulate elytral intervals, or elytral costae, restricted to species from Kauai, is one of the more remarkable evolutionary patterns exhibited by the Hawaiian Platynini. These costae occur in various configurations coded as five-state combinations of five characters numbered 146-150 (Liebherr & Zimmerman 1998); slightly rounded costae on intervals 1, 3 and 7, or 1, 3, 5, and 7 (1, 0, 0, 0, 0: *B. curtipes*, *B. elegans*, *B. kauaiensis*); larger costae in these intervals accompanied by smaller rounded costae on intervals 2, 4, 6, and 8 (1, 1, 0, 0, 0: *B. optima*, *B. transiens*, *B. alternans*, and *B. opaca*); smaller rounded costae on intervals 1, 3, 5, 6, and 7 (1, 0, 1, 0, 0: *B. maculata*); angulate costae on intervals 1, 5, and 7 with a rounded costa on interval 6 (1, 0, 0, 1, 0: *B. micantipennis*); and angulate costae on intervals 1, 3, 5, 6, 7, and 8 (1, 0, 0, 1, 1: *B. costata*, and *B. waialeale*). The lone non-Kauai species to exhibit these costae is the sister species to *B. elegans*—i.e., *B. kamehameha* from Oahu (Fig. 9, Δ). These taxa represent five separate derivations of elytral costae implicating 11 of the 24 Kauai species. The remaining 13 Kauai species are arrayed in four convex groups. One at the base of Division 2 gives rise to costate species in the clade subtended by *B. kauaiensis*. 
Examining the habits of costate species sheds some light on possible selective forces leading to development of costae. Though distinct carinae occur in species with flight wings (e.g., *B. costata*) they are not observed in species specialized as climbers of vegetation (e.g., *B. aterrima, B. erythropus*). The generalist Division 1 species *B. maculata*—found on the ground as well as on trees—exhibits costae. Other costate Division 1 species such as *B. costata, B. curtipes, B. elegans, B. kamehameha, B. micantipennis, and B. waialeale* have been found only on the ground. Known recorded habitats for the costate Division 2 species are also primarily from ground level, though *B. kauaiensis* and *B. alternans* have been observed climbing low understory ferns as well as shrubs and trees such as *Clermontia fauriei* H. Lév. and *ohia lehua*. Therefore, it appears that conditions associated with ground-level microhabitats on Kauai have preferentially led to development of these structures. This association with ground habitats coupled with the predominance of ground-dwelling lineages in the Kauai fauna (see Ecological Analysis below) has presented the optimal conditions for evolution of costae in the Kauaian lineages, among all lineages across the Hawaiian Islands. As a functional explanation, raised angulate elytral intervals reduce friction on the elytra as the beetle moves through extremely moist to wet, even muddy substrates, much like runners allow a sled to move through wet snow. Such a prediction is open to testing, though finding such a functional advantage to costae still leaves the question of whether such extremely wet conditions were typical of habitats occupied by platynine beetles during their evolutionary development on the Waialeale massif. If present-day ecological preferences held throughout these species' existence, then the relatively leeward distributions of *B. maculata* (Fig. 46) and *B. curtipes* (Fig. 97) suggest that at least these species evolved costae in less than extremely wet conditions.

**Pronotal setation.** Sharp (1903) based his generic classification of Hawaiian platynines on wing configuration, tarsal structure, and pronotal setation. He did this knowing that certain species variably possessed pronotal setae, either bilaterally lacking a seta, or possessing an anomalous pair of setae on one side versus a single seta on the other. He recognized first that such bilateral asymmetry represented a deficiency of development, not a sport (i.e., a natural variant based on mutation), and second that this instability was better represented in the Hawaiian fauna than in any other regional fauna of the tribe Platynini. In fact, 17 of the 129 Hawaiian platynine species (13%) exhibit variable presence of either the lateral or basal pronotal setae (Liebherr & Zimmerman 1998, characters 97, 98), or both (Fig. 9). Instability of setal presence seems a pervasive force, at least across the pronotal sclerite, as 9 of the 17 polymorphic species exhibit instability in both pairs of setae. Such pervasive instability occurs in a variety of phylogenetic contexts, with sister groups to polymorphic species basally optimized to either setal presence or absence of either seta. It is also not uncommon for patristically close species to represent absolutely opposite setal configuration: e.g., *B. optima, B. opaca, and B. alternans* with +/− lateral/basal pronotal setae embracing *B. transiens* with a −/+ setal configuration; or *B. fractistriata* (−/+ ) versus *B. fordi* and *B. foveolata* (both +/−).

Examination of the complex pattern of variability of pronotal setae during the radiation of Hawaiian Platynini illustrates the utter uselessness of these characters for defining natural groups. Nonetheless, some general, though violated, rules follow. First, the Hawaiian radiation clearly first exhibited a pronotum bearing basal setae only (formula −/+). This formula is retained through much of Division 1, though exceptions exist in that clade, including the loss of basal pronotal setae (*B. perkinsi* and *B. koebeli*) and the isolated
recurrence of lateral setae in *B. terebrata*. The basal monophyly of Division 2—i.e., when it was a monophyletic group composed of only a few Kauai species—was defined by a +/- pronoatal setal formula. This condition holds for many, though by no means all, of the species in the abacoid clade. The preponderance of Oahu species exhibit glabrous pronota. Six of these species are basal in the abacoid clade, which gave rise to propagules to Maui Nui that exhibit a variety of pronoatal configurations. Most of the primarily foliage-inhabiting species of Maui Nui—the clade subtended by *B. hakeakapa*—exhibit the plesiomorphic pronoatal configuration of lateral setae absent, basal present (-/+). Based on our preferred cladogram, this occurrence is a reversal from the opposite state (+/-).

**Tarsal configuration.** Sharp's (1903) third character system for classifying the Hawaiian platynines included characters of the tarsi, especially the dorsolateral grooves or sulci evident on tarsomeres 1-4 (Liebherr & Zimmerman 1998, characters 188-191). These are best examined and compared among species by observing their configuration in the metathoracic legs (Figs. 20, 130-133). Plesiomorphically, the tarsi appeared to bear very fine dorsolateral sulci, as observed in the cladistically basal species for the entire radiation, *B. (Protocaccus) mandibularis*, and the cladistically basal species of Division 2, *B. kahili*. Tarsal configuration has proceeded in two different directions with regard to this character: toward distinct sulci, as observed in subgenus *Colpocaccus* and the remainder of Division 2 (Fig. 9, T-), alternatively to loss of dorsolateral sulci and thickening of the tarsomeres in Division 1 (Fig. 9, T). Grooved tarsomeres are characteristic of many lightly built, long-legged carabids, especially across the Platynini, presumably because the sulci provide structural integrity to the thin-walled tarsal tube. Heavy-bodied taxa, such as beetles in the tribe Pterostichini, are not characterized by such grooved tarsi. Instead they evolved toward broader, heavier tarsi with convex dorsal surfaces; such is the situation in Division 1 (Fig. 29). The only Division 1 species to have reverted to the more plesiomorphic condition of grooved tarsomeres is the lone cave inhabitant, *B. aanae* (Fig. 9, T-). This species possesses the long legs typically seen in cave beetles, and no doubt the reacquiring of grooved tarsi is associated with the need to maintain strength in the very thin, long leg segments.

Other aspects of the tarsi also vary dramatically across this radiation. The ventral setation of the tarsi is the means by which the beetle maintains its purchase on the substrate (Liebherr & Zimmerman 1998, characters 186-187). As one would guess, arboreal species exhibit very different ventral tarsal surfaces than do predominantly terrestrial species. Plesiomorphically the tarsi bear two ventrolateral rows of setae—each of these rows composed of three staggered series of fine setae—separated by a broad median lacuna (Fig. 130). In arboreal species this median lacuna becomes constricted by the broadening of the ventrolateral setal series (Figs. 29D, 133D, F, H; Fig. 9, v). This thickening of the ventral setation is associated with elongation of the apical corners of metatarsomere 4 (MT4) so that they form apical lobes (Liebherr & Zimmerman 1998, characters 192-194; Fig. 9, λ). These lobes on the fourth tarsomere work in opposition to the fifth tarsomere, bearing the claws, providing a broad, hairy surface that can adhere to plant surfaces. Analogous structures are characteristic of legs in other beetle groups such as Coccinellidae and Chrysomelidae, though evolved in those groups from different tarsal segments (Stork 1980). In the Hawaiian Platynini, then, we have two independent origins of highly modified, arboreally suited tarsi: (1) in the Division 1 clade subtended by *B. lucipetens* and *B. kukui*; and (2) in the Division 2 clade subtended by *B. bartletti*. A third independent instance of the evolution of increased ventral setation and lobate tarsomere 4 is represented.
by the Division 2 species *B. caliginosa* and *B. mutabilis*. Tarsomerers in these species appear less specialized for arboreality as a narrow median lacuna remains and the ventral setae are not as long (Fig. 131F, H). Consistent with this, both species are found in terrestrial and arboreal situations.

**Reproductive structures.** Though the male genitalia vary more among the Hawaiian Platynini than in contral continental taxa, the various configurations of the male aedeagus define limited groupings of taxa, and it is difficult to associate particular aspects of the male intromittent organ with characters observed in the female reproductive tract. The aedeagal tip rests in a dorsal pouch of the bursa copulatrix, when such a pouch is present. Our species treatments show the various male aedeagal configurations and associated configurations of the female bursae. One generalized synapomorphy that unites most of the Hawaiian platynines involves the evolution of a depressed area on the ventroapical surface of the aedeagal shaft: the ventral excavation of the aedeagus (Liebherr & Zimmerman 1998, character 49; Fig. 9, X). This character is not observed in the cladistically basal *B. mandibularis*, and is seen in all of the remaining Hawaiian species except *B. mystica* (Fig. 9, X-).

Within the female reproductive tract, the development of cristate microtrichia on the lumenal surface of the bursa copulatrix (Liebherr & Zimmerman 1998, characters 20, 21; Fig. 9, E) is observed in many of the species of Division 1 and serves as the means to choose among the many cladogram topologies resolving Division 2. The plesiomorphic configuration of the platynine bursa copulatrix relative to the Hawaiian radiation includes the presence of a median band of spikelike microtrichia encircling the bursa copulatrix (Figs. 17E, 30B). These microtrichia face toward the gonopore, and are in the appropriate position to hold the male aedeagal internal sac during copulation, or to hold the egg as it is held in the bursa during fertilization. Moreover, the egg would glide toward the gonopore at oviposition on this carpet of spikes. These microtrichia are expressed in a different form in most species of Division 1 and in *B. kahili*, considered by us to represent the basal adelphotaxon to the rest of Division 2. In these species the microtrichia take a cockscomb arrangement, with from three to seven cristae arising from a common base (Fig. 30A). Two species have these cristate microtrichia mixed with the spikelike form: coincidently the not closely related but microsympatric *B. atra* and *B. kahili*. The occurrence in the former is treated as a reversal from the completely cristate condition, whereas that of the latter is interpreted as primary transformation from the plesiomorphic state. The remainder of the Division 1 species, with the exception of the clade subtended by *B. octoocellata*, exhibit a well-developed ring of cristate microtrichia. Conversely, this condition is lost within Division 2 (Fig. 9, E-): i.e., *B. kahili* is the only Division 2 species for which these setae have been observed. The *B. octoocellata* clade of Division 1 also exemplifies the loss of this apomorphy (Fig. 9, E-E-), as the bursal microtrichia in these four species are completely spikelike.

The most distinctive structures of the female reproductive tract are the bursal glands that occur in three species of Division 1 (Fig. 9, Ø): *B. costata* (Fig. 52D), *B. micantipennis* (Fig. 115D), and *B. waialeale* (Fig. 117D). These structures have not been observed before in Platynini, though numerous taxa have been examined (Liebherr & Will 1999). The only other occurrences of such structures include similarly positioned glands in *Tricondyla* tiger beetles (Carabidae: Cicindelini) (Deuve 1993) and pterostichine carabids of the genus *Abaris* Dejean (K.W. Will, pers. comm.). Though these structures are compellingly similar
in position and appearance, they are clearly not homologous among the three tribes in which they occur, and they are not homologous even among the three Hawaiian species! Based on information from all characters, the evolutionary origin of glands in B. costata is independent from that in the other two species that retain this structure from their common ancestor. If one wishes to accept homology for these glands among these three species, one must assume an extra 10 steps on a revised cladistic hypothesis. Interestingly, these three species also exhibit the highest development of elytral costae in the Kauai platynine fauna. They also all occur in streamside or very wet habitats; B. waialeale lives on wet clay soil and along creeks on the summit of Waialeale, the wettest spot on Earth. Perhaps all of these attributes have been acquired in parallel due to existence in an essentially aquatic/terrestrial habitat. Conversely, we may be misled by the other characters upon which we are basing our preferred cladogram. The only means to test either of these alternatives is to add characters to our estimation of phylogenetic affinity among these and the other species.

**Biogeographic Analysis**

Examining taxon-area relationships implicit in the preferred cladogram clearly shows the basal divergence of this radiation on Kauai, then on Oahu, with Maui Nui and Hawaii being the last islands colonized and diversified upon. Relationships within Maui Nui are more complicated, with species on Haleakala and West Maui, or West Maui and Molokai alternatively considered most closely related in various portions of the cladogram.

The best-fitting hierarchy of area relationships for the Hawaiian platynines was determined using items of error analysis (Page 1990, 1993), whereby the observed taxon-area cladogram (Fig. 9) was used to determine the best-fitting fundamental area cladograms. As in Liebherr & Zimmerman (1998) we used the COMPONENT computer program of Page (1993) to search for the best-fitting area cladograms. In this analysis, widespread species were mapped as associates, meaning that widespread distributions were assumed to indicate that the occupied areas were historically related at the level of the widespread distribution. Criteria sought for optimization included number of added leaves, duplications, and losses. Added leaves symbolize hypothetical taxa that must be added to the observed taxon-area cladogram to make it fit a particular fundamental area pattern. They may be thought of as taxa yet to be found, or taxa that have suffered extinction while others have persisted and perhaps diversified. To make that best fit, certain portions of the cladogram must be duplicated; in essence the taxon-area cladogram is filled in with hypothetical higher-level constructs so that it represents a single highly replicated pattern. Duplications signify the number of times portions of the tree must be duplicated to facilitate this best fit. They can be envisioned as “past dispersal events that resulted in sympathy amongst two previously allopatric vicariant sister taxa, with subsequent vicariance of the secondarily sympatric taxa resulting in parallel diversification of [the] two sympatric lineages” (Liebherr & Zimmerman 1998, 157). COMPONENT can also optimize the analysis to minimize a criterion called losses—i.e., the number of monophyletic sets of added leaves needed to make the observed cladogram fit the fundamental area cladogram pattern. Using this criterion suggests that we wish to minimize the number of times lineages colonize new islands and diversify there (i.e., concentrate the lack of fit based on lineages not being able to colonize new islands). This criterion is sensible for a host-parasite system where extinction of a host species eliminates all parasite species in that host, thereby ending
further colonization. It makes less sense in a dispersal/colonization biogeographic system such as Hawaii because concentrating added leaves in larger groups favors hypothesizing earlier extinction events (i.e., the fitting procedure is skewed toward grouping missing taxa in fewer larger groups). As we show below, this criterion is also sensitive to the distribution of species in the various areas, as it unites depauperate areas in its attempt to concentrate added leaves in fewer monophyletic sets of areas. The subtree pruning/regrafting routine was used to search for best-fitting trees for each subanalysis minimizing added leaves, duplications, or losses.

One best-fitting fundamental area cladogram was found for each optimization criterion of added leaves, duplications, and losses (Fig. 10, Table 6). Each of the fundamental area cladograms agrees on the basal position of Kauai relative to all other islands, with the divergence of Oahu next in sequence. The area cladogram that minimizes added leaves (Fig. 10A), or hypothetical taxa, favors resolution of relationships among Maui Nui volcanoes uniting the windward duo of East Molokai (Kamakou) and West Maui (Puu Kukui), this area-pair in a sister-area relationship with East Maui (Haleakala), relationships first reported in Liebherr (1997). The leeward, depauperate mountain of Lanai (Lanaihale) is the basally divergent representative area of Maui Nui. Maui Nui is then sister area to Hawaii Island, and these two youngest island complexes sister to Oahu.

If duplications are minimized (Fig. 10B), the only difference involves a closer area relationship of Lanai to West Maui and East Molokai, with Haleakala being the basally divergent Maui Nui volcano. However, this best fit via minimizing duplications requires five more added leaves than required for the fundamental area cladogram unifying the three windward Maui Nui volcanoes. We prefer to minimize added leaves instead of duplications for several reasons. First, there is much more substantial evidence of a close relationship among the windward triad of Maui Nui simply because there are more representative species living in those windward forests, and more area representations on the taxon-area cladogram. Second, added leaves represent hypothetical missing taxa whereas duplications represent historical dispersal events. A choice between saving five of the former versus one of the latter is a simple decision if the parsimony criterion is invoked.

The third criterion, losses, results in a fundamental area cladogram that groups the two most depauperate areas—Lanai and Hawaii—exclusive of the windward Maui Nui triad of Kamakou, Puu Kukui, and Haleakala (Fig. 10C). This result can be intuitively predicted if we note the many species triplets from Molokai, West Maui, and East Maui. These “real” triplets make fitting our taxon-area cladogram to the fundamental area cladogram topology of Fig. 10C best accomplished by adding monophyletic sets of these three areas, at the same time adding either Hawaii or Lanai to the alternate representations of those two areas. This artifact of taxonomic diversity in the various areas compounds the difficulties of skewed fitting by fewer larger sets of areas noted above.

In our estimation, probably the best fit criterion to use in biogeographic analysis is the numbers of added leaves, as these represent hypothetical taxa that can be added singly or in larger groups, in duplicated portions of a tree or as single interpolated leaves. This freedom to associate hypothetical constructs with real taxa in the production of an optimality criterion of fit seems the most assumption-free way to compare tree topologies.

Given the preferred biogeographic relationships of the various islands, several conclusions are inescapable. First, the Hawaiian Platynini have been present and diversifying in the Hawaiian Island chain since the time Kauai became covered with rain
Fig. 10A-C. Most parsimonious fundamental area cladograms (FAC) derivable from taxon-area cladogram (TAC). A. FAC that minimizes numbers of leaves added to reconcile TAC. B. FAC that minimizes duplications to reconcile TAC. C. FAC that minimizes losses to reconcile TAC. Island codes include: K, Kauai; O, Oahu; Mk, Molokai; WM, West Maui; EM, East Maui; L, Lanai; H, Hawaii Island. Fig. 10D. Map of major islands in the Hawaiian Island chain (after Zimmerman 1948).

Forest, probably 4.5-5.0 Ma. Second, interisland colonization has occurred repeatedly, even between totally oceanic complexes such as Kauai and Oahu, and Maui Nui and Hawaii. These dispersal events have been accomplished by both flight-capable and brachypterous taxa. For example, colonization of Hawaii Island has occurred most likely six times so far from Maui Nui or Haleakala (Fig. 9): two times by taxa possessing fully developed flight wings (*B. hawaiiensis* and the ancestor of *B. kukui* and *B. lucipetens*), once by a taxon with short and possibly functional flight wings (*B. molokaiensis*), and three times by brachypterous taxa (*B. ewingi*, *B. incendiaria*, and *B. kilauea*). At least at the scale of
Table 6. Fit values of added leaves, duplications, and losses for the three best-fitting fundamental area cladograms derivable from the taxon-area cladogram of Hawaiian Platynini (Fig. 9). Island abbreviations are: K, Kauai; O, Oahu; H, Hawaii; L, Lanai; Mk, Molokai; EM, East Maui; WM, West Maui.

<table>
<thead>
<tr>
<th>Fundamental area cladogram</th>
<th>Added leaves</th>
<th>Duplications</th>
<th>Losses</th>
</tr>
</thead>
<tbody>
<tr>
<td>K(O(H(L(EM(Mk,WM))))))</td>
<td>153</td>
<td>39</td>
<td>97</td>
</tr>
<tr>
<td>K(O(H(EM(L(Mk,WM))))))</td>
<td>158</td>
<td>38</td>
<td>99</td>
</tr>
<tr>
<td>K(O((L,H)(EM(Mk,WM))))</td>
<td>166</td>
<td>41</td>
<td>91</td>
</tr>
</tbody>
</table>

the Hawaiian archipelago, interisland colonization by platynine carabid beetles does not require flight ability. Of course, specializations evolving subsequent to wing loss may be associated with lower colonization ability. One obvious candidate for a specialization associated with lowered colonizing ability are the elytral costae that evolved on Kauai. Save for B. kamehameha now walking in the mountains of Oahu, this specialization has remained restricted to Kauai.

Ecological Analysis

The ecological situations of Hawaiian Platynini can be examined both in light of phylogenetic relationships and on the basis of island distribution of species. We recognize five different microhabitat situations within which platynine beetles occur. The occurrence of species in the various microhabitat situations was determined from label data and personal field observations. These may be described by five categories:

0 = species found along streamsides and other water margins—e.g., wet rock faces, bogs, seeps;
1 = forest-floor habitats in mesic and wet forest, such as koa/ohia lehua mesic and wet forest, and ohia wet forest;
2 = dryland habitats such as leeward Deschampsia/Sophora savannah, and open scrubland above timberline;
3 = twilight to dark zones of caves;
4 = arboreal moss mats, liverworts, or among bark flaps and layers on exfoliating trunks of ohia lehua and large koa.

Microhabitat 4 may be immediately adjacent geographically to microhabitats 0 and 1, depending on whether the forest occurs in gulches surrounding streams, or occurs on well-drained slopes. Moreover, if brachypterous individuals normally live in arboreal situations, but must disperse periodically to find new habitat patches, they must travel on the ground during dispersal periods. Not surprisingly, therefore, many of the species have been found in more than one of the microhabitat categories 0, 1, and 4. The microhabitat categories 2 and 3, dryland and caves, differ substantially from the other three, and only a few taxa on Haleakala and Hawaii Island are found in these situations. This restriction is historical, as most lava tube caves have collapsed or have been filled on the older islands, and above-
timberline habitats require large, newly developed volcanoes recently past the end of their
shield-building phase, such as Haleakala and Mauna Kea.

We view ecological preferences in a phylogenetic context by examining the ecological
preferences of species in the four major clades of Hawaiian Platynini, the subgenera
Protocaccus, Colpocaccus, Blackburnia, and Metromenus. These clades have very unequal
species numbers, due at least in part to different dispersal powers associated with these
microhabitat types. Therefore, examination of patterns of ecological change must discount
species diversity and concentrate on the ecological situations utilized in the various clades.

Based on the extant taxa, the Hawaiian platynine radiation appears to have originated
from a progenitor that included streamside habitats in its ecological repertoire. Known
collecting habitats for the basal species, B. (Protocaccus) mandibularis, include several
collections at light, and one capture along a stream (Table 7). The next most basal clade,
the four-species clade considered subgenus Colpocaccus (Fig. 9), includes three generalist
species, found either along streams, or on forest floors, or climbing vegetation, and one
species recorded only from vegetation. Blackburnia tantalus, one of the former three
species, has not been seen alive since 1940, and so we are left with old label data that at best
lists a host plant name. This species is scored in habitats 0, 1, and 4 based on Perkins
statement, “Colpocaccus tantalus is very common in many situations, and fifty or a hundred
individuals are sometimes found in a single batch” (Perkins 1906, 48). The fourth species,
B. hawaiiensis of Hawaii Island, is commonly found within mosses and bark flaps on large
koas. It has also been collected in a house at light (D. Foote to JKL, pers. comm. 1997),
suggesting that it disperses by flight. Arboreality is symptomatic of carabids on Hawaii
Island, and may be an ecological response to the poorly developed soils and torrential
runoff of that young island.

For the 51 species of subgenus Blackburnia, we have label data for 39. These are
variously found in all types of microhabitats we recognize, with seven species found in
streams and adjacent forest floors (categories 0 and 0, 1). This subgenus is the only one of
the four containing dryland species, all found on either Haleakala or Hawaii Island: B.
frigida, B. rupicola, and B. incendiaria. In addition, we did not score B. lenta, a member
of this subgenus found by Perkins on Haleakala, “from 9,500 to the top, or to within 100
or 200 ft. short of the top. The soil perhaps too much like ashes on the top” (Perkins 1894a,
April 11). Therefore it appears that at least these four species in subgenus Blackburnia are
able to survive what most platynine carabid beetles would find a dry, stressful situation.
The modal ecological situation found for Blackburnia species is an exclusively arboreal
existence, though we suggest that this fidelity to the trunks and moss mats of forest trees
must be broken during dispersal phases of these beetles.

The subgenus Metromenus comprises 73 species, of which ecological data are available
for 64. Modally, species in this clade are found in arboreal situations such as moss mats and
trunks, plus on the surrounding forest floor under logs (microhabitats 1, 4). These are
relatively stable ecological situations, unlike stream banks subject to flooding, befitting the
homogeneous occurrence of brachyptery among all Metromenus species. An additional 13
Metromenus have been found only in arboreal situations, meaning that fully 75% of species
with associated ecological data are found in either terrestrial or arboreal forest
microhabitats. Only three Metromenus appear restricted to the forest floor—B. opaca of
Kauai, B. barda and B. cuneipennis of Oahu. Only one has been recorded exclusively from
streamside situations: the single pair of specimens of B. platyophthalmica fogged out of
Table 7. Distribution of species in various habitat types and their combinations for the four major clades of Hawaiian Platynini (percentages of species in each habitat type or combination in parentheses). Habitat types listed by numbers in text.

<table>
<thead>
<tr>
<th>Subgenus</th>
<th>0</th>
<th>0, 1</th>
<th>1</th>
<th>0, 1, 4</th>
<th>1, 4</th>
<th>2</th>
<th>3</th>
<th>4</th>
</tr>
</thead>
<tbody>
<tr>
<td>Protocaccus</td>
<td>1(100)</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Colpocaccus</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>3(75)</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1(25)</td>
</tr>
<tr>
<td>Blackburnia</td>
<td>4(10)</td>
<td>3(8)</td>
<td>4(10)</td>
<td>5(13)</td>
<td>7(18)</td>
<td>3(8)</td>
<td>1(2)</td>
<td>12(31)</td>
</tr>
<tr>
<td>Metromenus</td>
<td>1(2)</td>
<td>0</td>
<td>3(5)</td>
<td>11(17)</td>
<td>35(55)</td>
<td>0</td>
<td>1(2)</td>
<td>13(20)</td>
</tr>
</tbody>
</table>

moss along a small stream on Molokai. Seven other species are extreme generalists, living along streams, on the forest floor, in arboreal vegetation, including moss mats.

Cave habitation has evolved twice in the platynine radiation, once each, so far as we know, in each subgenus Blackburnia and Metromenus. Unlike the stressful dryland situations, the stressful cave environments appear open to geographically appropriate colonists from across the radiation. The movement into caves from near-surface, moss-covered voids in the floor of rain forest habitats is the colonization model best supported by platynine carabids. In both cases—B. aae and B. howarthi—the epigean and cave-inhabiting species are geographically proximate, and the cave-inhabiting species are recently derived (Howarth 1987). Both cave species have their closest phylogenetic relatives composed of rarely encountered taxa (B. polhemusi + B. pilikua for B. aae, and B. debilis + B. kuki for B. howarthi, Fig. 9), suggesting that species with low-density distributions are those most likely to include the small, peripheral populations likely to undergo speciation when isolated in caves.

Taken island by island, the platynine radiation exhibits trends not unlike those seen viewing ecology in relation to phylogeny, not surprising as the radiation is rooted on Kauai. Nonetheless, viewing the data in a geographic dimension illustrates how island attributes may influence habitat preferences of resident carabid beetles. The general trend observed island by island is the heavier presence of strictly arboreal species on Maui Nui (microhabitat 4, Table 8), and the general tendency for species on Kauai to be more closely associated with streamside or terrestrial, forest-floor situations (microhabitats 0, 1, Table 8). Nonetheless, over half of the Kauai species have been recorded from arboreal microhabitats, and nearly half of the Maui Nui species may be found running on the forest floor at night, as well as on foliage. Hawaii Island has a habitat preference distribution skewed away from streamside habitats, no doubt because of the scarcity of such habitats on a newly evolved island. Nonetheless, species on Hawaii are not all generalists in their habits, with nearly half of the species restricted to arboreal microhabitats. Two of these species—B. lucipetens and B. kukui—are ready fliers with very well-developed flight apparatus, suggesting that they may be truly arboreal, never needing to walk on the ground. These species also exhibit highly modified tarsi, with the fourth tarsomere strongly bilobed. This combination of characters—fully developed flight apparatus and broadly lobed tarsi—
Table 8. Distribution of species in various habitat types and their combinations for the four major island groups of Hawaii. Percentages of species in each habitat type or combination in parentheses. Habitat types listed by numbers in text.

<table>
<thead>
<tr>
<th>Island</th>
<th>0</th>
<th>0, 1</th>
<th>1</th>
<th>0, 1, 4</th>
<th>1, 4</th>
<th>2</th>
<th>3</th>
<th>4</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kauai</td>
<td>3(15)</td>
<td>0(0)</td>
<td>4(20)</td>
<td>2(10)</td>
<td>9(45)</td>
<td>0</td>
<td>0</td>
<td>2(10)</td>
</tr>
<tr>
<td>Oahu</td>
<td>1(4)</td>
<td>0(0)</td>
<td>4(15)</td>
<td>4(15)</td>
<td>11(41)</td>
<td>0</td>
<td>0</td>
<td>6(13)</td>
</tr>
<tr>
<td>Maui Nui</td>
<td>2(5)</td>
<td>2(5)</td>
<td>0(0)</td>
<td>1(2)</td>
<td>18(43)</td>
<td>2(5)</td>
<td>2(5)</td>
<td>15(36)</td>
</tr>
<tr>
<td>Hawaii</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1(14)</td>
<td>2(29)</td>
<td>1(14)</td>
<td>0</td>
<td>3(43)</td>
</tr>
</tbody>
</table>

is also observed among the species of the West Indian *Platynus bromeliarum* group that are restricted to life within arboreal bromeliads (Liebherr 1986).

Cladistic analysis of the Hawaiian platynine taxa plus a variety of circum-Pacific outgroups (Liebherr & Zimmerman 1998) found the genus *Lorostema* Motschulsky to be most closely related to the Hawaiian *Blackburnia*. This taxon comprises six species—we consider *Lorostemmoides* Habu to be synonymous with *Lorostema* (Lorenz 1998a)—distributed from Sri Lanka eastward across the Indo-Malayan archipelago and northward throughout the Philippines to Japan. One widespread species—*Lorostema bothriophora* (Redtenbacher)—is distributed eastward in the Pacific to Tahiti. *Lorostema informalis* Darlington was found to be a winged, streamside hygrophile by Darlington (1952, 1971), an ecological preference identical to that of *B. mandibularis*, the cladistically basal Hawaiian platynine from Kauai. The genera *Lorostema* and *Notagonum* Darlington were considered by him to represent the more generalized lineages from which New Guinean specialist montane taxa were derived (1971). These montane taxa may be quite geographically restricted. The genus *Nebriagonum* Darlington comprises six species restricted to the Bismarck Range. Other New Guinea genera of Darlington and their habitat preferences include: (1) *Altagonum*, *Fortagonum*, *Laevagonum*, and *Montagonum* living in montane rain forest; (2) *Potamagonum* living along turbulent mountain brooks, and (3) *Maculagonum* living arboreally, at least partly on grass. It should be noted that the poxed *Maculagonum* species (Darlington 1952) and the Hawaiian species triplet (*B. maculata* + (*B. mystica + B. tibialis*)) are the only carabids known that share the irregularly flecked elytra, wherein melanic fields are randomly interspersed with flavous, less-pigmented areas. Darlington suggested that these montane specialists were independently derived from generalist taxa, possibly some of those placed in the genus of convenience, *Notagonum*. By this, Darlington’s hypothesis of New Guinea platynine radiation helped lay foundation for Wilson’s (1961) taxon cycle, wherein lowland generalist taxa that persist evolutionarily must specialize over time, colonizing and adapting to upland habitats. Those taxa that do not colonize and adapt face extinction due to aggressive colonization by later colonists to the unstable lowland habitats.

The overall pattern of ecological specialization during the diversification of Hawaiian Platynini recalls aspects of the taxon cycle, interpreted in a cladistic context (Liebherr &
Hajek 1990). Aspects in accord with the taxon cycle include: (1) the occupation of streamside habitats in the cladistically most basal species, *B. mandibularis*; and (2) the general trend toward occupation of arboreal habitats in the faunas of the younger islands Maui Nui and Hawaii, those faunas also tending to be composed of the more recently derived species in the radiation. As shown by the biogeographic analysis, however, island colonization within the archipelago can occur by terrestrial or arboreal colonists. Therefore, Wilson’s scenario—whereby each island or volcano is colonized by generalist lowland species with intraisland habitat specialization then ensuing—does not occur. Instead, colonization and speciation tend not to profoundly disturb the ecological preference of the resultant species, with clades comprising species of similar habitat usage spanning several islands—e.g., the three streamside species of Division 1 (*B. costata*, *B. corrusca*, and *B. molokaiensis*, Fig. 9), the nine terrestrial species of Division 1 (from *B. micantipennis* to *B. kipahulu* in Fig. 9), or the five arboreal species including *B. bartletti* and its sister group. Moreover, given the ecological plasticity inherent in many of the species, the nature of the island may define the species’ ecological preference. For example, *B. hawaiiensis* of Hawaii Island has only been recorded from arboreal habitats, but belongs to a clade with two other generalist species, *B. posticata* of Kauai and *B. lanaiensis* of Maui Nui. It is reasonable to suggest that *B. hawaiiensis* may more extensively utilize terrestrial microhabitats as soils continue to develop on Hawaii Island (Vitousek et al. 1997).

**Conservation Status**

We conducted extensive geographic sampling of platynine carabids partially to answer the question “What has the past 100 years of Hawaiian development meant for these beetles?” Several points are abundantly clear in this regard. Most important, many rain forest localities within Hawaii still support what appear to be undisturbed native communities, at least restricting consideration to insects and plants. The abundance and diversity of native carabid beetles can be astounding, with up to 10 species or more of Platynini inhabiting any one site. Clearly any efforts spent in preserving such situations is much warranted. Nonetheless, several patterns of diminution of diversity appear evident, and we describe those below: (1) the loss of diversity in lower elevations; and (2) the loss of diversity in leeward situations. To some degree, observing these changes is possible because such sites were sampled 100 to 125 years ago by Blackburn and Perkins. Moreover, Perkins’ experiences in the 1890s allowed him to personally witness the destruction of habitats in sites he visited repeatedly (Liebherr & Polhemus 1997a). For the wetter montane situations that have been visited first during the recent survey efforts, our present-day documentation will assist those who study these sites in the future.

As the most objective means of ascertaining the status of the various platynine species, we have used two criteria related to the known dates of last existence (DLE)—i.e., species seen no later than 50 years ago, and species not seen within the past 100 years (Table 9). These two DLE levels can be related to significant events in the history of Hawaiian natural history. The shorter time span is associated with activities after World War II, and the increase in commercial and military traffic by both air and sea. The longer time span approaches that since the comprehensive survey of the Hawaiian insect fauna by R.C.L. Perkins completed in 1902.
Table 9. Number of species with date of last existence (DLE) (1) more than 50 years ago but less than 100 years, or (2) more than 100 years ago, and percentage of all such endangered species within the platynine fauna of each Hawaiian Island.

<table>
<thead>
<tr>
<th>Island</th>
<th>No. w/DLE &gt; 50 yrs.</th>
<th>No. w/DLE &gt; 100 yrs.</th>
<th>% platynine fauna</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kauai</td>
<td>3</td>
<td>1*</td>
<td>16.7</td>
</tr>
<tr>
<td>Oahu</td>
<td>2</td>
<td>2</td>
<td>12.5</td>
</tr>
<tr>
<td>Molokai</td>
<td>2</td>
<td>0</td>
<td>9.1</td>
</tr>
<tr>
<td>West Maui</td>
<td>0</td>
<td>2</td>
<td>11.8</td>
</tr>
<tr>
<td>East Maui</td>
<td>3</td>
<td>5</td>
<td>23.5</td>
</tr>
<tr>
<td>Lanai</td>
<td>1**</td>
<td>1</td>
<td>40.0</td>
</tr>
<tr>
<td>Hawaii</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Total</td>
<td>10**</td>
<td>11*</td>
<td>16.3</td>
</tr>
</tbody>
</table>

*Single known locality of *B. transiens* currently inaccessible on private property.  
**B. lanaiensis** has been observed on Molokai and Maui within the past 50 years.

The greatest potential loss of platynine diversity in Hawaii is likely to have occurred on Maui, especially East Maui. Fully seven species—*B. agonoides, B. anomal, B. haleakala, B. koebel, B. komohana, B. lenta,* and *B. terebrata*—have not been seen since Perkins' time on Maui, with another three having last dates of existence documented as 1902 (*B. octoocellata* and *B. sharpi*) or 1913 (*B. polipoli*). This loss is concentrated in the leeward portions of the two volcanoes (Fig. 11E). As mentioned above, this pattern is somewhat attributable to the pattern of sampling whereby Perkins did not have access to wetter regions to the east on Haleakala and was largely thwarted by bad weather from entering the West Maui Mountains (Liebherr & Polhemus 1997a). However, historical contractions of species distributions in *B. rupicola* (Fig. 38) and *B. frigida* (Fig. 86) also indicate the decline of habitat qualities needed for carabid beetles in these leeward areas. Species in this assemblage from lower elevations—1000-1500 m—were associated with forest dominated by *Acacia koa* and ohia lehua. Based on distributions of the carabid beetles, the communities in which these species lived probably centered on koa/ohia montane mesic forest (Gagné & Cuddihy 1990), extending to the forest's leeward edge. Perkins makes mention of collecting *B. terebrata* under a dead log in association with finding anobiids under bark of koa (Perkins 1894a, 7 April). He also observed *B. octoocellata* ovipositing in the chinks of koa bark (Perkins in Sharp 1903). This suggests that his "Haleakala 4000 ft." and "Haleakala 5000 ft." localities of 1894 and 1896 (Anonymous n.d.) were near the receding edge of native koa forest as it was progressively destroyed by pasturing cattle and logging. Comparison of pre-human distributions of mesic forest on Haleakala with that present today illustrates the immense changes that faced this community over the past century or more (Pratt & Gon 1998). The most promising site for rediscovery of the missing
Fig. 11. Sites on the Hawaiian Islands from which species were collected that have their last known dates of existence (DLE) more than 50 years ago. Small circles represent sites with one such species, larger circles represent sites with two or more species. A. Kauai. B. Oahu (sites for B. tantalus not shown; see text and Fig. 24). C. Molokai. D. Lanai. E. Maui.

East Maui species lies south of Haleakala's southwest rift zone at elevations comparable to historical collection sites, though this flank is many kilometers from where Perkins collected in the 1890s, and may represent another area of endemism on the mountain.

Patterns of diminution do not appear so extreme on other islands, though in the case of Lanai it is due to a paucity of species living on the island relative to the much more diverse Haleakala. Lanai's fauna has suffered the highest potential extinction, with two of the more leeward occurring species lost from recent records (Fig. 11D). This level of extinction is in accord with the successive ecological catastrophes visited on this island (Hobdy 1993). Of the two missing species, B. lanaiensis is found on Molokai and Maui as well, so in a
conservation context this extinction on Lanai is less significant. The absence of the endemic *B. lanaihalensis* since 1894 is the more significant loss. Its single known locality in Kaiholena Gulch is the most likely—though not likely—site of rediscovery.

Of all the islands with moderate to high levels of platynine diversity, Molokai is the least disturbed (Fig. 11C). The two species missing since 1902—*B. perkinsi* and *B. debilis*—are known from five and one specimens, respectively, so these species were never commonly encountered. That *B. debilis* most likely came from near Perkins' base camp at Makakupaia suggests that like the potentially lost Maui species it preferred mesic rather than wet forest.

The Waialeale volcanic caldera broadly supports the Alakai Swamp, which is drained by numerous leeward-directed river valleys uniting into the Waimea River. As on Maui, comparison of recent patterns of diversity with those of Perkins' time is confounded by the different geographical array of sample sites (Fig. 3). Also, like Maui, species not observed in the past 50 years tend to concentrate on the leeward reaches of the Waialeale massif. The single species from the more southern spur of Waialeale above the Makaweli River—*B. transiens*—was found by Perkins with the assistance of local sugarcane planters. Such cooperation does not now exist, so its current status remains in doubt. The other three species found farther north that have not been seen in the last 50 years—*B. ambiens*, *B. opaca*, and *B. optima*—were collected from Kalalau Valley south to the Waialae River, and should be sought throughout that large challenging region. Sampling during 1995 in the vicinity of Waialae Cabin above Waialae Falls on the Waialae River suggests that invasion of grasses may have significantly disturbed native forest floors south and east of that area. Patches of undisturbed forest at lower elevations along the Waialae River and Koaie Stream should be searched for these missing species.

Oahu, the Hawaiian Island bearing the brunt of human population, might be expected to bear the most loss of diversity. However, such losses are concentrated in areas directly uphill from Honolulu, and given the large, sympatric distributions of many of the Oahu species, loss of diversity has been less than that observed on Maui (Fig. 11B). *Blackburnia blaptoides*, collected from “Konahuanui 1500 ft.” by Blackburn, and *B. paloloensis*, found from Palolo Valley to Pauoa Valley during the early 1900s, are missing from recent samples in the Koolau Range. A single Waianaes endemic, *B. mystica*, remains unobserved since Blackburn walked into the Waianaes from Wahiawa in 1877. The most dramatic loss involves *B. tantalus*, the most commonly collected Oahu carabid in the nineteenth century (Liebherr & Polhemus 1997b). Even though it accounted for 40% of the total captures in the last century, and it possessed a vast historical range that covered Oahu (Fig. 24), its date of last known existence is 1940. The last captures of this species during the 1930s were in Haleauau Gulch on the windward side of Mt. Kaala, and in Kaipapau Valley and on the Castle Trail in the north Koolau Range. These areas require further study to determine the status of this previously abundant species.

From what we know of habitat preferences in Hawaiian Platynini, it appears that patterns of habitat utilization remain conservative within taxonomically diversifying clades. This means that loss of biodiversity is concentrated in those clades occurring in the most disturbed mesic and leeward habitats. The sister group of *B. curtipes* (Fig. 9)—i.e., *B. polipoli*, *B. sharpi*, *B. perkinsi*, and *B. koebelei*—constitute one such potentially devastated clade. Similarly, of the species called “big-heads” in correspondences between Sharp and Perkins (the clade subtended by *B. agilis*, Fig. 9), three of the seven species are missing from collections made during the past 100 years: *B. anomala*, *B. lenta*, and *B. terebrata*. 
Such observations support the utility of phylogenetic criteria in any evaluation of how taxa will respond to habitat change and loss.

**Classification**

We have taken a nomenclaturally conservative course for classifying the Hawaiian Platynini, in that we have synonymized the many genera proposed by Blackburn (1878a) and Sharp (1884, 1903) under *Blackburnia* Sharp, 1878. This decision is based on the desire to emphasize the monophyletic nature of the native Hawaiian Platynini—i.e., its founding in the archipelago by a single colonizing taxon. In so doing, we have proposed a genus that is disparate morphologically, meaning its members lack a sufficient level of overall similarity to permit recognition of member species by habitus alone. Indeed, the many morphologically disparate elements in *Blackburnia* coupled with the ease of recognizing pronotal setation and flight-wing configuration were the underlying reasons that Sharp (1903) proposed his many genera in *Fauna Hawaiensis*. For habitus recognition, we suggest users first focus on the subgeneric rank, as each subgeneric assemblage offers substantial morphological similarity (though extensive diversification of form is especially evident within Division 1, Fig. 9). We have not defined any groups below the subgenus for the simple reason that we believe classification should reflect phylogenetic affinity and the recognition of monophyletic groups. Such an effort presupposes a robustly supported phylogenetic hypothesis so that future additions of taxa or characters do not radically change taxon membership. As of now, morphological data unambiguously support monophyletic subgenera as we have defined them, but groupings of species within subgenera are not as well supported. The development of molecular sequence data for native Hawaiian platynines is ongoing (M. F. Whiting & J. R. Cryan, pers. comm.), and the combination of morphological and molecular data should serve to produce a more robust phylogenetic hypothesis for all levels of this radiation than morphological data alone. As such, we await further phylogenetic data before codifying species relationships in a more elaborate classification. When that classification is proposed, the most efficacious approach will be to add monophyletic species groups as an informal taxonomic rank within the subgenera *Blackburnia* and *Metromenus*. 
This identification key is based almost exclusively on external anatomical characters, though for one cryptic species pair from Oahu—*B. optata* and *B. hihia*—a male specimen must be dissected for positive determination of a series. To use this key, one should have available a stereomicroscope preferably capable of 125× magnification, though lower magnifications may be used if the user is willing to try both alternate couplets when the couplet decision involves microsculptural characters. Colors and textures described in this key and in the descriptions were assessed under fiber-optic halogen illumination, with a ring-light attachment used on the microscope. Specimens should be clean, or at least free of most dirt so that microsculpture on the pronotum and elytra can be examined. One eyepiece should contain a measuring reticle or ocular grid so that relative proportions can be calculated for various structures.

Line illustrations for the male aedeagus are presented for all species for which males are known. The platynine carabid aedeagus, as for many of the tribes in Harpalinae, is held within the abdominal apex in a position rotated 90° from the symmetrically held, everted position. For the Hawaiian *Blackburnia* and other members of the subtribe Platynina, the aedeagus is rotated 90° clockwise when moved to repose—viewed facing toward the beetle head—so that the apex of the aedeagal median lobe is directed toward the left side of the body when held between the abdominal sclerites. For all species of *Blackburnia* we present line drawings for two views of the median lobe of the aedeagus: (1) a view of the anatomically right (or ventral) side in repose; and (2) a view of the anatomically ventral (or anterior) side in repose.

During copulation, the male aedeagus of *Blackburnia* beetles is everted, rotated 90° counterclockwise and directed forward. Therefore the anatomically ventral side of the aedeagus is oriented dorsally as the aedeagus enters the female vagina and bursa copulatrix while the male beetle maintains a superior position riding on the female’s dorsum. The aedeagal tip enters the bursa as far as the dorsal pouch of the bursa (e.g., Fig. 52D), or presumably to that position if a pouch is not evident. The view from the anatomically right side of the aedeagal median lobe allows one to evaluate curvature of the anatomically ventral surface, the extent of the ventral excavation, and the length of the apex beyond the ovoid ostium at which point the internal sac evaginates during copulation. The view from the anatomically ventral perspective is intended to focus on the shape of the apex of the median lobe, be it gradually narrowed to a rounded tip (e.g., Fig. 23B) as in *B. tantalus*, narrowed to a pointed tip (e.g., Fig. 41B) as in *B. lucipetens*, or attenuate (e.g., Fig. 106B) as in *B. medeirosi*. This ventral view was drawn with the apical quarter of the median lobe horizontal in the field of view. Because the curvature of the aedeagal median lobe differs among the species, keeping the apex horizontal as a comparative reference for the apex necessarily distorts the views of the basal 3/4 of the lobe and the parameres. Nonetheless we have included these features in the drawings to permit alignment of the dissection and proper comparison for the purposes of identification.

There is much structural variation in female reproductive tracts of Hawaiian Platynini, as our illustrations demonstrate. We have labeled illustrations to permit easy identification of the structures; Liebherr & Zimmerman (1998) should be consulted for the evolutionary aspects of these characters.
Male and female genitalic dissections are most easily accomplished by first relaxing the specimen in near-boiling distilled water containing a small amount of detergent. After soaking for approximately 30 min., male specimens can be removed from their point or pin, and the intersegmental membrane apicad sternite VII and mediotergite VIII cut with a sharpened minute needle. The assembly comprising the median lobe plus associated laterotergites and antecostal apodemes of segments VIII and IX (Deuve 1988) can then be removed and soaked in cold 10% KOH overnight to clear the tissues. The dissected parts can be gently acidified in cold dilute acetic acid after clearing, and then transferred to glycerin for viewing and storage in a genitalia vial attached to the specimen pin.

Dissection of the female reproductive tract follows a similar procedure, except that it is best to disarticulate the entire abdomen after relaxing the specimen in hot water, and then soak the abdomen in 10% cold KOH overnight. As the spermatheca and associated spermathecal gland are quite fragile and surrounded by tracheae and dissolved fat body, the cleared abdomen should be dissected in the following sequence: (1) remove the abdominal tergites along the pleural membranes to the position of abdominal segments VIII and IX (the invaginated genitalic segments) by gripping the edge of the basal tergite at one of its pleural margins and pulling the tergites posteriorly with one pair of forceps while holding firmly to the basal sternite with a second pair of forceps; (2) remove the membranous tergites plus the genitalic segments VIII and IX from the external sternites (II-VII), then remove the membranous basal tergites from the genitalic segments; (3) place the genitalic segments and associated bursal assembly, hindgut, and defensive glands in methyl cellosolve (ethylene glycol monomethyl ether) containing dissolved Chlorazol Black stain (Eastman Kodak Corp.) for 10-15 min.; (4) carefully remove the sclerites of the eighth abdominal segment, and attached tracheae and undissolved fat body associated with the bursa copulatrix, spermatheca, and gland; (5) carefully distend the bursa to determine its length relative to the length of the common oviduct; and (6) mount the stained preparation in glycerine under a cover slip on a compound microscope slide. After examination, the preparation can be stored in a genitalia vial attached to the specimen pin.

Identification of the adults of Hawaiian Platynini depends to a large degree upon accurate observation of chaetotaxy. Standard terms used to identify the setae (Fig. 12) follow usage in other carabid identification guides—e.g., Lindroth (1969). Finding and/or counting setae requires a clean specimen; if too dirty, the specimen may be immersed in hot, soapy, distilled water for a time to allow removal of the obscuring material. If the seta is broken, the articulatory base will be evident, though in some Hawaiian platynine Carabidae the setae are exceedingly short and thin, and the sockets are difficult to discern without high magnification. There is much infraspecific variation in setal presence; this variation is accounted for by permitting species to key via more than one route in the keys below. We also report such variation under the appropriate species treatments. Sharp used the presence or absence of lateral and basal pronotal setae as the basis for generic diagnosis in his 1903 classification. In the context of parsimony analysis, these characters are exceedingly homoplastic, and they may define natural groups at very low taxonomic levels (Liebherr & Zimmerman 1998). Nonetheless, these characters are easy to discern in the field—assuming a sunny day or a well-lit cabin—and we use them where possible to sort species among the key couplets.

We give body lengths as the sum of three measurements: (1) the distance from the median labral apex to the cervical collar or shallow ridge at the back of the head just below
the anterior margin of the pronotum in normal beetle posture; (2) the distance from the
medial anterior to medial posterior margins of the pronotum; and (3) the distance from the
scutellar ridge—i.e., the front of the exposed triangular surface of the scutellum held
between the elytra—to the tip of the left elytron (the elytron not usually pinned). This body
length does not take into account the length of the mandibles (of uncertain position in any
specimen) and the exposed portions of the abdomen (considerable in well-fed and or gravid
individuals). As such our overall, or standardized body length values may seem slightly too
small for those accustomed to field identification; however, they combine maximally
reliable repetition of measurements with a value as close to the actual body size as possible.

We have quantified several aspects of head shape using ratios. The ocular ratio is the
maximal distance across the outer surface of the compound eyes, measured from the dorsal
side of the specimen, divided by the minimal distance between the eyes on the vertex (Fig.
13). The development of the eyes and size of the head capsule does not vary in a monotonic
manner among either individuals of different species, nor among conspecific individuals
of different sizes. Therefore we use this measurement judiciously, and as a later resort to
identification than other more reliable, qualitative characters. Several Hawaiian platynines
exhibit elongation of the mandibles. For those taxa we have used the ratio of the distance
from the left mandibular apex to its dorsal condyle divided by the distance from where the
lateral labral apex overlies the lateral margin of the mandible to the dorsal condyle.
Determining this ratio necessitates estimation of the labral-mandibular overlap position if
the mandibles are either widely opened or tightly closed. Again, this ratio is used sparingly
as an adjunct to other characters.

Flight wing size varies even among species possessing full venation, and for which
specimens have been collected in flight. We quantify this variable development using the
wing ratio (defined earlier in the “Character Evolution, Brachyptery” section), which
compares wing area to elytral area, thus giving a rough guide to the amount of wing area
per unit body size.

We make substantial use of microsculpture, especially for diagnosing closely related
species. We follow the terms of Lindroth (1974) to describe the configuration of the
cuticular surface. The isodiametric mesh represents the most common configuration of
cuticular microsculpture both within Platynini and in the family Carabidae at large (Fig.
14A). This shape is observed in the most basal Hawaiian platynine taxa, and as such
represents the plesiomorphic microsculpture condition in this radiation. Several taxa exhibit
modification of the isodiametric mesh whereby each individual sculpticell becomes
elevated, giving the overall surface a rough or granulate appearance (Fig. 14B). By far the
most broadly occurring microsculptural condition among Hawaiian platynines involves
transverse orientation of the individual sculpticells, resulting in a transverse mesh (Fig.
14C). Transverse and isodiametric meshes often co-occur on various parts of an individual
beetle—e.g., the pronotal laterobasal depressions may be lined with more or less
isodiametric sculpticells, whereas the pronotal disc is covered with transversely elongate
sculpticells. Similarly, the inner elytral intervals may be covered with flat transverse
sculpticells whereas the outer, or eighth interval, will be covered with isodiametric, or
possibly elevated, granulate isodiametric sculpticells. The most highly derived form of
sculpticell configuration entails numerous transverse parallel lines that are only
occasionally joined longitudinally, forming at best an irregular mesh (Fig. 14D). Such
parallel lines result in an iridescent cuticular surface. The function of iridescent cuticle
Fig. 12. *Metacolpodes buchanani* (Hope). A. Dorsal view. B. Ventral view. aas, apical abdominal setae of male; bs, basal pronotal seta; ds, dorsal elytral setae; hu, humeri, showing rounded humeral angle; les, lateral elytral setae; ls, lateral pronotal seta; ms, mentum seta; msa, mesofemoral anteroventral setae; msr, mesocoxal ridge seta; mta, metafemoral anteroventral seta; mtc, metacoxal
setae; p, pedicel; ppv, profemoral posteroventral setae; sa, sutural apex; sas, subapical sinuation of elytra; sc, scape; sct, scutellar setae; sms, submentum setae; sos, supraorbital setae. Abdominal sternite number indicated by Roman numerals.
in predominantly nocturnal creatures has been long questioned (Lindroth 1974), and enough counter examples exist for any single interpretation to leave any or all answers wanting. Among Hawaiian platynines, *B. sulcipennis* and *B. curtipes* of Kauai both exhibit profoundly parallel microsculpture and are found in drier forest situations (Figs. 62, 97). Conversely, Maui Nui species most closely related to *B. curtipes* also inhabit drier forest situations, and two of them—*B. perkinsi* and *B. koebelei*—exhibit among the most granulate elytral microsculpture in all Hawaiian Platynini. Lindroth's conclusion that these various configurations are evolutionarily maintained as "not harmful" is perhaps the best answer presently available to their evolutionary significance. Their taxonomic significance is indisputable, and careful attention to microsculpture will ease species identification.
Key 1

Introduced Species and Subgenera of Native Species

1. Prosternal process apically marginate, bead delimiting ventral surface (Fig. 15A-B); tarsal claws with long pectinations or short serrations on mesal surfaces (Fig. 15D-E) ................................................................. 2
   — Prosternal process unmarginated (Fig. 15C); tarsal claws smooth (Fig. 15F) ..... 3

2(1). Pronotum with sinuate lateral margin and angulate hind angles, hind pronotal seta located in distinct marginal bead; tarsal claws serrate, the serration deepest near base of claw (Fig. 15D); integument piceous, elytra with faint bluish metallic luster
   — Pronotum with convex lateral margin and rounded hind angles, basal pronotal seta located in mesal faint marginal bead; tarsal claws markedly pectinate, 3-5 long pectins on basal 2/3 of claw (Fig. 15E); elytral disc brunneous, pronotum and head dorsally rufous ...................... *Laemostenus complanatus* (Dejean) (p. 462)

3(1). Elytral apex rounded or smoothly angulate at suture; elytral disc with or without metallic luster, if shiny metallic green, humeri markedly reduced and flight wings vestigial ....................................................... 4
   — Elytral apex with small denticle at sutural angle; elytral disc a vivid metallic green, pronotum and head shiny rufous, with slight greenish luster, legs rufotestaceous, femoral apices piceous; humeri broad; macropterous ......................
      ............................................................. *Metacolpodes buchanani* (Hope) (p. 466)

4(3). Mandibles foreshortened to elongate, but distance from articulation to apex not more than 2× distance from articulation to median apical margin of labrum; fifth tarsomere glabrous or setose ventrally; macropterous or brachypterous ................................................................. 5
   — Mandibles extremely elongate, distance from mandibular dorsal articulation to apex greater than 2× distance from articulation to median apical margin of labrum (Fig. 13); fifth tarsomere glabrous ventrally; macropterous; Kauai .......
      *Blackburnia* (Protocaccus) *mandibularis*, new subgenus, new species (p. 83)

5(4). Brachypterous, or if winged, basal two tarsomeres of middle and hind legs rounded dorsally, without evidence of dorsolateral grooves ...................... 6
   — Macropterous AND basal two tarsomeres of middle and hind legs with evident dorsolateral grooves; grooves on outer dorsolateral margin more developed or not than those on mesal margin ..................................................................................
      ............................................................. *Blackburnia* subgenus *Colpocaccus* (Key 2, p. 58)

6(5). Basal tarsomeres of middle and hind legs with variously developed inner and outer dorsolateral grooves, at least outer groove evident on basal metatarsomere; all species vestigially winged ................................................................. 7
   — Basal tarsomeres of middle and hind legs without evidence of dorsolateral grooves ..................................................................................
      ............................................................. *Blackburnia* sensu stricto, in part (Key 3, p. 59)
Fig. 15. Prothoracic and tarsal structures of Platynini known to occur in Hawaii. A. Prothorax of *Laemostenus complanatus*, ventral view, procoxae removed. B. Prothorax of *Calathus ruficollis*, ventral view, procoxae removed. C. Prothorax of *Blackburnia posticata*, ventral view, procoxae removed. D. Metatarsal claws of *Laemostenus complanatus*, ectal view. E. Metatarsal claws of *Calathus ruficollis*, ectal view. F. Metatarsal claws of *Blackburnia posticata*, ectal view. pepm, proepimeron; pepp, proepipleuron; peps, proepistemum; ps, prosternum; psp, prosternal process.
Eyes much reduced, only four ommatidia visible; apex of scape and pedicel, entire length of antennomere 3 densely setose; apex of femora densely setose; pronotum with sinuate lateral margins, and a single basolateral seta situated 0.20× pronotal length before hind angle; Haleakala cave species

\[ \text{Blackburnia s.s. aaeae (Samuelson & Liebherr) (p. 187)} \]

Eyes less reduced; apex of scape without dense pelage of setae; femora apically glabrous; pronotal setation differing, if single basolateral seta, it is less than 0.20× pronotal length cephalad hind angle

\[ \text{Blackburnia subgenus Metromenus (Key 4, p. 66)} \]

Key 2

Adults of the subgenus *Colpocaccus* Sharp

1. Pronotal disc shiny, transverse mesh microsculpture not as deep, surface barely iridescent, laterobasal depressions with isodiametric mesh microsculpture, the center of each sculpticell shiny; basal metatarsomere with broadly convex median area bounded by moderate inner and outer dorsolateral grooves...

\[ \text{Blackburnia posticata (Sharp) (p. 87)} \]

2. Femora rufotestaceous, distinctly paler than elytral epipleura, pale legs and elytral epipleura contrasted against darker thoracic and abdominal venter; male aedeagal median lobe apex of moderate length, broadly rounded (Figs. 25A, 27A)

\[ \text{Blackburnia tantalus (Blackburn) (p. 92)} \]

3. Pronotal lateral margins of equal breadth cephalad laterobasal depressions (Fig. 19C), contrasting paler against brunneneous disc; femora testaceous, contrasted with infuscated tibiae and tarsi; Maui Nui

\[ \text{Blackburnia lanaiensis (Sharp) (p. 95)} \]

3(2). Pronotal lateral margins narrower in apical half than closer to laterobasal depressions (Fig. 19D), pronotal coloration without strong contrasts, though center of disc darker or not than margins; femora concolorous with tibiae and tarsi, or if partly paler, femoral ventral margin infuscated and concolorous with tibiae; Hawaii Island

\[ \text{Blackburnia hawaiiensis (Sharp) (p. 98)} \]
CARABIDAE PART I: PLATYNINI

Key 3
Adults of the subgenus Blackburnia Sharp
Division 1 of Sharp (1903)

1. Elytra coloration a mosaic of irregular, bilaterally asymmetrical flavous and brunneous blotches and flecks ......................................................... 2
   — Elytra concolorous throughout, from piceous with metallic luster to rufous ..... 4

2(1). All elytral intervals equally convex, nearly flat; macropterous .................. 3
   — Elytral interval 3 slightly carinate, intervals 5-7 more distinctly carinate; brachypterous, metathoracic wings extended only ½ length elytra; Kauai ..........
   ........................................................................................................ Blackburnia maculata (Sharp) (p. 123)

3(2). Pronotal dorsum as pale as flavous portions of elytra, head darker, brunneous; males with metatibiae bent, markedly bowed mesally at midpoint of length; Oahu, Waianae Range ......................... Blackburnia tibialis (Sharp) (p. 128)
   — Pronotal dorsum as dark as brunneous portions of elytra, center of disc concolorous with vertex of head; males with straight metatibiae, not bowed near midpoint; Oahu, Waianae Range ........................................ Blackburnia mystica (Blackburn) (p. 125)

4(1). Antennomere 3 covered with secondary setae throughout length in addition to the apical whorl of setae, secondary setae about 1/4 to 1/3 as long as breadth of antennomere .................................................. 5
   — Third antennomere glabrous or apparently glabrous; if sparse secondary setae present they are less than 1/10 x breadth of antennomere .................. 11

5(4). At least elytral intervals 1, 5, and 7 carinate, distinctly raised above others ..... 6
   — All elytral intervals equally convex ...................................................... 7

6(5). Pronotum glabrous, basal seta lacking; elytral intervals 1, 3, 5, and 7 strongly carinate throughout length, intervals 6 and 8 less strongly carinate; apical palpal segments covered with secondary setae; Kauai ........................................................................................................ Blackburnia waialeale, new species (p. 229)
   — Basal pronotal seta present; elytral intervals 1, 5, and 7 carinate throughout length but interval 3 raised at base only, intervals 6 and 8 only slightly more convex than intervals 2-4; apical palpal segments glabrous; Kauai ........................................ Blackburnia micantipennis (Sharp) (p. 226)

7(5). Eyes not or only slightly more convex than outline of head, but with 20 or more ommatidia across horizontal diameter; integument melanized, brunneous to piceous; mandibles foreshortened, robust, apex more blunt ...................... 8
   — Eyes flat, reduced to cluster of 4 ommatidia; integument pallid; mandibles of normal proportions, with acuminate apex; Haleakala cave species (could also key out in Key 1, couplet 7 due to tarsal configuration) .................... Blackburnia aaeae (Samuelson & Liebherr) (p. 187)
8(7). Elytral striae punctate, punctures isolated or connected by continuously depressed stria, all intervals equally convex; dorsal body surface matte, forebody microsculpture granulate isodiametric, elytral microsculpture granulate and slightly transverse .................................................. 9

— Elytral striae smooth, continuous, intervals 1, 3, 5, and 7 subcarinate, slightly more elevated than other intervals; dorsal body surface shiny, microsculpture isodiametric on head, transverse on pronotum and elytra; Kauai ................................................................. Blackburnia curtipes (Sharp) (p. 196)

9(8). Pronotum lacking basal seta, hind angle glabrous; pronotal lateral margins and front angles not prominent, surface with granulate microsculpture, but only slightly punctate on center of disc ................................................................. 10

— Pronotum with basal seta present; pronotal lateral margins protruding, front angles prominent, surface pronouncedly wrinkled or punctate throughout; Haleakala ....................................................... Blackburnia sharpi (Blackburn) (p. 202)

10(9). Inner five elytral striae more or less discontinuous, some specimens with two punctures joined together by oblong depressions; elytral microsculpture markedly granulate; Molokai ................................ Blackburnia perkinsi (Sharp) (p. 203)

— Inner five elytral striae distinctly punctate, but punctures joined by continuously depressed striae; elytral microsculpture granulate, but shinier than pronotum (single male holotype); West Maui .... Blackburnia koebelei (Sharp) (p. 206)

11(4). Vertex of head covered with irregular, deep, circular, pitlike punctures isolated by shiny cuticle .................................................................................................................. 12

— Vertex of head without deep pitlike punctures, although smaller punctures present or not posteriorly along cervical depression .......................................................... 15

12(11). Eyes slightly convex, visibly extended beyond supraorbital ridge in dorsal view; humeri more rounded, forebody broader relative to elytra (Fig. 124B-D) ................. 13

— Eyes flat, not extended beyond supraocular ridge; head and pronotum narrow relative to broad humeri (Fig. 124A); Oahu, Koolau Range ........................................ Blackburnia blaptoides Blackburn (p. 240)

13(12). Pronotal basal seta present; humeri less rounded, basal carina present or not ... 14

— Pronotum lacking basal seta, hind angle glabrous; humeri narrow, rounded, basal carina barely visible; Haleakala ... Blackburnia kipahulu, new species (p. 247)

14(13). Pronotal lateral margin prominent, reflexed, lateral gutter present; humeral anterolateral margin markedly carinate; Molokai ........................................ Blackburnia puniciceps (Sharp) (p. 243)

— Pronotal lateral margin narrow, convexity of disc extended to lateral bead in anterior half of pronotum; humeral anterolateral margin with slight carina, obscured or not by deep pitlike punctures extended along base of elytra; Haleakala ........................................ Blackburnia deroderana (Sharp) (p. 245)
15(11). Pronotal disc markedly wrinkled or punctate throughout, punctures either large and pitlike or smaller ................................................................. 16
— Pronotal disc smoother, laterobasal depressions on median base of pronotum punctate or not .................................................................................. 19

16(15). Lateral portions of basal abdominal sternites variously wrinkled or punctate, but always more than one puncture .............................................. 17
— Single large pitlike fovea between abdominal sternites II and III; Oahu, Koolau Range ....................... Blackburnia kamehameha, new name, in part (p. 236)

17(16). Pronotal punctures smaller, median longitudinal impression shallower; legs brunneous to flavous, contrasted with piceous venter; Kauai ................. 18
— Pronotal punctures large and pitlike, median longitudinal impression deeply sulcate; legs concolorous with rest of body; Oahu ........................................ Blackburnia insignis Sharp (p. 237)

18(17). Basal pronotal seta lacking, hind angles rounded; elytral striae with deep, round, pitlike punctures, third interval lacking dorsal elytral setae (anterior seta rarely present) ........................................ Blackburnia elegans (Sharp) (p. 232)
— Basal pronotal angles setose, obtuse-angulate; elytral striae indistinctly punctate, interval 3 with three dorsal elytral setae .. Blackburnia costata (Sharp) (p. 131)

19(15). Pronotum without, or with only basolateral setae; elytra without foveae associated with eighth elytral stria ........................................................................ 20
— Pronotum with two pairs of lateral setae, one pair before rounded hind angles and one pair at apical 1/3 of length; elytra with four pale-bottomed foveae associated with anterior half of eighth elytral stria; Haleakala ................................ Blackburnia terebrata (Blackburn) (p. 223)

20(19). Pronotum glabrous (polymorphic species key both ways) ......................................................... 21
— Pronotum with single pair of basolateral setae ................................................................................ 24

21(20). Abdominal sternites II and III not encompassing a large pitlike fovea ......................... 22
— Single large pitlike fovea between abdominal sternites II and III; Oahu, Koolau Range ......................... Blackburnia kamehameha, new name, in part (p. 236)

22(21). Pronotal lateral margins evident to front angles, though reflexion may be narrow; elytral striae continuous, at most minutely punctulate ........................................ 23
— Pronotal lateral margins entirely smooth, or indicated by faint groove; elytral striae distinctly punctate, punctures more or less isolated on disc; dorsum with metallic green luster; Oahu ......................... Blackburnia micans (Sharp) (p. 153)
23(22). Pronotum transverse, lateral margins broadly reflexed in apical half; dorsal surface with granulate microsculpture, matte, bruneous to piceous; overall body length 12.2-15.7 mm; Hawaii Island ................................................................. Blackburnia incendiaria (Blackburn), in part (p. 114)

— Pronotum only slightly wider than long, lateral margins very narrow in apical half; dorsal surface with transverse microsculpture, shiny, elytra with faint bluish luster; overall body length 8.9-9.0 mm; Haleakala ................................................................. Blackburnia agonoides (Sharp) (p. 164)

24(20). Tarsomeres 2-4 broadened apically, fourth tarsomeres bilobed, lobes longer than tarsomere base, ventral surfaces of basal four tarsomeres densely setose .... 25

— Tarsomeres 2-4 may be broader apically, but fourth tarsomere not distinctly bilobed, base longer than median emargination, ventral surfaces of basal four tarsomeres medially glabrous ................................................................. 26

25(24). Pronotum subquadrate, width ≤ 1.10× median length; lateral pronotal reflexion of equal width from laterobasal depression to front angle; male aedeagus extremely narrow in apical half, apex long, markedly curved (Fig. 44A-B); Hawaii Island ................................................................. Blackburnia kukui, new species (p. 120)

— Pronotum transverse, width 1.20-1.30× median length; lateral pronotal reflexion narrowest toward front angles; male aedeagus broader, apex more bluntly rounded (Fig. 41A-B); Hawaii Island (also Maui Nui and Oahu records) ........ Blackburnia lucipetens (Blackburn) (p. 115)

26(24). Macropterous, fully developed metathoracic flight wings present (visible along suture by slightly lifting one elytron) ................................................................. 27

— Flight wings brachypterous or vestigial, at most extended ½ length of elytron as a narrow strap ................................................................. 29

27(26). Pronotal disc with granulate transverse microsculpture and metallic cupreous luster; elytral striae punctate basally; overall body length 8.1-10.5 mm .... 28

— Pronotal disc bruneous, without metallic reflection; elytral striae smooth, without punctations; overall body length 11.1-13.6 mm ................................................................. Blackburnia octooccellata (Karsch) (p. 106)

28(27). Pronotum subquadrate, width 1.10-1.15× median length, basolateral margins more sinuate before hind angles (Fig. 49C); Oahu ................................................................. Blackburnia corrusca (Erichson) (p. 134)

— Pronotum more transverse, width 1.18-1.25× median length, basolateral margins less sinuate before hind angles (Fig. 49D); Maui Nui, Hawaii Island ................................................................. Blackburnia molokaiensis (Sharp) (p. 137)
29(26). Pronotum with reflexed lateral margin, discal convexity separated from margin by a concave gutter evident from hind to front angles, laterobasal depressions broad, impunctate or nearly so, with or without faint punctures or wrinkles mesad or cephalad depressions ........................................... 30
  — Pronotal lateral margin narrower, discal convexity extended to just inside marginal bead, concave gutter not extended to front angles, laterobasal depressions punctate, or reduced to single punctate depression ........................................... 36

30(29). Pronotum ovoid, hind angles obsolete, basolateral margin evenly rounded ...... 31
  — Pronotum with evident hind angles, basolateral margin with distinctly varying curvature ........................................................................................................ 32

31(30). Scutellar setae (Fig. 12A) present between base of scutellar striales and first striae, fully developed, in rare instances unilaterally doubled; Hawaii Island .................... Blackburnia incendiaria (Blackburn), in part (p. 114)
  — Scutellar setae absent, or if present, very small; Haleakala .................................... Blackburnia rupicola (Blackburn) (p. 112)

32(30). Eighth elytral stria with 15-18 lateral elytral setae (e.g., Fig. 12A) ............... 33
  — Eighth elytral stria with 9-11 lateral elytral setae .................................................. 34

33(32). Elytral microsculpture dense transverse lines, surface with an iridescent luster; elytral intervals broadly convex, striae impunctate except for minute basal punctulae; Kauai Blackburnia sulcipennis (Sharp) (p. 140)
  — Elytral microsculpture granulate isodiametric sculpticells arranged in transverse rows; elytral intervals flat between the deep, broad striae that are deeply punctate in basal half of length; Hawaii Island ........................................ Blackburnia ewingi, new species (p. 108)

34(32). Pronotal hind angles obtuse; elytral striae basally punctulate, minute punctures throughout basal half in lateral striae; overall body length 10.9-12.7 mm ... 35
  — Pronotal hind angles about right; elytral striae evidently punctate throughout length, striae partially discontinuous on disc; overall body length 7.8 mm; Haleakala ...................... Blackburnia polipoli, new species (p. 199)

35(34). Humeri distinctly developed, elytra subparallel; pronotal hind angles situated before median base, moderately reflexed lateral margin evident to front angles (Fig. 92A); Molokai Blackburnia polhemusi, new species (p. 189)
  — Humeri reduced, elytra suboviform; pronotal hind angles extended caudad, the basal margin trisinuate, reflexed lateral margin narrower in apical half than cephalad laterobasal depression, narrowest at front angles (Fig. 92B); Haleakala Blackburnia pilikua, new species (p. 194)
36(29). All elytral striae punctate and discontinuous on disc, punctures irregularly grouped in isolated longitudinal depressions; dorsal body surface with reduced microsculpture, colored a shiny metallic blue-green; Oahu ........................................... 37
— Elytral striae continuous on disc, punctures various, most distinct or not on lateral portions of elytra; dorsal body surface not both metallic and with reduced microsculpture .................................................. 38

37(36). Pronotal laterobasal depressions smooth, without punctures; male aedeagal median lobe with markedly recurved medioventral surface, apex angled relative to shaft (Fig. 73); Waianae Range ........ Blackburnia hihia, new species (p. 160)
— Pronotal laterobasal depressions punctate, with 8-18 fine irregular punctures; male aedeagal median lobe with straight to slightly recurved medioventral surface, apex not markedly angled to rest of shaft (Fig. 71); Koolau Range ..........................
................................................................................................ Blackburnia optata (Sharp) (p. 157)

38(36). Pronotal median base smooth, impunctate, laterobasal depressions shallow, sparsely punctate to impunctate; body color Brunneous to piceous, shiny, but without metallic reflection ................................................................. 39
— Pronotal median base distinctly punctate or rugose, laterobasal depressions finely to deeply punctate; body piceous with metallic blue, green, or cupreous reflection .................................................................................................................. 48

39(38). Head and pronotum shiny, microsculpture reduced; pronotal laterobasal depressions smooth or with less than 10 indistinct punctures on mesal surface .. ................................................................. 40
— Head with well-developed isodiametric mesh microsculpture across vertex, pronotal disc with transverse mesh microsculpture, surface slightly iridescent; pronot al laterobasal depressions with 10-15 small punctures on mesal surface; Kauai ........................................ Blackburnia atra, new species (p. 145)

40(39). Pronotal lateral and basal margins distinctly developed .................................. 41
— Pronotal lateral and basal margins almost completely obsolete, fine line visible caudad front angles, fine linear impressions visible behind laterobasal depressions; Haleakala ................ Blackburnia lenta (Sharp) (p. 224)

41(40). Mesepisterna sparsely to deeply punctate across its surface .................................. 42
— Mesepisterna not punctate; if slightly wrinkled, wrinkles restricted to part of sclerite, its surface shiny to alutaceous ................................................................. 43

42(41). Pro- and metepisterna punctate; rufous femora markedly contrasted with piceous ventral body surface; pronotum quadrate, as wide as long (Fig. 77D); Kauai ........................................ Blackburnia bryophila, new species (p. 175)
— Pro- and metepisterna not punctate; rufous femora only slightly paler than Brunneous venter; pronotal width 1.2 × median length, lateral margins broadly rounded (Fig. 60C); Kauai .......................... Blackburnia erythropus (Sharp) (p. 148)
43(41). Dorsal elytral setae absent, elytral humeri reduced, elytral margins subparallel to oviform in medial half of length; head broad, robust, width across eyes 0.81-0.89× pronotal width; pronotal hind angles evident caudad basal setae ...... 44

   Three dorsal elytral setae, elytral humeri broad, elytral margins parallel in median half of length; head gracile, width across eyes 0.72-0.76× pronotal width; pronotal hind angles rounded, obsolete; Kauai ......... Blackburnia aterrima (Sharp) (p. 150)

44(43). All elytral striae punctate in basal half of length, impunctate apically ...... 45

   Elytral striae 1-4 smooth, impunctate throughout length; West Maui ......... Blackburnia cephalotes (Sharp) (p. 219)

45(44). Basal four metatarsomeres more gracile, second tarsomere 1.5× length inner tibial spur; humeri reduced, elytra more oviform ............................................................. 46

   Basal four metatarsomeres broadened apically, second tarsomere subequal to length of inner tibial spur; humeri more distinct, elytral margins subparallel in basal half; Molokai Blackburnia brevipes (Sharp) (p. 217)

46(45). Elytral microsculpture reduced, surface shiny; male aedeagal median lobe apex shorter, acuminate and slightly downturned in lateral view (Figs. 103A, 106A), slightly to moderately attenuate in ventral view (Figs. 103B, 106B) ....

   Elytra with transverse mesh microsculpture, surface iridescent; male aedeagal median lobe apex elongate, bluntly rounded in lateral view (Fig. 107A), attenuate in ventral view (Fig. 107B); Haleakala Blackburnia anomala (Blackburn) (p. 215)

47(46). Elytral striae 7-8 continuous between punctures, stria 7 indicated throughout length; male aedeagal median lobe slightly attenuate in ventral view (Fig. 103B); Haleakala Blackburnia agilis (Sharp) (p. 207)

   Elytral striae 7-8 interrupted throughout length, stria 7 obsolete apically; male aedeagal median lobe attenuate in ventral view (Fig. 106B); Haleakala Blackburnia medeirosi, new species (p. 211)

48(38). Vertex of head shiny, microsculpture sculpticells not visible, though transversely oriented isodiametric mesh visible behind eyes .......... 49

   Vertex of head with distinct isodiametric mesh, sculpticell margins easily visible at 50× ........................................................................................................ 50

49(48). Pronotal hind angles obsolete; laterobasal depression a linear gutter, basal pronotal seta located in well-defined marginal bead; abdominal sternites with granulate isodiametric microsculpture; Haleakala Blackburnia frigida Blackburn (p. 178)

   Pronotal hind angles indicated by sinuate lateral margin just cephalad basal pronotal seta; laterobasal depression broader, lateral margin expanded basally, lateral margin not distinct at basal pronotal seta; abdominal sternites shiny, with reduced transversely oriented microsculpture; Molokai Blackburnia munroi (Perkins) (p. 182)
50(48). Scutellar seta (Fig. 12A) absent; pronotal median base densely covered with a combination of rugose wrinkles and punctures; elytra with more distinctly developed transverse sculpticells producing more granulate appearance ... 51
— Scutellar seta present; pronotal median base sparsely punctate, the punctures small and isolated; elytra shiny metallic aeneous, with transverse microlines producing iridescent luster; West Maui .......................................................... Blackburnia viridis, new species (p. 184)

51(50). Upper body surface with metallic purple, green, or blue reflection, surface shiny; femora brunneneous, paler than ventral body surface; Maui ....................... 52
— Upper body surface coal black, microsculpture with granulate appearance; femora dark, infuscated, barely paler than abdominal sternites; Molokai ............ .................................................................. Blackburnia longipes (Sharp) (p. 167)

52(51). Elytral striae 1-3 discontinuous at some point on disc, strial punctures longitudinal, not markedly expanding width of stria; male aedeagal median lobe with tip shorter, only slightly downturned (Fig. 81A); Haleakala ...................... Blackburnia fracta (Sharp) (p. 173)
— Elytral striae 1-3 continuous on disc, strial punctures circular, the surrounding depression 3-4x width of stria between punctures; male aedeagal median lobe with tip longer, more downturned (Fig. 80A); West Maui ....................... Blackburnia pukalaina, new species (p. 170)

Key 4
Adults of subgenus Metromenus Sharp
Division 2 (Sharp 1903), excluding subgenus Colpocaccus Sharp

1. Pronotal lateral and basal setae present (polymorphic species key both ways) .. 2
— Pronotal lateral seta or basal seta absent, or both absent .................................. 7

2(1). Eyes convex, approximately 20 or more ommatidia across horizontal diameter; mandibles shorter, distance from dorsal articulation to apex ≤ 1.50× that from articulation to median labral apex ................................................. 3
— Eyes nearly flat, 12-15 ommatidia across horizontal diameter; mandibles elongate, distance from dorsal articulation to apex 1.90× that from articulation to median labral apex; Haleakala cave species .................................................. Blackburnia howarthi (Samuelson & Liebherr) (p. 336)

3(2). Humeri distinctly angulate ............................................................................. 4
— Humeri rounded, not distinctly angulate .......................................................... 5
4(3). Basal elytral carina slightly arcuate, margin at humerus not elevated into a tooth; pronotal basal margin broadly elevated just inside hind angles, not marginate; Haleakala ........................................... Blackburnia calathiformis (Sharp) (p. 334)
— Basal elytral carina arcuate, margin at humerus distinctly elevated into a tooth; pronotal base marginate just inside hind angles, margin continuous with basolateral margin; Haleakala ................................................................. Blackburnia abaxoides, new species, in part (p. 350)

5(3). Metatarsomeres medially carinate, dorsolateral grooves deeply incised; pronotal lateral margin narrow in anterior half, margin not broader at tightly rounded front angles (most specimens of these species lack the basal pronotal setae) ................................................................................................................................. 6
— Metatarsomeres with broad median convexity, dorsolateral grooves shallow; pronotal lateral margin broad to broadly rounded front angles; Kauai (all known specimens with basal pronotal setae) ................................................................. Blackburnia ambiens (Sharp) (p. 270)

6(5). Broader, basal pronotal width 0.70-0.80× maximum pronotal width, laterobasal pronotal margin broadly elevated; elytra broad, suboviform, humeri moderately reduced; Molokai .... Blackburnia vagans (Sharp), in part (p. 368)
— Narrower, basal pronotal width 0.65-0.70× maximum pronotal width, laterobasal pronotal margin more narrowly elevated; elytra narrow, oviform, humeri reduced; West Maui ........ Blackburnia auana, new species, in part (p. 370)

7(1). Pronotum with basal pronotal seta present, lateral seta absent ..................... 8
— Pronotum with lateral seta present and basal seta absent, or both setae absent .. 31

8(7). Elytral intervals of equal convexity, none carinate ........................................ 9
— Elytra with intervals 1, 3, 5, 7, and 8 carinate, intervals 2, 4, 6, and 9 subcarinate; Kauai ....................................................... Blackburnia transiens (Sharp) (p. 281)

9(8). Dorsal elytral setae associated with small depressions that are much smaller than width of third elytral interval ................................................................. 10
— Dorsal elytral setae located in deep foveae, each depression broader than third elytral interval, striae 2 and 3 approaching each other in foveae; Oahu, Koolau Range ............................................. Blackburnia fractistriata (Perkins) (p. 389)

10(9). Metatarsomere 4 lobate, with inner and outer lobes as long or longer than length of tarsomere basad articulation of fifth tarsomere (Fig. 133E) ..................... 11
— Metatarsomere 4 with lobate to straight apical margin; if lobate, apical lobes are shorter than median length of tarsomere basad articulation of fifth tarsomere (Fig. 130G) .................................................. 13
11(10). Lobes of metatarsomere 4 narrower, tightly rounded to pointed at apex; legs testaceous, dorsal body surface brunneous to piceous .................. 12
— Lobes of metatarsomere 4 very broad, broadly rounded at apex; legs concolorous with dorsum, body color extremely variable, from rufous to piceous in apparently fully sclerotized individuals (most specimens of this species lack basal pronotal setae); Oahu ................................................................. Blackburnia palmae (Blackburn), in part (p. 444)

12(11). Elytra with distinctly developed transverse sculpticells arranged in rows, sculpticells clearly visible across entire disc; male aedeagal median lobe slender in ventral view (Fig. 269B); Molokai .......................................................... Blackburnia platynoides (Sharp) (p. 442)
— Elytral microsculpture more transverse and reduced, transversely stretched isodiametric sculpticells difficult to trace across entire disc; male aedeagal median lobe broader in ventral view (Fig. 267B); West Maui ............................................................. Blackburnia gracilis (Sharp) (p. 437)

13(10). Pronotal hind angles distinctly angulate (Figs. 180A, 192B-C, 209A, 250C-D, 278A) .............................................................. 14
— Pronotal hind angles rounded, either broadly or tightly, but not angulate (doubtful species keys to both couplets) .......................................................... 19

14(13). Pronotum quadrate to cordate, width across basal setae subequal to 1.30× width across front angles; elytral margin slightly broader or not near humeri, but not elevated and translucent .......................................................... 15
— Pronotum trapezoidal (Fig. 180A), width across basal setae 1.50× width across front angles, laterobasal depressions with very large round tubercle; elytral margin broadly elevated in basal half, translucent; Molokai .................................................. Blackburnia cheloniceps (Perkins) (p. 320)

15(14). Microsculpture of dorsum distinctly developed, pronotum with transverse mesh, and elytra with isodiametric sculpticells in transverse rows; pronotum with lateral margins distinctly sinuate before basal setae .................................................. 16
— Microsculpture of dorsum reduced microlines, barely traceable, surface shiny; pronotum (Fig. 278A) quadrate with basolateral margins barely sinuate before basal setae; Haleakala species ........ Blackburnia fulgida, new species (p. 452)

16(15). Pronotal basal margin straight to concave medially, extended caudad laterally so that hind angles are caudad median base; all elytral intervals with similar microsculpture .................................................................................. 17
— Pronotal basal margin (Fig. 209A) straight medially, convex laterally, hind angles slightly cephalad median base; elytral intervals 1-7 with shiny isodiametric sculpticells, intervals 8-9 with granulate sculpticells .......................................................... Blackburnia kilaeua, new name, in part (p. 362)
17(16). Pronotal laterobasal depressions without tubercle; elytra with isodiametric sculpitcels, surface not granulate ......................................................... 18
- Pronotal laterobasal depressions broadly tuberculate (Fig. 192B); elytra with granulate isodiametric mesh; Molokai .............................................. Blackburnia debilis (Perkins) (p. 339)

18(17). Elytral lateral margin expanded behind humeral angle; eyes only slightly convex, <20 ommatidia across horizontal diameter; overall body length 6.1-6.3 mm .................................................. Blackburnia kuiki, new species (p. 340)
- Elytral lateral margin not expanded behind humeral angle; eyes convex, >30 ommatidia across horizontal diameter; overall body length 8.1-9.8 mm .................................. Blackburnia sphodriformis (Sharp), in part (p. 422)

19(13). Elytra uniformly colored, testaceous to piceous ........................................... 20
- Elytra bicolored, intervals 1, 8, and 9, and elytral base and apex pale flavous, concolorous with pronotum, center of each elytron darker, smoky brunneous; Molokai Blackburnia hakeakapa, new species (p. 415)

20(19). Head, pronotum, and elytra concolorous, rufous to piceous .............................. 21
- Head, meso-, and metatema, and abdominal sternites rufous to brunneous, darker than rest of body, which is pale, flavous; Oahu, Waianae Range Blackburnia metromenoides (Perkins) (p. 380)

21(20). Elytral epipleura brunneous to piceous, apical portion not contrasted with abdominal sternites; elytral microsculpture similar on all intervals .......... 22
- Elytral epipleura flavous, contrasted with brunneous to piceous abdominal sternites; elytral intervals 8 and 9 with isodiametric microsculpture rougher, more granulate than on inner 7 intervals (best observed near subapical sinuation of elytra); Hawaii Island Blackburnia kilaua, new name, in part (p. 362)

22(21). Legs brunneous to piceous, concolorous with thoracic and abdominal venter .. 23
- Legs testaceous to rufous, paler than brunneous to piceous venter ......................... 25

23(22). Apical emargination of metatarsomere 4 deeper, lateral lobes >0.5× distance basad articulation with metatarsomere 5 (e.g, Fig. 133C, D); elytral disc with isodiametric sculpticells arranged in transverse rows ........................................... 24
- Metatarsomere 4 slightly emarginate apically, lateral lobes <0.5× distance basad articulation with metatarsomere 5 (e.g., Fig. 133A, B); elytral disc shiny, microsculpture obsolete; Lanai Blackburnia filipes (Sharp) (p. 460)

24(23). Metatarsomere 4 emarginate apically, emargination 0.6× as deep as length basad articulation with metatarsomere 5, West Maui ................................................ Blackburnia bartletti, new species (p. 434)
- Metatarsomere 4 lobate, apical lobes subequal to tarsomere length basad articulation with metarsomere 5 (Fig. 133C, D); Haleakala Blackburnia dyscolea (Sharp) (p. 440)
25(22). Microsculpture distinctly developed over entire dorsum, isodiametric on head, transverse on pronotal disc, and isodiametric in transverse rows on elytra; pronotum and elytra with iridescent luster ........................................ 26
— Microsculpture of pronotal disc of indistinct microlines, isodiametric sculpticells of head and elytra visible or not, but surface shiny, not iridescent .......... 29

26(25). Elytral humeri narrower, elytra oviform; pronotum (Figs. 251A, C, 273A) narrower, more cordate, lateral margin opaque near basal angles, narrow in front half, microsculpture within gutter obscured .......................... 27
— Elytral humeri broader, elytra suboviform; pronotum (Fig. 251B) broader, more quadrate, lateral margin broader and translucent basally, microsculpture within gutter visible to front angles; West Maui ........................................................................ Blackburnia longula (Sharp) (p. 429)

27(26). Elytra more evenly convex, disc not depressed; dorsal body surface brunneous, less contrasted with testaceous legs ........................................ 28
— Elytral disc with intervals 2-5 depressed relative to interval 1 (caudal view), the elytra appearing flat; dorsal body surface piceous, distinctly contrasted with testaceous legs; Lanai ......................... Blackburnia depressa (Sharp) (p. 446)

28(27). Humeri very narrow, lateral marginal groove behind humeral angle obsolete, without visible microsculpture; male aedeagal median lobe narrower in ventral view (Fig. 259B); Molokai .................. Blackburnia constricta (Sharp) (p. 427)
— Humeri slightly broader, lateral marginal groove behind humeral angle broad, with visible isodiametric microsculpture; male aedeagal median lobe broader in ventral view (Fig. 263B); Haleakala ................................ Blackburnia erro (Blackburn) (p. 432)

29(25). Third and fourth antennomeres concolorous with other segments; elytral disc with isodiametric sculpticells arranged in transverse rows ................ 30
— Third and fourth antennomeres with smoky infuscation, distinctly darker than pedicel or apical antennomeres; elytral disc with or without reduced micro­sculpture, shiny; (most individuals of this species lack basal pronotal setae); Molokai ................................ Blackburnia fraudator (Sharp), in part (p. 457)

30(29). Elytral subapical sinuation deep, distinctly developed (Fig. 278B); abdominal sternites shiny, transverse mesh microsculpture faint; Haleakala ................................................................. Blackburnia insociabilis (Blackburn), in part (p. 456)
— Elytral subapical sinuation shallow, elytra broader in apical half (Fig. 273B); abdominal sternites with distinct transverse mesh microsculpture, surface iridescent; West Maui .................... Blackburnia kauwa, new species (p. 449)

31(7). Pronotum with lateral setae bilaterally or unilaterally present, and basal setae absent ............................................................................................................ 32
— Pronotum glabrous, bilaterally lacking both lateral and basal setae ........... 60
32(31). Elytral intervals 1, 5, and 7 subcarinate or carinate throughout length, other intervals carinate or not .......................................................... 33
— All elytral intervals of equal convexity ........................................ 36

33(32). Elytral intervals 1, 3, 5, and 7 distinctly carinate, interval 6 subcarinate; head, pronotum, and elytra concolorous, OR, if head darker, dorsal surface with granulate isodiametric microsculpture ........................................ 34
— Elytral intervals 1, 5, and 7 subcarinate to triangularly carinate, other intervals rounded, not carinate; vertex of head rufopiceous, darker than rufobrunneous pronotum and elytra AND dorsum of body shiny; Kauai .................................................. Blackburnia kauaiensis (Sharp) (p. 275)

34(33). Pronotum and elytra shinier due to less distinct microsculpture; elytral carinae on intervals I, 3, 5, and 7 complete, smooth dorsally, except on third interval where carinae are interrupted by articulatory pits of dorsal elytral setae ..... 35
— Pronotum and elytra with distinct microsculpture, transverse mesh on pronotum, and granulate isodiametric mesh on elytra; crest of elytral carinae crenulate, occasionally interrupted; Kauai .................. Blackburnia opaca (Sharp) (p. 283)

35(34). Eyes less convex, head elongate, dorsal impression of neck deep, broad; pronotal hind angles narrowly rounded; overall body length 5.0-6.6 mm; females with 2 setae each side on abdominal sternite VII; Kauai .......................................................... Blackburnia alternans (Sharp) (p. 284)
— Eyes more convex, head less elongate, making dorsal impression less obvious; pronotal hind angles broadly rounded; overall body length 6.6-6.7 mm; females with 3 setae each side on abdominal sternite VII; Kauai .................. Blackburnia optima (Sharp) (p. 277)

36(32). Metatarsomere 4 asymmetrically lobate, outer lobe longer, 1.0-1.4× tarsomere length basad articulation of metatarsomere 5; humeri narrow, elytra oviform .................................................................................. 37
— Metatarsomere 4 emarginate to straight apically, lobes no more than about 0.5× mediobasal length; humeri broader, elytra suboviform to subparallel .......... 38

37(36). Elytral margins flavous, paler than infuscated disc; outer lobe of metatarsomere 4 subequal to mediobasal length; elytra iridescent due to distinct isodiametric sculpticells arranged in transverse rows; Kauai ................................................................ Blackburnia asquithi, new species (p. 263)
— Elytra more uniformly brunneous, at most lateral margin outside interval 9 paler; outer lobe of fourth metatarsomere 1.4× mediobasal length; elytra shiny, margins of isodiametric sculpticells less incised; Kauai ........................................ Blackburnia kahili, new species (p. 259)

38(36). Pronotal hind angles broadly rounded, basolateral margins convex or straight before basal setae .......................................................... 39
— Pronotal hind angles well defined, either obtuse to nearly right, OR basolateral margin sinuate before basal setae ........................................... 40
39(38). Elytral humeri tightly rounded, not distinctly angulate; eyes convex, surface curvature extended beyond curve defined by gena (Fig. 241B); Kauai .............. Blackburnia pavida (Sharp), in part (p. 407)

- Elytral humeri distinctly angulate; eyes less convex, lateral surface barely more convex than curve defined by genal expansion of head capsule (Fig. 137C); Kauai Blackburnia pauma, new species (p. 266)

40(38). Dorsal elytral setae present and located in depressions that extend across third interval, striae 2 and 3 approach each other in depression or not ............ 41

- Dorsal elytral setae located in small depressions that do not extend across third interval, or setae absent ................................................................. 43

41(40). Pronotal disc and laterobasal depressions with transverse microsculpture, depressions not granulate in appearance; elytral marginal groove narrow behind humeral angle, without granulate microsculpture ................. 42

- Pronotum with distinct transverse mesh microsculpture on disc, granulate isodiametric microsculpture in laterobasal depressions; elytral marginal groove broad behind humeral angle, covered with granulate microsculpture; Oahu, Koolau Range Blackburnia fossipennis (Blackburn), in part (p. 297)

42(41). Elytra with evident isodiametric sculpticells arranged in transverse rows, disc brunneous, apex paler, flavous; overall body length 4.6-5.1 mm; Oahu, Koolau Range Blackburnia fordii, new species (p. 391)

- Elytral microsculpture much reduced, microlines difficult to trace, surface shiny, disc and margins concolorous, ferrugineous; overall body length 6.5-7.0 mm; Haleakala Blackburnia foveolata, new species (p. 395)

43(40). Apical segment of maxillary and labial palpi glabrous ........................................ 44

- Apical segment of maxillary and labial palpi setose, covered with a sparse pelage of fine setae; Oahu, Waianae Range Blackburnia hukula, new species (p. 287)

44(43). Eyes not reduced, more convex, >20 ommatidia across horizontal diameter .... 45

- Eyes reduced, outer surface barely convex, approximately 16 ommatidia across horizontal diameter; West Maui Blackburnia lihau, new species, in part (p. 314)

45(44). Mandibles less elongate, distance from dorsal articulation to apex <1.8× distance from articulation to labral apex; pronotal basolateral margin broader, reflexed, either broadly elevated or conformed as a marginal bead before hind angles ....................................................... 46

- Mandibles elongate, distance from dorsal articulation to apex 1.8-2.1× distance from articulation to median labral apex; pronotal lateral margin extremely narrow, no lateral bead or marginal elevation cephalad hind angles; Haleakala Blackburnia haleakala, new name, in part (p. 360)
46(45). Pronotum quadrate to trapezoidal, basolateral margins slightly sinuate before quadrate hind angles ................................................................. 47

47(46). Pronotum more constricted basally, basolateral margins sinuate to straight before angulate to rounded hind angles ........................................... 51

48(47). Elytral humeri rounded, elytral basal carina raised to meet broadly elevated lateral margin at humerus, no humeral tooth present, lateral marginal depression broad and translucent from humerus to subapical sinuation ............... 48

49(48). Elytral humeri markedly angulate, humeral angle produced forward beneath or laterad pronotal hind angles, lateral margin elevated at humeral angle to form tooth or not, lateral marginal depression narrower, opaque from humerus to subapical sinuation (specimens of *B. abaxoides* from mid-elevational sites [i.e., 1000-1200 m] may key to this couplet; see Table 11, p. 354) ............. 49

50(49). Elytral disc with distinct isodiametric sculpticells in transverse rows, surface slightly iridescent ........................................................................ 50

51(46). Pronotal laterobasal margins less explanate, laterobasal depressions not as broad nor deep, pronotal base not as strongly concave, lateral margins narrower ...... 52

52(51). Pronotal laterobasal margins less explanate, laterobasal depressions not as broad nor deep, pronotal base not as strongly concave, lateral margins narrower ...... 52

... *Blackburnia paludicola*, new species (p. 293)
52(51). Elytral humeri narrow AND rounded, not angulate
Elytral humeri broader, or if narrow, then humeri are distinctly angulate

53(52). Broader, basal pronotal width 0.70-0.80 x maximum pronotal width, laterobasal pronotal margin (Fig. 209C) broadly elevated; elytra broad, suboviform, humeri moderately reduced; Molokai

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<td>Blackburnia vagans (Sharp), in part (p. 368)</td>
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53(52). Narrower, basal pronotal width 0.65-0.70 x maximum pronotal width, laterobasal pronotal margin (Fig. 209D) more narrowly elevated; elytra narrow, oviform, humeri reduced; West Maui

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<tr>
<th>Specimen</th>
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<tr>
<td>Blackburnia auana, new species, in part (p. 370)</td>
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54(52). Elytral humeri broader, with humeral angle either tightly rounded or angulate; elytra suboviform to subparallel, disc not greatly elevated above level of scutellum

54(52). Narrower, elytra oviform, convex, disc elevated above level of scutellum; Lanai

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<th>Specimen</th>
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<td>Blackburnia lanaihalensis, new name (p. 366)</td>
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55(54). Pronotal base constricted, basolateral margins clearly sinuate before obtuse hind angles; humeri narrow, elytral margin broadly arcuate laterad humeri

55(54). Pronotal base (Fig. 157B) less constricted, basolateral margins not so sinuate before obtuse or obtuse-rounded hind angles; humeri moderate to broad, lateral elytral margin less broadly arcuate; Oahu

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<tr>
<th>Specimen</th>
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<td>Blackburnia muscicola (Blackburn) (p. 291)</td>
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56(55). Pronotal disc with distinct transverse mesh microsculpture, surface slightly iridescent, laterobasal depressions with granulate microsculpture; elytral humeri more rounded (if angulate in some individuals, then angle distinctly obtuse)

56(55). Pronotal disc shiny, transverse mesh microsculpture reduced, laterobasal depressions covered with shiny transverse and isodiametric sculpticells; elytral humeri angulate, slightly obtuse to nearly right; Haleakala, 450-1100 m

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<th>Specimen</th>
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<tr>
<td>Blackburnia abaxoides new species, in part, lowland specimens (p. 350)</td>
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57(56). Basolateral pronotal margins narrowly elevated laterad narrower or tuberculate laterobasal depressions; elytra with lateral margins not laterally expanded behind humeri

57(56). Basolateral pronotal margins (Fig. 199B) broadly elevated laterad broadly concave laterobasal depressions; elytra broad basally, lateral margins expanded behind rounded-angulate humeri; West Maui

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<tr>
<th>Specimen</th>
<th>Note</th>
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<tr>
<td>Blackburnia concolor (Sharp) (p. 348)</td>
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58(57). Pronotal base straight or concave, hind angles laterad or caudad median base; microsculpture on elytral intervals 8 and 9 little contrasted with that of disc ................................................................. 59
— Pronotal hind angles (Fig. 209A) slightly cephalad median base due to convex laterobasal margins, basolateral margins sinuate or not; elytral disc with shiny isodiametric sculpticells arranged in transverse rows that contrast with granulate microsculpture in intervals 8 and 9; Hawaii Island .................................
........................................................................ Blackburnia kilaeua, new name, in part (p. 362)

59(58). Pronotal hind angles (Fig. 199A) distinctly angulate, laterally projecting, laterobasal margins sinuate; pronotal base straight or concave, laterobasal depressions often with broad, rounded tubercle; Molokai ............................................................ Blackburnia tricolor (Sharp) (p. 345)
— Pronotal hind angles (Fig. 144A) more rounded, laterobasal margins straight to slightly convex; pronotal base straight, laterobasal depressions usually flat between convex median base and elevated lateral margin ........................................ Blackburnia ulaula, new species (p. 271)

60(31). Dorsum with evident microsculpture on at least one somite; striae 6-8 evident, not obsolete ........................................................................................................ 61
— Microsculpture obsolete on dorsum, body highly polished; elytral striae 6 and 7 markedly reduced, difficult to trace; stria 8 shallow, indistinct between foveate lateral elytral setae; striae 1-5 smooth, sulcate; Oahu, Koolau Range ........................ Blackburnia perpolita (Sharp) (p. 413)

61(60). Metatarsomere 4 lobate, inner and outer lobes 1.4-1.7× length of tarsomere basad articulation with metatarsomere 5 (Fig. 133E, F) ................................................. 62
— Metatarsomere 4 either truncate apically, or emarginate, but lobelike projections less than medial length of tarsomere basad articulation with metatarsomere 5 (Fig. 131A, B) ............................................................... 64

62(61). Elytral disc convex, elytra oviform, inflated; inner lobes of metatarsomere 4 narrower than outer, pointed apically; head darker than pronotum or elytra, elytral epipleura flavous basally, much paler than metepisterna and lateral reaches of basal abdominal sternites .................................................. 63
— Elytral disc flat, elytra depressed; inner and outer lobes of metatarsomere 4 broad, rounded or truncate apically; head, pronotum, and elytra concolorous, elytral epipleura concolorous with metepisterna and lateral reaches of basal abdominal sternites; Oahu ........................................................................ Blackburnia palmae (Blackburn), in part (p. 444)
63(62). Elytra very broad, flavous to brunneous with a darker, infuscated band the width of intervals 8 and 9 across elytral apex; head piceous to brunneous, contrasted with brunneous to flavous pronotal disc; head not appearing elongate, with moderately impressed neck; Oahu, Koolau Range ................................................................. Blackburnia mutabilis (Blackburn) (p. 384)
— Elytra narrower, brunneous to piceous, base or lateral margins paler or not, no apical infuscation; head usually concolorous with pronotal disc (or slightly darker); head with markedly impressed neck, head appearing elongate; Oahu, Koolau Range ......................... Blackburnia caliginosa (Blackburn) (p. 381)

64(61). Each elytron with smoky brunneous disc; base, lateral two intervals, apex, and sutural interval paler, flavous; head brunneous, pronotum contrastingly paler, flavous .......................................................... 65
— Elytra of more uniform coloration, lateral margins and apex paler or not; head and pronotal disc concolorous ................................................................. 66

65(64). Elytral intervals 4-6 markedly convex basally, subcarinate; elytra with distinctly developed isodiametric sculpticells arranged in transverse rows; Kauai ................................................................. Blackburnia limbata (Sharp) (p. 404)
— Elytral intervals 4-6 flat basally, striae obsolete on elytral base; elytra with microsculpture of distinctly tranverse sculpticells; Oahu, Waianae Range ........ Blackburnia hilaris (Perkins) (p. 377)

66(64). Elytra broad or narrow, but not with depressed disc or truncate apex .......... 67
— Elytra broad, disc depressed, apex truncate, with setose apical half of penultimate, and all of apical tergite visible beyond abbreviated apex; Kauai Blackburnia pavida (Sharp), in part (p. 407)

67(66). Anterior and posterior (of three) dorsal elytral setae located in depressions that extend across third interval, striae 2 and 3 convergent in depressions .......... 68
— Dorsal elytral setae located in smaller depressions that do not extend across third interval, striae not convergent adjacent to depressions (several of six dorsal setae absent or not) ................................................................. 69

68(67). Pronotum (Fig. 169D) broad basally, hind angles rounded, basolateral margins convex; middle dorsal elytral setae located in depressions that do not extend across third interval; Oahu, Koolau Range ................................................................. Blackburnia paloloensis, new species (p. 307)
— Pronotum (Fig. 157D) narrower basally, hind angles obtuse angulate, basolateral margins slightly sinuate; all three dorsal elytral setae located in depressions that extend across third interval; Oahu, Koolau Range Blackburnia fossipennis (Blackburn), in part (p. 297)

69(67). Eyes reduced, almost flat, 16-18 ommatidia across horizontal diameter .......... 70
— Eyes convex, >20 ommatidia across horizontal diameter ............................... 72
70(69). Pronotum (Fig. 169C) elongate, narrow relative to broad, inflated elytral base, median length and maximum width subequal, basolateral margins slightly sinuate; Oahu, Koolau Range .......... Blackburnia oceanica (Blackburn) (p. 313)

— Pronotum (Figs. 176A, 180B) broader, appearing quadrate, upraised hind angles nearly as wide as distance between humeri, median length 0.77-0.80 × maximum width, basolateral margins straight to sinuate before slightly obtuse to right hind angles .

71(70). Vertex of head and pronotal disc shiny, sculpticell margins shallow, indistinct; tarsomeres longer, basal metatarsomere 1.8 × length of inner tibial spur; West Maui

— Vertex of head and pronotal disc slightly iridescent due to distinct microsculpture, isodiametric on head, transverse on pronotal disc; tarsomeres shorter, basal metatarsomere 1.3 × length of inner tibial spur .

72(69). Head with granulate isodiametric microsculpture; pronotal disc and elytra with dense transverse sculpticells arranged in mesh, surface iridescent; elytra convex dorsally, domelike, disc elevated above level of scutellum (doubtful species keys to both couplets) .

— Microsculpture of head isodiametric but not granulate; pronotal disc with transverse mesh microsculpture, elytra with isodiametric sculpticells arranged in transverse rows, iridescence less distinct; elytra not convex dorsally, scutellum and sutural interval more planar .

73(72). Pronotum narrower, maximum width <1.25 × median length, basolateral margins sinuate before obtuse hind angles .

— Pronotum (Fig. 169B) transverse, maximum width 1.25-1.33 × median length, basolateral margins straight to convex before rounded hind angles; Oahu, Koolau Range ................. Blackburnia barda (Blackburn) (p. 310)

74(73). Elytral epipleura flavous, contrasted with brunneous to piceous metepisterna; head, pronotal and elytral disc piceous, pronotal and elytral margins paler, brunneous to flavous, elytral apex broadly paler or not .

— Elytral epipleura and metepisterna concolorous, rufous to brunneous; dorsal body surface uniformly rufous to piceous . Blackburnia cuneipennis (Blackburn) (p. 411)

75(74). Pronotum with granulate microsculpture broadly across base, basolateral margins (Fig. 164A) broadly elevated inside hind angles, barely sinuate; body size larger, overall body length 6.0-8.2 mm; Oahu, Koolau Range ................. Blackburnia fugitiva (Blackburn) (p. 299)

— Pronotum with microsculpture of laterobasal depressions more granulate than on median base, basolateral margins (Fig. 164B) more abruptly elevated inside hind angles, sinuate; body size smaller, overall body length 5.2-6.7 mm; Oahu, Koolau Range .......... Blackburnia proterva (Blackburn), in part (p. 301)
76(72). Elytral microsculpture shinier on disc, margins may be granulate and isodiametric or not; microsculpture of pronotal disc less contrasted with that of laterobasal depressions ................................. 77

— Elytra with uniformly granulate isodiametric microsculpture, humeri broad, angulate; pronotal disc shiny, with reduced transverse mesh microsculpture, contrasted with granulate isodiametric laterobasal depressions; Molokai ...........

.......................................................... Blackburnia moerens (Sharp) (p. 421)

77(76). Pronotum constricted basally, hind angles either rounded or angulate, basolateral margins sinuate; elytral base broad or narrow, but not with humeral tooth .......

.......................................................... 78

— Pronotum quadrate, base broad, hind angles nearly right, basolateral margins at most slightly sinuate; elytra subparallel, humeri extremely angulate, often elevated as a humeral tooth ............... 85

78(77). Elytral microsculpture much reduced, shiny, isodiametric sculpticells arranged in transverse rows, microlines difficult to trace; dorsal and ventral body surfaces nearly uniformly piceous, elytral epipleura hardly paler 79

— Elytral microsculpture distinct at least laterally, disc with evident isodiametric sculpticells arranged in transverse rows; body paler, flavous to piceous, elytral epipleura contrasted with darker metepisterna ................................. 80

79(78)1. Third and fourth antennomeres with smoky infuscation, distinctly darker than pedicel or apical antennomeres; elytral disc usually with reduced microsculpture, shiny (most individuals of this species lack basal pronotal setae); Molokai ............... Blackburnia fraudator (Sharp), in part (p. 457)

— Third and fourth antennomeres concolorous with other segments; elytral disc with isodiametric sculpticells arranged in transverse rows; Haleakala ................................. Blackburnia insociabilis (Blackburn), in part (p. 456)

80(78). Pronotum transverse, distinctly broader than long, basolateral margins at most moderately sinuate before more rounded hind angles; overall length 4.9-7.8 mm ......................................................... 81

Pronotum (Fig. 250C-D) elongate, median length and maximum width subequal, basolateral margins with elongate sinuation before slightly obtuse, well-marked hind angles; overall body length 8.1-9.8 mm; Maui Nui ............... Blackburnia sphodriformis (Sharp), in part (p. 422) ........................................................................

81(80). Pronotal laterobasal depressions broad, concave, or flat, and extended to raised lateral margin ................................. 82

— Pronotal laterobasal depressions (Fig. 226B) linear, bounded laterally by broad tubercle that extends to narrowly raised lateral margin; Oahu ................................. Blackburnia meticulosa (Blackburn) (p. 386)

1. Undescribed species from Puu Lua, eastern Molokai, will key to this couplet. It is being described separately.
82(81). Elytral marginal groove of equal width across elytral base, or nearly so, not broad enough to be filled with granulate microsculpture; isodiametric microsculpture of head not distinct, the surface shiny ........................................ 83
   — Elytral marginal groove much broader inside and caudal humeral angle than more mesally cephalad scutellar seta, filled with granulate microsculpture; head with distinct isodiametric microsculpture, the surface matte; Oahu, Koolau Range ....................... Blackburnia proterva (Blackburn), in part (p. 301)

83(82). Basal metatarsomere longer, ≥4.0× as long as broad; elytral disc either shiny or more granulate, but not contrasted greatly with lateral intervals ........... 84
   — Basal metatarsomere short, about 3.0× as long as broad; elytral disc shiny, reduced microsculpture contrasted with granulate microsculpture on lateral two intervals; Hawaii Island .......... Blackburnia kilauea, new name, in part (p. 362)

84(83). Elytra with distinctly developed isodiametric microsculpture across disc, rough-margined sculpticells arranged in transverse rows; head and elytra concolorous, brunneous to piceous, pronotum and sutural interval of elytra slightly paler (elytral apex rarely paler); overall body length 6.7-7.8 mm; Oahu ........................................................ Blackburnia epicurus (Blackburn) (p. 375)
   — Elytra shiny iridescent, disc with flat-margined isodiametric sculpticells arranged in transverse rows; color immensely variable, head, pronotal disc, and elytral disc concolorous, flavous to piceous, body entirely pale, rufous to flavous (aequalis form), or darker, brunneous to piceous, with pale pronotal and elytral margins, elytra sometimes with broadly paler apex; overall body length 5.6-6.6 mm; Oahu ......................... Blackburnia fraterna (Blackburn) (p. 398)

85(77). Pronotum at least slightly constricted basally, basolateral margins less broadly elevated, separated or not from laterobasal depressions by a convex tubercle; elytral humeri angulate, elytral lateral margin only slightly expanded caudal humeri ................................................................. 86
   — Pronotum (Fig. 176B) cychroid, basolateral margins broadly and evenly elevated laterad broadly concave laterobasal depressions; pronotal lateral margins straight to convex before nearly right hind angles; elytral humeri rounded, elytral lateral margin broadly reflexed caudal humeri; Haleakala .............. Blackburnia calathoides (Sharp), in part (p. 318)

86(85). Mandibles shorter, length <1.8× distance from dorsal mandibular articulation to median labral apex; pronotal marginal bead at least indicated mesad or cephalad hind angles; elytral humeri more converging, humeri angulate and sometimes more broadly elevated ........................................ 87
   — Mandibles elongate, length from dorsal articulation to apex 1.8-2.1× distance from dorsal articulation to median labral apex; pronotal basolateral margin markedly sinuate before right hind angles, marginal bead lacking mesad and cephalad hind angles; elytra parallel-sided, humeri angulate with immense humeral tooth; Haleakala .. Blackburnia haleakala, new name, in part (p. 360)
87(86). Pronotum constricted basally, basolateral margins sinuate before obtuse hind angles, front angles less convergent, distance between front angles 0.75-0.92× distance between hind angles; eyes convex ........................................ 88
— Pronotum (Fig. 169A) trapezoidal, basolateral margins straight cephalad right hind angles, front angles convergent, distance between front angles about 0.67× distance between hind angles; eyes little convex; Oahu, Waianae Range ........
........................................................................................................ Blackburnia audax (Perkins) (p. 303)

88(87). Pronotal disc shiny, transverse microlines difficult to trace, laterobasal depressions with isodiametric to reduced, shiny isodiametric microsculpture .......... 89
— Pronotal disc with distinct transverse mesh microsculpture, slightly iridescent, laterobasal depressions with granulate isodiametric microsculpture; Molokai ................................................................. Blackburnia latifrons (Sharp) (p. 331)

89(88). Pronotum (Fig. 206A) narrower, lateral margins narrow in apical half, marginal groove narrowly lined with isodiametric microsculpture in apical 1/3, maximum pronotal width 1.22-1.27× median length; Haleakala ..............
........................................................................................................ Blackburnia putealis (Blackburn) (p. 358)
— Pronotum (Fig. 199D) more transverse, lateral margins broader in apical half, marginal grooves broadly lined with granulate isodiametric microsculpture to front angles, maximum pronotal width 1.29-1.31× median length; West Maui ................................................................. Blackburnia komohana, new name (p. 356)
TAXONOMY OF *BLACKBURNIA* SHARP, 1878

In this section we provide brief diagnoses, geographic distributions, ecological information, and information on type selection and deposition for all species. The diagnoses are accompanied by sections on flight-wing development (Pterothorax), and male genitalia and female reproductive tract characters. The former section will be of interest to those studying the evolution of flightlessness. The latter two sections present information not heretofore available. Both the male and female genitalic characters can be used to corroborate identification based on external characters. As mentioned above, in several species male genitalic characters are the primary means of accurate identification. In addition, we include a brief paragraph presenting the phylogenetic relationships of each species, including both the hypothesized adelphotaxon, or sister group, and a short discussion of the chorological or biogeographical consequences of that relationship. In this way, the geography associated with speciation can be more easily understood. Finally, for all newly described species in this treatment, we also provide comprehensive descriptions including aspects of the head, prothorax, elytra, legs, abdomen, coloration, microsculpture, and etymology.

Based on cladistic principles and an analysis including numerous Pacific-Rim outgroups (Liebherr & Zimmerman 1998), the genus *Blackburnia* Sharp was placed as the adelphotaxon of *Lorostema* Motschulsky. These taxa are members of the platynine subtribe Platynina.

*BLACKBURNIA* SHARP, 1878

*Blackburnia* Sharp, 1878 (January): 179 (type species *Blackburnia insignis* Sharp by original monotypy, not original designation as per Lorenz [1998b])

*Atrachycnemis* Blackburn, 1878a (October): 120 (type species *Atrachycnemis sharpi* Blackburn by original monotypy, new synonymy)

*Disenochus* Blackburn, 1878a (October): 121 (type species *Disenochus anomalus* Blackburn by original monotypy, new synonymy)

*Metromenus* Sharp, 1884: 217 (type species *Dyscolus palmae* Blackburn designated by Lorenz [1998b], new synonymy)

*Colpodiscus* Sharp, 1884: 217 (type species *Anchomenus lucipetens* Blackburn designated by Lorenz [1998b], new synonymy)

*Barypristus* Sharp, 1884: 217 (type species *Anchomenus sharpi* Blackburn by original designation, new synonymy)

*Mauna* Blackburn, 1884: 25 (type species *Blackburnia frigida* Blackburn by original monotypy, new synonymy)

*Deropristus* Sharp, 1903: 192 (type species *Blackburnia blaptoides* Blackburn designated by Lorenz [1998b], new synonymy)

*Anchotefflus* Sharp, 1903: 195 (type species *Anchotefflus gracilis* Sharp by original designation, new synonymy)

*Pseudobroscus* Sharp, 1903: 196 (type species *Pseudobroscus lentus* Sharp by original monotypy, junior homonym, preoccupied by *Pseudobroscus* Semenov, 1888 [Semenov 1906])

*Derobroscus* Sharp, 1903: 197 (type species *Derobroscus micans* Sharp designated by Lorenz [1998b], new synonymy)
**DIAGNOSIS.** A group of extremely diverse habitus, but with following synapomorphic diagnostic characters: 1, antennal scape with 1-2 small apical setae in addition to a single, longer, outer apical seta (except for *Blackburnia atra*); 2, hind pronotal setae, if present, located before hind angles (setae at hind angles only in *B. hawaiiensis, B. maculata, B. insignis, B. blaptoides*); 3, metameral dorsoapical surface glabrous (plesiomorphic setose condition present in 15 species (*B. tantalus, B. lucipetens, B. kukui, B. maculata, B. mystica, B. tibialis, B. costata, B. corrusca, B. molokaiensis, B. aanae, B. erythropus, B. bryophila, B. micantipennis, B. waialeale, and B. kilauea*). Given current geographic distributions of Platynini, *Blackburnia* can be distinguished from non-native Platynini by the presence of 1-2 or more extra setae at the apex of the antennal pedicel. Many native species exhibit substantial cuticular modifications, such as carinate ridges on the elytral intervals (Kauai species), pitting on the vertex of head or pronotum, and reduction of elytral striae into dashes or isolated pits. Most species characterized by such striking modifications (with the exception of *B. costata, B. corrusca, and B. molokaiensis*) have the metathoracic flight wing reduced to a vestigial flap that may extend only to the posterior margin of the metanotum, or slightly more caudal to the first or second abdominal tergite. The many species of subgenus *Metrornenus* are vestigially winged but lack cuticular pitting. These species have evolved a variety of different body shapes, including substantially reduced humeri resulting...
in an "ant-waist" habitus (Figs. 137A, C, 192A, C), and marked lateral expansions of the pronotum and humeri resulting in an ovoid habitus (Figs. 176, 180, 187).

**Protocaccus Liebherr, new subgenus**

DIAGNOSIS. This subgenus is characterized by the following apomorphic characters: 1, mandibles elongate; 2, submentum with 7 setae each side arranged in an anterior row of 4 and a posterior row of 3; 3, tarsomeres 1-3 with fine outer and obsolete inner dorsal sulci; 4, tarsomeres with ventral vestiture arranged in dense lateral rows of fine setae bordering a narrow median space; 5, female abdomen with 5 setae each side of apical sternite VII; and 6, lateral ensiform setae of female gonocoxite 2 very large and broad, over 0.23× length of gonocoxite (Fig. 17D). The single included species, described below, provides the basis for the subgeneric description.

**Blackburnia (Protocaccus) mandibularis Liebherr, new species**  
(Figs. 13, 16, 17, 18)

DIAGNOSIS. Easily recognizable by very elongate mandibles (Fig. 13), extended more than half their length beyond apical margin of labrum; pronotum quite narrow, about 1.25× as wide as head width at eyes (Fig. 16), basal marginal bead nearly complete, only slightly effaced medially; wings fully developed for flight (Fig. 17A); tarsomere 5 apparently glabrous ventrally, very short setae in two ventrolateral rows visible at 125×. Standardized body length 8.4-9.3 mm.

DESCRIPTION. Head. Neck elongate, dorsal impression distinct; eyes moderately convex, ocular ratio 1.55-1.57; labrum subquadrate, anterior margin slightly protruded medially; vertex longitudinally wrinkled mesad eye behind anterior supraorbital setae; mandibles elongate, straight terebral margin extended as far beyond anterior labral margin as distance from dorsal mandibular condyle to that margin (Fig. 13); mentum quadrisetose, two longer setae laterally complementing shorter median pair; submentum with 6-7 setae laterad mentum pits each side, 3-4 in anterior row along mentum-submentum suture, 3 in posterior row, outer seta in posterior row longest; antennae long, extended to basal 1/3 of elytra.

Prothorax. Pronotum narrow relative to broad humeri (Fig. 16), lateral marginal depressions narrow in anterior half; widened caudad to wrinkled, impunctate laterobasal depressions; lateral margins sinuate before obtuse-rounded hind angles; lateral setae absent, basolateral setae present; basal marginal bead absent behind laterobasal depressions, traceable medially; median dorsal impression fine, with strong transverse wrinkles extended laterally onto pronotal disc; anterior transverse impression smooth, delimiting an elevated anteromedial callus; anterior marginal bead effaced medially, well developed near only slightly projecting, rounded front angles. Prosternal process evenly rounded posteriorly, convex medioventrally, unmargined.

Elytra elongate, slightly expanded laterally in middle 1/3; humeri not broad, basal groove evenly rounded at humerus; intervals only slightly convex; striae smooth, impunctate, only slightly sinuous; subapical sinuation slight; 3 dorsal elytral setae; 14-16 lateral elytral setae.
Fig. 16. *Blackburnia (Protocaccus) mandibularis*, new species, habitus, dorsal view.

**Pterothorax.** Metepisternum elongate, lateral margin length 2.2 to 2.7× anterior margin length; flight wings fully developed (Fig. 17A), wing area 3.1 to 3.3× elytral area (see wing ratio in “Character Evolution, Brachyptery” section).

**Legs.** Profemur lacking anterior setae, with 2 posteroventral setae; mesofemur with 2-3 anteroventral setae; metacoxa bisetose, mesal seta absent; metafemur with 2-3 anteroventral setae; tarsomeres slightly broadened apically, ventral vestiture of broad lateral brushes with a median space, inner dorsal sulcus lacking on tarsomeres 1-3, outer sulcus obsolete;
Fig. 17. Blackburnia (Protocaccus) mandibularis, new species. A. Right metathoracic flight wing, dorsal view. B. Male aedeagal median lobe, right lateral view. C. Male aedeagal median lobe, euventral view. D. Left female gonocoxa, ventral view. E. Female reproductive tract, dorsal view. ans, apical nematiform setae; as, apical fringe setae of gonocoxite 1; bc, bursa copulatrix; co, common oviduct; des, dorsal ensiform seta; gc1, basal portion of gonocoxite; gc2, apical portion of gonocoxite; les, lateral ensiform seta; sg, spermathecal gland; smt, spikelike microtrichia; sp, spermatheca.
metatarsomere 4 with outer lobe 1.35× longer than inner lobe, outer lobe 0.75× length of median base, apical setal position slightly subapical, equidistant from lateral and dorsal surface of tarsomere.

**Abdomen.** Males with 1 seta on each side on apical margin of sternite VII; females with 5 setae each side.

**Coloration.** Head capsule dark, piceous, contrasted with rufotestaceous palpi and antennae; pronotum rufous with smoky cast; elytral disc piceous, base cephalad of humeral groove and epipleura rufotestaceous, paler than rufous venter, concolorous with femora and tibiae; pterothoracic and abdominal venter may exhibit mottled pattern of smoky infuscation.

**Microsculpture.** Vertex with distinct isodiametric mesh, stronger near wrinkles mesad eyes; pronotal disc with distinct transverse mesh that causes slight iridescence between transverse wrinkles; pronotal laterobasal depressions and median base with marked, granulate isodiametric mesh; elytral disc with isodiametric sculpticells arranged in transverse rows.

**Male genitalia.** Median lobe of male aedeagus unique among native Hawaiian platynines in being evenly curved ventrally, and lacking a ventral excavation near apex; sagittal crest little developed on basal bulb (Fig. 17B); apex slightly constricted laterally (Fig. 17C).
Female reproductive tract. Gonocoxa with double row of setae at apex of gonocoxite 1, gonocoxite 2 with 2 long, broad lateral ensiform setae (Fig. 17D), apical nematiform setae moderate, 0.33× length of gonocoxite 2; bursa copulatrix with indistinct dorsal pouch, symmetrical (Fig. 17E); spermatheca ovoid with distinct constrictions on reservoir; spermathecal gland duct short, entering near base of reservoir.

**Holotype** labeled “III/15/69 3500’ Waipoo Falls, Kauai R.C.A. Rice” (BPBM).

**Paratypes.** Kauai: 1210 m, 04-IV-1919, Kusche (CASC, 4), 05-IV-1919, Kusche (CASC, 1); Alakai Swamp Tr., Rice (BPBM, 1); Kokee S.P., Koai Str. bank, Montgomery (UHEM, 1), picnic area 0.4 mi before Alakai, UV light, 10-VI-1989, Jamieson (BPBM, 2).

**Distribution.** This species is known only from the Waimea River and its tributaries, Kauai (Fig. 18).

**Etymology.** The species epithet *mandibularis* refers to the very elongate mandibles.

**Habits.** Little is known about this species. It has been collected at light during June, and along Koai Stream and at Waipoo Falls. It should be searched for along stream banks.

**Phylogenetic relationships.** This species is the basal adelphotaxon of the rest of the native Hawaiian Platynini (Fig. 9). Its distribution on Kauai supports the presence of Hawaiian platynine taxa for at least as long as Kauai has existed as a forested island.

### Subgenus Colpocaccus Sharp, 1903

**DIAGNOSIS.** This basal clade of four species, as *B. mandibularis*, includes species characterized by functional flight wings, elongate elytra without modified intervals or striae, and sinuate pronota with only basal setae present (Fig. 19). Species of the subgenus *Colpocaccus* have obvious ventral setae on metatarsomere 5 (Fig. 20A), enabling them to be diagnosed from *B. mandibularis*. The basal tarsomerers, best viewed on the metathoracic leg, possess distinct inner and outer dorsal sulci (Fig. 20B-D). The dorsal sulci of the tarsi permit these species to be diagnosed from the large subgenus *Blackburnia*, treated next. The other large clade to follow, subgenus *Metromenus*, is comprised totally of species exhibiting vestigial flight wings. The male aedeagal median lobe of *Colpocaccus* spp. and all others to follow differs from that of *B. mandibularis* by the medioventral excavation of the shaft, producing a recurved ventral margin in lateral view (e.g., Fig. 21B).

**Distribution.** Each major island complex—Kauai, Oahu, Maui Nui, and Hawaii Island—supports a representative species of this subgenus.

**Phylogenetic relationships.** Species-area relationships of this subgenus are totally congruent with the summary area cladogram: (Kauai(Oahu(Maui Nui + Hawaii))) (Fig. 9).

*Blackburnia (Colpocaccus) posticata* (Sharp), new combination

(Figs. 2C, E, 14A, 15C, F, 19A, 20, 21, 22, 30D)

*Colpocaccus posticatus* Sharp, 1903: 215.

*Colpocaccus marginatus* Sharp, 1903: 215 (new synonymy).

**DIAGNOSIS.** Distinguishable from other species of subgenus by the distinct transverse mesh microsculpture on pronotal disc, and the broader pronotal lateral depressions (Fig. 19A) lined with isodiamic sculpticells. The elytral apex is variously paler, in most
Brosconymus Sharp, 1903: 198 (type species Brosconymus optatus Sharp by original monotypy, new synonymy)
Anchonymus Sharp, 1903: 199 (type species Anchonymus agonoides Sharp by original monotypy, new synonymy)
Chalcomenus Sharp, 1903: 206 (type species Anchomenus corruscus Erichson designated by Lorenz [1998b], new synonymy)
Baryneus Sharp, 1903: 209 (type species Anchomenus sharpi Blackburn by original monotypy, junior objective synonym of Barypristus Sharp, 1884)
Prodisenochus Sharp, 1903: 210 (type species Disenochus terebratus Blackburn by original monotypy, new synonymy)
Apteromesus Sharp, 1903: 211 (type species Apteromesus maculatus Sharp by original monotypy, new synonymy)
Mysticomenus Sharp, 1903: 212 (type species Mysticomenus tibialis Sharp designated by Lorenz [1998b], new synonymy)
Colpocaccus Sharp, 1903: 213 (type species Dyscolus tantalus Blackburn designated by Lorenz [1998b], new synonymy)
Atelothrus Sharp, 1903: 216 (type species Atelothrus politus Sharp designated by Lorenz [1998b], new synonymy)
Mesothricus Sharp, 1903: 222 (type species Mesothricus vagans Sharp designated by Lorenz [1998b], new synonymy)
Mecostomus Sharp, 1903: 229 (type species Mecostomus perkinsi Sharp by original monotypy, new synonymy)
Mecomenus Sharp, 1903: 230 (type species Mecomenus koebelei Sharp designated by Lorenz [1998b], new synonymy)
Broscomimus Semenov, 1906: 19 (replacement name for Pseudobroscus Sharp, new synonymy)

DIAGNOSIS. A group of extremely diverse habitus, but with following synapomorphic diagnostic characters: 1, antennal scape with 1-2 small apical setae in addition to a single, longer, outer apical seta (except for Blackburnia atra); 2, hind pronotal setae, if present, located before hind angles (setae at hind angles only in B. hawaiensis, B. maculata, B. insignis, B. blaptoides); 3, metathoracic dorsoapical surface glabrous (plesiomorphic setose condition present in 15 species (B. tantalus, B. lucipetens, B. kukui, B. maculata, B. mystica, B. costata, B. blaptoides); 3, metathorax dorsoapical surface glabrous (plesiomorphic setose condition present in 15 species (B. tantalus, B. lucipetens, B. kukui, B. maculata, B. mystica, B. costata, B. corrusca, B. molokaiensis, B. aaeae, B. erythropus, B. bryophila, B. micantipennis, B. waialeale, and B. kilaeua). Given current geographic distributions of Platynini, Blackburnia can be distinguished from non-native Platynini by the presence of 1-2 or more extra setae at the apex of the antennal pedicel. Many native species exhibit substantial cuticular modifications, such as carinate ridges on the elytral intervals (Kauai species), pitting on the vertex of head or pronotum, and reduction of elytral striae into dashes or isolated pits. Most species characterized by such striking modifications (with the exception of B. costata, B. corrusca, and B. molokaiensis) have the metathoracic flight wing reduced to a vestigial flap that may extend only to the posterior margin of the metanotum, or slightly more caudad to the first or second abdominal tergite. The many species of subgenus Metromenus are vestigially winged but lack cuticular pitting. These species have evolved a variety of different body shapes, including substantially reduced humeri resulting
in an “ant-waist” habitus (Figs. 137A, C, 192A, C), and marked lateral expansions of the pronotum and humeri resulting in an ovoid habitus (Figs. 176, 180, 187).

ProtoCaccus Liebherr, new subgenus

DIAGNOSIS. This subgenus is characterized by the following apomorphic characters: 1, mandibles elongate; 2, submentum with 7 setae each side arranged in an anterior row of 4 and a posterior row of 3; 3, tarsomeres 1-3 with fine outer and obsolete inner dorsal sulci; 4, tarsomeres with ventral vestiture arranged in dense lateral rows of fine setae bordering a narrow median space; 5, female abdomen with 5 setae each side of apical sternite VII; and 6, lateral ensiform setae of female gonocoxite 2 very large and broad, over 0.23× length of gonocoxite (Fig. 17D). The single included species, described below, provides the basis for the subgeneric description.

Blackburnia (ProtoCaccus) mandibularis Liebherr, new species

(Figs. 13, 16, 17, 18)

DIAGNOSIS. Easily recognizable by very elongate mandibles (Fig. 13), extended more than half their length beyond apical margin of labrum; pronotum quite narrow, about 1.25× as wide as head width at eyes (Fig. 16), basal marginal bead nearly complete, only slightly effaced medially; wings fully developed for flight (Fig. 17A); tarsomere 5 apparently glabrous ventrally, very short setae in two ventrolateral rows visible at 125×. Standardized body length 8.4-9.3 mm.

DESCRIPTION. Head. Neck elongate, dorsal impression distinct; eyes moderately convex, ocular ratio 1.55-1.57; labrum subquadrate, anterior margin slightly protruded medially; vertex longitudinally wrinkled mesad eye behind anterior supraorbital setae; mandibles elongate, straight terebral margin extended as far beyond anterior labral margin as distance from dorsal mandibular condyle to that margin (Fig. 13); mentum quadrisetose, two longer setae laterally complementing shorter median pair; submentum with 6-7 setae laterad mentum pits each side, 3-4 in anterior row along mentum-submentum suture, 3 in posterior row, outer seta in posterior row longest; antennae long, extended to basal 1/3 of elytra.

Prothorax. Pronotum narrow relative to broad humeri (Fig. 16), lateral marginal depressions narrow in anterior half, widened caudad to wrinkled, impunctate laterobasal depressions; lateral margins sinuate before obtuse-rounded hind angles; lateral setae absent, basolateral setae present; basal marginal bead absent behind laterobasal depressions, traceable medially; median dorsal impression fine, with strong transverse wrinkles extended laterally onto pronotal disc; anterior transverse impression smooth, delimiting an elevated anteromedial callus; anterior marginal bead effaced medially, well developed near only slightly projecting, rounded front angles. Prosternal process evenly rounded posteriorly, convex medioventrally, unmargined.

Elytra elongate, slightly expanded laterally in middle 1/3; humeri not broad, basal groove evenly rounded at humerus; intervals only slightly convex; striae smooth, impunctate, only slightly sinuous; subapical sinuation slight; 3 dorsal elytral setae; 14-16 lateral elytral setae.
Fig. 16. Blackburnia (Protococcus) mandibularis, new species, habitus, dorsal view.

**Pterothorax.** Metepisternum elongate, lateral margin length 2.2 to 2.7× anterior margin length; flight wings fully developed (Fig. 17A), wing area 3.1 to 3.3× elytral area (see wing ratio in “Character Evolution, Brachyptery” section).

**Legs.** Profemur lacking anterior setae, with 2 posteroventral setae; mesofemur with 2-3 anteroventral setae; metacoxa bisetose, mesal seta absent; metafemur with 2-3 anteroventral setae; tarsomeres slightly broadened apically, ventral vestiture of broad lateral brushes with a median space, inner dorsal sulcus lacking on tarsomeres 1-3, outer sulcus obsolete;
Fig. 17. Blackburnia (Protocaccus) mandibularis, new species. A. Right metathoracic flight wing, dorsal view. B. Male aedeagal median lobe, right lateral view. C. Male aedeagal median lobe, euventral view. D. Left female gonocoxa, ventral view. E. Female reproductive tract, dorsal view. ans, apical nematiform setae; as, apical fringe setae of gonocoxite 1; bc, bursa copulatrix; co, common oviduct; des, dorsal ensiform seta; gc1, basal portion of gonocoxite; gc2, apical portion of gonocoxite; les, lateral ensiform seta; sg, spermathecal gland; smt, spikelike microtrichia; sp, spermatheca.
metatarsomere 4 with outer lobe 1.35× longer than inner lobe, outer lobe 0.75× length of median base, apical setal position slightly subapical, equidistant from lateral and dorsal surface of tarsomere.

**Abdomen.** Males with 1 seta on each side on apical margin of sternite VII; females with 5 setae each side.

**Coloration.** Head capsule dark, piceous, contrasted with rufotestaceous palpi and antennae; pronotum rufous with smoky cast; elytral disc piceous, base cephalad of humeral groove and epipleura rufotestaceous, paler than rufous venter, concolorous with femora and tibiae; pterothoracic and abdominal venter may exhibit mottled pattern of smoky infuscation.

**Microsculpture.** Vertex with distinct isodiametric mesh, stronger near wrinkles mesad eyes; pronotal disc with distinct transverse mesh that causes slight iridescence between transverse wrinkles; pronotal laterobasal depressions and median base with marked, granulate isodiametric mesh; elytral disc with isodiametric sculpticells arranged in transverse rows.

**Male genitalia.** Median lobe of male aedeagus unique among native Hawaiian platynines in being evenly curved ventrally, and lacking a ventral excavation near apex; sagittal crest little developed on basal bulb (Fig. 17B); apex slightly constricted laterally (Fig. 17C).
**Female reproductive tract.** Gonocoxa with double row of setae at apex of gonocoxite 1, gonocoxite 2 with 2 long, broad lateral ensiform setae (Fig. 17D), apical nematiform setae moderate, 0.33× length of gonocoxite 2; bursa copulatrix with indistinct dorsal pouch, symmetrical (Fig. 17E); spermatheca ovoid with distinct constrictions on reservoir; spermathecal gland duct short, entering near base of reservoir.

**Holotype.** ♀ labeled "III/15/69 3500' Waipoo Falls, Kauai R.C.A. Rice" (BPBM).

**Paratypes.** Kauai: 1210 m, 04-IV-1919, Kusche (CASC, 4), 05-IV-1919, Kusche (CASC, 1); Alakai Swamp Tr., Rice (BPBM, 1); Kokee S.P., Koaie Str. bank, Montgomery (UHEM, 1), picnic area 0.4 mi before Alakai, UV light, 10-VI-1989, Jamieson (BPBM, 2).

**Distribution.** This species is known only from the Waimea River and its tributaries, Kauai (Fig. 18).

**Etymology.** The species epithet *mandibularis* refers to the very elongate mandibles.

**Habits.** Little is known about this species. It has been collected at light during June, and along Koaie Stream and at Waipoo Falls. It should be searched for along stream banks.

**Phylogenetic relationships.** This species is the basal adelphotaxon of the rest of the native Hawaiian Platynini (Fig. 9). Its distribution on Kauai supports the presence of Hawaiian platynine taxa for at least as long as Kauai has existed as a forested island.

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**Subgenus Colpocaccus** Sharp, 1903

**DIAGNOSIS.** This basal clade of four species, as *B. mandibularis*, includes species characterized by functional flight wings, elongate elytra without modified intervals or striae, and sinuate pronota with only basal setae present (Fig. 19). Species of the subgenus *Colpocaccus* have obvious ventral setae on metatarsomere 5 (Fig. 20A), enabling them to be diagnosed from *B. mandibularis*. The basal tarsomers, best viewed on the metathoracic leg, possess distinct inner and outer dorsal sulci (Fig. 20B-D). The dorsal sulci of the tarsi permit these species to be diagnosed from the large subgenus *Blackburnia*, treated next. The other large clade to follow, subgenus *Metromenus*, is comprised totally of species exhibiting vestigial flight wings. The male aedeagal median lobe of *Colpocaccus* spp. and all others to follow differs from that of *B. mandibularis* by the medioventral excavation of the shaft, producing a recurved ventral margin in lateral view (e.g., Fig. 21B).

**Distribution.** Each major island complex—Kauai, Oahu, Maui Nui, and Hawaii Island—supports a representative species of this subgenus.

**Phylogenetic relationships.** Species-area relationships of this subgenus are totally congruent with the summary area cladogram: (Kauai(Oahu(Maui Nui + Hawaii)))) (Fig. 9).

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**Blackburnia (Colpocaccus) posticata** (Sharp), new combination

(Figs. 2C, E, 14A, 15C, F, 19A, 20, 21, 22, 30D)

*Colpocaccus posticatus* Sharp, 1903: 215.

*Colpocaccus marginatus* Sharp, 1903: 215 (new synonymy).

**DIAGNOSIS.** Distinguishable from other species of subgenus by the distinct transverse mesh microsculpture on pronotal disc, and the broader pronotal lateral depressions (Fig.19A) lined with isodiametric sculpticells. The elytral apex is variously paler, in most
Fig. 19. **Blackburnia** species habitus, dorsal view. A. B. (Colpocaccus) posticata. B. B. (Colpocaccus) tantalus. C. B. (Colpocaccus) lanaiensis. D. B. (Colpocaccus) hawaiensis.
Fig. 20. Scanning electron micrographs of tarsal structures, female *B. (Colpocaccus) posticata*. A. Left protarsomeres, ventral view, showing two rows of 3 ventral setae on tarsomere 5; 119x. B. Right protarsomeres, dorsal view, showing indistinct dorsal sulci on basal two tarsomeres; 120x. C. Right mesotarsomeres, dorsal view, showing evident dorsal sulci on tarsomeres 1-3; 119x. D. Right metatarsomeres, dorsal view, showing evident dorsal sulci on tarsomeres 2-3; 118x.
Fig. 21. *B. (Colpocaccus) posticata*. A. Right metathoracic flight wing, dorsal view. B. Male aedeagal median lobe, right lateral view. C. Male aedeagal median lobe, euventral view. D. Left female gonocoxa, ventral view. E. Female reproductive tract, dorsal view. F. Female spermatheca, ventral view.
specimens from half the distance behind posterior dorsal elytral seta to apex, in some specimens only caudad junction of seventh and second striae. Standardized body length 6.4-8.8 mm.

**Pterothorax.** Metepistemum elongate, lateral margin 2.1 to 2.3× length of anterior margin; wings fully developed (Fig. 21A), wing area 3.1 to 3.7× elytral area.

**Male genitalia.** Aedeagal median lobe with recurved medioventral surface, and short, bluntly rounded apex (Fig. 21B); shaft slightly constricted laterally beyond middle, and evenly rounded at apex (Fig. 21C).

**Female reproductive tract.** Gonocoxa with single series of apical setae on gonocoxite 1; gonocoxite 2 with 3 lateral ensiform setae, 1 dorsal ensiform seta, and 2 short apical nematiform setae, their length 0.2× length of gonocoxite 2 (Fig. 21D); bursa copulatrix slightly asymmetrical with dextral expansion (Fig. 21E), broad dorsal pouch and dorsal sclerotization of bursal wall, appearing flavous in cleared specimens; spermatheca ovoid, bulge opposite spermathecal duct, as well as apical constrictions of reservoir (Fig. 21F).

**Variation.** Sharp (1903) considered individuals exhibiting differentially paler elytral apex to represent a distinct species—*Colpocaccus marginatus*—a decision made untenable given the large number of mixed series now available for study. In collections made during
the 1990s, roughly half the individuals exhibit a broadly pale elytral apex, the other half possess elytra with only a thin pale band, or in some cases a concolorous apex and disc. This variability does not appear to have any basis in maturity of adults. Of 148 specimens collected on the Alakai Swamp Trail in July and August 1991, 78 (53%) exhibit broad pale apical bands on the elytra. Of 99 specimens collected near Waialae Cabin in May of 1995, 61 (62%) have pale bands. Judging from the presence of teneral individuals in the Alakai Swamp Trail series, adults are newly eclosing in July and August. In May, conversely, individuals are mating and producing larvae, indicating that all adults have likely overwintered. Thus the percentage of pale-banded individuals does not appreciably change from July/August to the next May, and elytral pattern is presumably determined shortly after eclosion in the first stages of sclerotization and melanization.

Lectotypes. For *Colpocaccus posticatus*, ♀ lectotype labeled “♀ Colpocaccus posticatus Type D.S. Khlm. Kauai. 16.IV.1895 Perkins (BMNH)” hereby designated. For *Colpocaccus marginatus*, ♂ lectotype labeled “Colpocaccus marginatus Type D.S. Koholuamano Kauai, 4000 ft. Perkins, iv.1895.” The type locality for both of these names is now called Kaholuamano, and is SSW of Waialae Cabin on the Waialae River, in the eastern reaches of Waimea Canyon.

Distribution. This species is widespread in montane forests of Kauai, including the outlying Mt. Kahili ridge to the south and the Makaleha mountains to the east (Fig. 22).

Localities. Broadly distributed across the high swamp habitats of Kauai, having been collected near Kalalau, along the Pihea and Alakai Swamp Trails, on the plateau above Waialae Cabin, and to the west at Kaholuamano. It has also been found on the isolated ridge of Mt. Kahili. Collection localities range from 605 to 1515 m elevation.

Habits. This species lives in most microhabitats within the montane forest. It appears to overwinter on the ground, being found under rocks and logs, and in moss mats from October to March. After dark during May it has been found active on the forest floor and on trails, but also climbing vegetation such as low ferns and *Clermontia*. During daytime in spring it can be found under bark flaps of *Metrosideros* (ohia lehua), and in arboreal moss mats. It can also be found occasionally along rocky or mossy stream banks during spring. Adults fly, and have been collected at light from June until August.

Phylogenetic relationships. This species is the adelphotaxon to the following three species of subgenus *Colpocaccus* (Fig. 9).

*Blackburnia (Colpocaccus) tantalus* (Blackburn), new combination
(Figs. 19B, 23, 24)

*Dyscolus tantalus* Blackburn, 1877: 147.
*Colpodiscus tantalus*: Sharp, 1884: 217.
*Colpocaccus tantalus*: Sharp, 1903: 214.

Diagnosis. Darker and shinier than other species of subgenus; head, pronotum, and elytra concolorous or nearly so, microsculpture of vertex slightly effaced isodiametric mesh; pronotal lateral margins are straight to convex before obtuse-rounded hind angles (Fig. 19B). Sharp (1903) also noted that in this species, the legs are more similar in color compared to the thoracic ventrites than in *B. posticata, B. lanaiensis*, and *B. hawaiiensis.*
Fig. 23. B. (Colpocaccus) tantalus. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, evventral view. C. Left female gonocoxa, ventral view. D. Female spermatheca, ventral view. exc, ventral excavation; other abbreviations as in Fig. 17.
In *B. tantalus*, the middle of the mesofemora is generally darker than the elytral epipleura. Standardized body length 7.6-10.3 mm.

**Pterothorax.** Metepisternum elongate, lateral margin 1.8 to 2.4× length of anterior margin; flight wings fully developed, wing area 3.3 to 4.2× elytral area.

**Male genitalia.** Aedeagal median lobe with marked medioventral expansion and apicoventral excavation, apex very short and bluntly rounded (Fig. 23A), shaft of median lobe slightly constricted laterally about midlength, evenly narrowed to apex (Fig. 23B).

**Female reproductive tract.** Gonocoxa with double series of apical setae on gonocoxite 1; 3-4 broad, elongate lateral ensiform setae, 1 dorsal ensiform seta, and 2 moderate apical nematiform setae, 0.3× length of gonocoxite 2 (Fig. 23C); bursa copulatrix with broad dorsal pouch lined with distinct transverse microsculpture, cuticle appearing yellow, leathery; spermatheca ovoid with fine constrictions, slightly bulged opposite entrance of spermathecal duct (Fig. 23D).

**Lectotype** ♀ labeled with two horizontal lines—the Blackburn code for Oahu (Zimmerman 1957)—and “tantalus” handwritten on reverse side (BMNH) hereby designated. Blackburn (1877) found this species in the “Oahu mountains; on various trees. Not scarce.”
Distribution. Historically distributed on the island of Oahu in both the Waianae and Koolau Ranges (Fig. 24).

Localities. In the Waianae Range, historically found on Mt. Kaala from 455 m elevation to the summit. Also found in Haleauau Gulch and in Kaumokonui Valley. Distributed along the length of the Koolaus, with collecting localities including Kawailoa, Kaipapau, Sacred Falls, Kualanui and Castle Trail, Helemano, Tantalus, Konahuanui, Mt. Olympus, Palolo Valley and Kaau Crater, and Waialae Iki. Koolau localities ranged in elevation from 455 m on Tantalus to 760 m along the northern crest at Kualanui and Helemano (Poamoho Trail).

Habits. PRESUMED EXTINCT. The last specimen collected of this species was found in 1940 on the slopes of Mt. Kaala (Liebherr & Polhemus 1997b). Blackburnia tantalus comprised 39% of the total specimens collected by Perkins on Oahu in the 1890s, and its disappearance is likely attributable to predation by the big-headed ant, *Pheidole megacephala* (F.). This species lived in habitats of lower elevation than other native Oahuan platynines, and depredations of big-headed ant were concentrated in the lower reaches of the montane forest, suggesting that the ant's spread in the late 1800s spelled the end for this species.

Because most specimens were collected many years ago, little is preserved regarding this species' habits. It has been collected under moss on ohia lehua (*Metrosideros*) in September, under bark in October, and under koa (*Acacia*) bark in January. During April and May it was collected on *Cibotium chamissoi*, *Pritchardia*, and *Astelia*. Perkins in Sharp (1903) wrote that it is found "Under bark of Koa commonly, at bases of the leaves of Freycinetia, under stones in wet places and in decaying vegetable matter. Very curious, compared with most of the other Carabids. The other species of this genus [subgenus *Colpocaccus*] are probably more or less indiscriminate in their choice." He also noted its abundance: "*Colpocaccus tantalus* is very common in many situations and fifty or a hundred individuals are sometimes found in a single batch" (Perkins 1906, 48). Perkins commonly observed aggregating behavior among species of this subgenus: "Colonies even of hundreds of individuals are sometimes found together, and sometimes other rarer Carabidae are found mixed in these colonies" (Perkins 1913, cxli). Such observations reiterate the great changes in abundance that have befallen this species.

Absence of flight records is probably symptomatic of the lack of proper labeling. Perkins (1913, cxli) noted that all *Colpocaccus* "are attracted by light at night in the forest region, to which they are restricted."

Phylogenetic relationships. This species is the adelphotaxon for the sister species pair *B. lanaiensis* of Maui Nui, and *B. hawaiiensis* of Hawaii Island (Fig. 9).

*Blackburnia (Colpocaccus) lanaiensis* (Sharp), new combination

(Figs. 19C, 25, 26)

*Colpocaccus lanaiensis* Sharp, 1903: 215.

DIAGNOSIS. Of *Colpocaccus* species with shiny pronotal discs, beetles of this species possess the palest legs, with testaceous femora lighter than the slightly infuscated tibiae; pronotal lateral marginal depressions are paler than the disc, and are of equal breadth in anterior half of the pronotum (Fig. 19C), as opposed to both *B. tantalus* and *B. hawaiiensis*,...
in which the lateral depressions are progressively narrowed toward the pronotal front angles. Standardized body length 7.2-8.6 mm.

**Pterothorax.** Metepisternum elongate, lateral margin 1.8 to 2.2× length of anterior margin; flight wings fully developed, wing area 3.3 to 3.9× elytral area.

**Male genitalia.** Aedeagal median lobe with a pronounced medioventral expansion, apical portion relatively straight, and bluntly rounded tip longer then in *B. tantalus* (Figs. 23A, 25A); median lobe slightly constricted laterally near midlength, tapered to a tightly rounded apex (Fig. 25B).

**Female reproductive tract.** Gonocoxa with partially doubled series of apical setae on gonocoxite 1; 3-4 broad, elongate lateral ensiform setae, 1 dorsal ensiform seta, and 2 moderate apical nematiform setae, 0.3× length of gonocoxite 2 (Fig. 25C); bursa copulatrix
with broad dorsal pouch lined with distinct transverse leathery microsulpture, cuticle appearing yellow; spermatheca ovoid, slightly constricted, slightly bulged opposite entrance of spermathecal duct.

**Lectotype** σ, right specimen on card labeled “σ, Lanai, 2000 ft. Perkins. 80. I.1894” (BMNH) hereby designated. The pin bears a second label, “No. 1225 examined by Prof. Thaxter for Laboulbeniaceae.” Perkins’ lot number 80 is described only as from “Lanai, Lanai, 2000 ft. I.1894” (Anonymous n.d.). This probably corresponds to higher elevations on Lanaihale.

**Distribution.** Known from all islands constituting Maui Nui: east Molokai, Lanai, and West and East Maui (Fig. 26).

**Localities.** On Molokai this species has been recorded from Kalae, Kalawao, and Puu Kolekole within the TNCH Kamakou Preserve. It has been found historically on Lanai at Lanaihale—i.e., the mountains behind Koele of Perkins—and at Kaua Valley. On West Maui, Perkins and Koebele records include Lahaina and Iao Valley. On East Maui, it remains abundant in Kipahulu Valley within Haleakala National Park, along the Central Pali Trail and Kaukauai Stream. Other sites include Keanae and Waihoi Valleys. The recorded elevational range within Kipahulu spans 450 to 1210 m.

**Habits.** Despite the many collecting sites from which this species is known, little has been recorded regarding its habits. In Kipahulu Valley it has been collected in a variety of situations during April and May, including under rocks along a stream bed; under boards, logs, and tarpaulins at an abandoned fence camp; by sifting leaf and moss litter from *Metrosideros* (ohia lehua); and by beating vegetation at night.

**Phylogenetic relationships.** This species is the adelphotaxon of *B. hawaiiensis* (Fig. 9).
Fig. 27. B. (Colpocaccus) hawaiiensis. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view.

**Blackburnia (Colpocaccus) hawaiiensis** (Sharp), new combination
(Figs. 19D, 27, 28, 30C)

*Colpocaccus hawaiiensis* Sharp, 1903: 214.
*Colpocaccus apicalis* Sharp, 1903: 215 (new synonymy).

**Diagnosis.** The combination of lateral marginal depressions narrowed toward front angles, and head contrastingly darker than pronotum and elytra (Fig. 19D) serves to distinguish this species from *B. tantalus* and *B. lanaiensis*. The femora are either concolorous with tibiae, or if paler, still retain a medioventral infuscated area against which tibiae would contact in retracted leg position. Standardized body length 7.3-8.6 mm.

**Pterothorax.** Metepistemum elongate, lateral margin 2.0 to 2.4× length of anterior margin; flight wings fully developed, wing area 3.7 to 4.3× elytral area.

**Male genitalia.** Aedeagal median lobe with a pronounced medioventral expansion, apical portion relatively straight and elongate, and bluntly rounded tip longer than in *B. tantalus* but shorter than in *B. lanaiensis* (Figs. 23A, 25A, 27A); median lobe slightly constricted laterally near midlength, tapered to a tightly rounded apex (Fig. 27B).

**Female reproductive tract.** Gonocoxa with partially doubled series of apical setae on gonocoxite 1; 4 broad, elongate lateral ensiform setae, 1 dorsal ensiform seta, and 2 moderate apical nematiform setae, 0.3× length of gonocoxite 2 (Fig. 27C); bursa copulatrix with broad dorsal pouch, cuticle appearing slightly yellow in cleared specimens due to
slight sclerotization; spermatheca ovoid, slightly constricted, slightly bulged opposite entrance of spermathecal duct.

**Variation.** Sharp (1903) diagnosed *Colpocaccus apicalis* by the broadly pale elytral apex, using the same criterion for recognition of *C. marginatus* (see *B. posticata* above). He acknowledged that the limited series of his "apicalis" comprised newly emerged individuals; in fact, all specimens representing this name were collected during August 1896 by Perkins. Nonetheless, other specimens collected during this month do not exhibit
a broad pale band, suggesting that this condition represents a color polymorphism, just as in B. posticata. In B. hawaiensis the pale-banded form appears much less common than in B. posticata; of August 1896 specimens, only 19 of 99 specimens (19%) exhibit the pale elytral apex.

**Lectotypes.** For *Colpaccus hawaiensis*, ♀ lectotype is hereby designated as right specimen on card labeled “Colpaccus hawaiensis, Hawaii Perkins 656” (BMNH). For *Colpaccus apicalis*, ♀ lectotype labeled “Hawaii 4000 ft. viii 96. C. apicalis Type D.S.” (BMNH) hereby designated. Perkins’ lot number 656 was collected at Kilauea, VIII.1896 (Anonymous n.d.).

**Distribution.** This species is found across Hawaii Island (Fig. 28).

**Localities.** In the Kohala Mountains, recorded from Puu Ohu and Puu Pala. On Mauna Kea found at Laupahoeoe Natural Area Reserve, at Nauhi Gulch, and at Kawaiik. Most records are along the Hilo-Kilauea road, from Glenwood, Olaa, Volcano, Kulani Hill, and Kipuka Puaulu. It is also known from farther west in Kau at Naalehu and at Haao Springs.

**Habits.** This species has been recorded mostly from arboreal situations, by beating *Cibotium* (tree fern, or hapuu) and *Metrosideros* (ohia lehua), and in moss on ohias and tree ferns. Records in flight include those in a window pane trap (June), and at light (July, August, and October).

**Phylogenetic relationships.** This is the adelphotaxon to *B. lanaiensis* of Maui Nui (Fig. 9).

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**Subgenus Blackburnia** Sharp, 1878

**DIAGNOSIS.** Sharp’s (1903, 190) diagnosis of his Division I—“Hind tarsi not sculptured.”—can be used today to diagnose the subgeneric taxon *Blackburnia*. In these species, the basal tarsomeres of all legs lack evidence of dorsolateral sulci, and instead are broadly convex dorsally (Fig. 29A, C, E-H). The single exception, *B. aae*, is a cave species restricted to Kipahulu Valley caves on Haleakala, Maui, and its long gracile legs show faint evidence of dorsal sulci, presumably secondarily derived in association with evolution for cave life. In addition, tarsomere 5 of species in subgenus *Blackburnia* are setose ventrally, with setae equal in length or longer than depth of metatarsomere 5 at the point of setal insertion (Fig. 29B, D). Only several species of the sister subgenus *Metromenus* possess setose fifth tarsomeres, and all of these exhibit evident dorsolateral sulci on the basal tarsomeres.

**Monophyly of subgenus.** The monophyly of this subgenus is robustly supported by a variety of characters (Liebherr & Zimmerman 1998). The female bursa copulatrix is asymmetrical, in most species with a large left-directed expansion near the entry of the common oviduct and spermathecal duct. The bursa also tends to be more elongate in this subgenus, in many species being more than 1.5× length of common oviduct from its insertion on the bursa to its division into lateral oviducts. Nearly all species of the subgenus—except *B. octoocellata*, *B. ewingi*, *B. rupicola*, *B. incendiaria*, and *B. elegans*—exhibit crista microtrichia extended from cuticular sculpticells lining the bursa copulatrix (Fig. 30A).

Extensive evolution of the ovipositor has accompanied this shift to crista bursal microtrichia, with gonocoxae evolving from the plesiomorphic triangular configuration
observed in subgenus *Colpocaccus* (Fig. 30C), to become more parallel (Figs. 31A-B, D, 32C-D), or more falcate, with a basolateral expansion and a curved, scimitarlike lateral margin (Figs. 31C, 32A-B). In most instances, the setal fringe at the apex of gonocoxite 1 is reduced (e.g., Fig. 31C), sometimes to as few as 1 or 2 setae, whereas the plesiomorphic condition is with a complete fringe of setae at the apex of gonocoxite 1 (Fig. 30C).

The setae of gonocoxite 2 are also evolutionarily derived in this subgenus. The lateral ensiform setae are relatively long in the plesiomorphic condition (Fig. 30C), but are generally shorter, sometimes much shorter in species of subgenus *Blackburnia* (Figs. 31, 32). The apical nematiform setae, situated in the apical sensory depression, are
Fig. 30A, B. Microtrichia lining the lumenal surface of bursa copulatrix in *Blackburnia* species. A. Cristate microtrichia characteristic of subgenus *Blackburnia*; B. (B.) *molokaiensis*; 1900×. B. Spikelike, plesiomorphic microtrichia characteristic of the subgenera *Protocaccus*, *Colpocaccus*, and *Metromenus*, as well as B. (Blackburnia) *octoocellata* and its adelphotaxon; B. (Metromenus) *sphodriformis*; 977×. Fig. 30C, D. Plesiomorphic triangular configuration of female gonocoxae. C. B. (Colpocaccus) *hawaiensis*, left gonocoxa, ventral view; 334×. D. B. (Colpocaccus) *posticata*, right gonocoxa, dorsal view; 300×.

Plesiormorphically about 0.2 to 0.3× length of gonocoxite 2 (Fig. 30D). In species of subgenus *Blackburnia*, these setae are almost always more than 1/3 length of gonocoxite 2; the exceptions include B. *ewingi*, B. *rupicola* (Fig. 31A), and B. *incendiaria*, which exhibit plesiomorphic shorter nematiform setae.

Finally, abdominal setation of the females of subgenus *Blackburnia* has undergone a reversal to the plesiomorphic condition within Platynini—i.e., there are 2 setae each side of sternite VII. In 2 of the other 3 subgenera of the radiation—*Colpocaccus*, and *Metromenus*—the groundplan condition is for the female sternite VII to have 3 apical setae each side. The cladistically most basal species—B. (Protocaccus) *mandibularis*—is autapomorphic for possession of 5 apical setae each side of the female sternite VII. The immediate outgroup to the Hawaiian radiation—the genus *Lorostema* Motschulsky—exhibits the plesiomorphic bisetose condition (Liebherr & Zimmerman 1998), so it is impossible to unambiguously ascertain the groundplan condition for this
Fig. 31. Scanning electron micrographs of female left gonocoxa, ventral view, for B. (Blackburnia) species. A. B. rupicola; 108×. B. B. lucipetens (mesal view showing both lateral ensiform seta to right, and dorsal seta to left); 138×. C. B. corrusca; 180×. D. B. sulcipennis; 177×.

caracter in the Hawaiian radiation, though cladistic optimization procedures (e.g., Farris optimization, Farris 1970) would decide in favor of the trisetose state as the groundplan condition.

**Distribution.** Species of the subgenus Blackburnia are distributed on all the major islands except Lanai. Species diversity in the subgenus is relatively evenly distributed across the islands, with Kauai supporting 11 species, Oahu 9, Molokai 7, West Maui 5, East Maui or Haleakala 17, and Hawaii Island 5. Two species are widespread across more than one island: B. molokaiensis on Molokai, West and East Maui, and Hawaii Island; and B. lucipetens obviously resident on Hawaii Island, but much more sporadically collected on East and West Maui, with only single collections at lights on Lanai and Oahu. This species is probably the strongest flier of the native species of Hawaiian Platynini, supporting the possibility that it repeatedly colonizes outlying areas from a core habitation on Hawaii Island.

**Phylogenetic relationships.** This clade of 51 species comprises the adelphotaxon to the subgenus Metromenus (Fig. 9). A basally divergent clade includes a mixture of winged,
flight-capable species—*B. octoocellata*, *B. kukui*, *B. lucipetens*, *B. mystica*, and *B. tibialis* (Fig. 9)—plus more derivative species that have undergone flight-wing reduction during their evolution. This primitively winged clade is the adelphaxon to a clade in which all 42 species exhibit at least some reduction of the flight wings. This clade includes a basally divergent clade of 3 species that live along streams, and exhibit slightly shortened metathoracic alae: *B. costata* of Kauai, *B. corrusca* of Oahu, and *B. molokaiensis* from Maui Nui and Hawaii Island. Subsequent in phylogeny, all species of the subgenus are vestigially winged. Firstly, *B. sulcipennis* of Kauai comprises the adelphaxon for two clades of moderate diversity: the 14-species *B. atra* clade, and the 24-species clade spanning *B. aace* to *B. kipahulu*. Both of these latter clades include species from Kauai, Oahu, and Maui Nui. The most recent speciation events in these groups consistent with the cladogram involve: 1, within-island speciation on Kauai, Oahu, or East Maui; or 2, vicariance among and speciation on Molokai, West Maui, and East Maui, areas that comprised the Pleistocene superisland Maui Nui. Maui Nui has progressively foundered over the past 200,000 years due to the weight of Hawaii Island pressing down the Pacific Plate (Moore 1987), providing present-day opportunities to observe the products and patterns of allopatric speciation.
Fig. 33. *Blackburnia* species habitus, dorsal view. A. *B. (Blackburnia) octoocellata*. B. *B. (Blackburnia) ewingi*, new species. C. *B. (Blackburnia) rupicola*. D. *B. (Blackburnia) incendiaria*. 
Blackburnia (Blackburnia) octoocellata (Karsch), new combination
(Figs. 33A, 34, 35)
Anchomenus sharpi Blackburn, 1878a: 122 (junior homonym of Atrachycnemis sharpi
Blackburn, 1878a: 120).
Colpodes octoocellatus Karsch, 1881: 3 (synonymy, Blackburn, 1882: 63).

DIAGNOSIS. A large piceous beetle, standardized body length 11.1-13.6 mm, with fully
developed flight wings and broad humeri (Fig. 33A), tarsomere 4 triangular, expanded
apically, but not bilobed, and tarsomere 5 with elongate ventral setae, longer than depth of
tarsomere at their point of insertion. The pronotum lacks indication of hind angles (Fig.
33A), except in some specimens there is a slight change in curvature of the laterobasal
margins behind the basal pronotal setae.

Pterothorax. The metepisternum is elongate, lateral margin 2.1× length of anterior
margin; flight wings fully developed, wing area 5.0× area of elytra in single specimen
measured.

Male genitalia. Aedeagal median lobe with medioventral expansion, shaft nearly straight
in middle portion, apex abruptly downturned to tightly rounded tip (Fig. 34A); apex
laterally constricted near tip, attenuate (Fig. 34B).

Female reproductive tract. Gonocoxa with 5-6 larger setae restricted to medial angle
of gonocoxite 1, about 5 very small setae laterad (Fig. 34C); gonocoxite 2 elongate,
subparallel, apex tightly rounded, with 2-3 very small lateral ensiform setae, and 1-2 very
small dorsal ensiform setae, each about 0.04× length of gonocoxite 2; apical nematiform
setae elongate, about 0.33× length of gonocoxite 2; bursa copulatrix elongate, about 1.9×
length of common oviduct, with a large left-directed expansion, and obvious ring of
spikelike luminal microtrichia (Fig. 34D); spermatheca elongate, without evidence of basal
projections, exhibiting numerous fine constrictions.

Lectotypes. For Anchomenus sharpi, σ lectotype hereby designated, labeled with three
parallel lines and a diagonal ink slash, signifying Maui among Blackburn's labels
(Zimmerman 1957), with “B. sharpi” handwritten on reverse side (BMNH). For Colpodes
octoocellatus, σ lectotype labeled “Type No: 60819 // Olinda, Finsch 8-ocellatus Karsch”
(MNHU) hereby designated. Karsch's type series is mixed; the σ lectotype and a σ
paratype represent this species, whereas the ♀ paratype represents B. rupicola.

Etymology. The species epithet octoocellatus does not fit well with the habitus of this
species, as nearly all specimens have 6 dorsal elytral setae located in depressions less than
half the width of the third elytral interval.

Distribution. This species is known only from material collected by Finsch in 1872, and
by Perkins in the 1890s, on the lower slopes of the Haleakala volcano near Olinda (Fig. 35).

Habits. One collection with accompanying ecological information was made by Perkins:
"under koa bark," date and year unknown. Perkins included this species in his lots 364 and
384, with those lots recorded as Olinda, 4000 ft., 31-III-1894, and Haleakala, 4500 to 5000
ft., III-1894. His lot 384 included 69 Blackburnia erro, 4 B. sphodriformis, 1 B. putealis,
and 1 B. octoocellata. Of these, “The large spec. [was] beaten from dead tree” (Anonymous
n.d.). This single large specimen was no doubt B. octoocellata. Perkins notes in Sharp
(1903) that B. octoocellata is “truly arboreal, and especially fond of Koa, and is found
Fig. 34. *B. (Blackburnia) octoocellata*. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view. D. Female bursa copulatrix, ventral view, showing medial band of spikelike microtrichia, left lateral expansion, and fusiform spermatheca with gland, attaching to common oviduct.
**Blackburnia (Blackburnia) octoocellata** (Karsch), new combination  
(Figs. 33A, 34, 35)

*Anchomenus sharpi* Blackburn, 1878a: 122 (junior homonym of *Atrachycnemis sharpi* Blackburn, 1878a: 120).


*Baryneus sharpi*: Sharp, 1903: 209.

*Colpodes octoocellatus* Karsch, 1881: 3 (synonymy, Blackburn, 1882: 63).

**DIAGNOSIS.** A large piceous beetle, standardized body length 11.1-13.6 mm, with fully developed flight wings and broad humeri (Fig. 33A), tarsomere 4 triangular, expanded apically, but not bilobed, and tarsomere 5 with elongate ventral setae, longer than depth of tarsomere at their point of insertion. The pronotum lacks indication of hind angles (Fig. 33A), except in some specimens there is a slight change in curvature of the laterobasal margins behind the basal pronotal setae.

*Pterothorax.* The metepisternum is elongate, lateral margin 2.1× length of anterior margin; flight wings fully developed, wing area 5.0× area of elytra in single specimen measured.

**Male genitalia.** Aedeagal median lobe with medioventral expansion, shaft nearly straight in middle portion, apex abruptly downturned to tightly rounded tip (Fig. 34A); apex laterally constricted near tip, attenuate (Fig. 34B).

**Female reproductive tract.** Gonocoxa with 5-6 larger setae restricted to medial angle of gonocoxite 1, about 5 very small setae laterad (Fig. 34C); gonocoxite 2 elongate, subparallel, apex tightly rounded, with 2-3 very small lateral ensiform setae, and 1-2 very small dorsal ensiform setae, each about 0.04× length of gonocoxite 2; apical nematiform setae elongate, about 0.33× length of gonocoxite 2; bursa copulatrix elongate, about 1.9× length of common oviduct, with a large left-directed expansion, and obvious ring of spikelike lumenal microtrichia (Fig. 34D); spermatheca elongate, without evidence of basal projections, exhibiting numerous fine constrictions.

**Lectotypes.** For *Anchomenus sharpi*, ♂ lectotype hereby designated, labeled with three parallel lines and a diagonal ink slash, signifying Maui among Blackburn’s labels (Zimmerman 1957), with “B. sharpi” handwritten on reverse side (BMNH). For *Colpodes octoocellatus*, ♂ lectotype labeled “Type No: 60819 // Olinda, Finsch 8-octocellatus Karsch” (MNHU) hereby designated. Karsch’s type series is mixed; the ♂ lectotype and a ♀ paratype represent this species, whereas the ♀ paratype represents *B. rupicola*.

**Etymology.** The species epithet *octoocellatus* does not fit well with the habitus of this species, as nearly all specimens have 6 dorsal elytral setae located in depressions less than half the width of the third elytral interval.

**Distribution.** This species is known only from material collected by Finsch in 1872, and by Perkins in the 1890s, on the lower slopes of the Haleakala volcano near Olinda (Fig. 35).

**Habits.** One collection with accompanying ecological information was made by Perkins: “under koa bark,” date and year unknown. Perkins included this species in his lots 364 and 384, with those lots recorded as Olinda, 4000 ft., 31-III-1894, and Haleakala, 4500 to 5000 ft., III-1894. His lot 384 included 69 *Blackburnia erro*, 4 *B. sphodrijormis*, 1 *B. putealis*, and 1 *B. octoocellata*. Of these, “The large spec. [was] beaten from dead tree” (Anonymous n.d.). This single large specimen was no doubt *B. octoocellata*. Perkins notes in Sharp (1903) that *B. octoocellata* is “truly arboreal, and especially fond of Koa, and is found..."
Fig. 34. *B. (Blackburnia) octoocellata*. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view. D. Female bursa copulatrix, ventral view, showing medial band of spikelike microtrichia, left lateral expansion, and fusiform spermatheca with gland, attaching to common oviduct.
**Blackburnia (Blackburnia) octoocellata** (Karsch), new combination

(Figs. 33A, 34, 35)

*Anchomenus sharpi* Blackburn, 1878a: 122 (junior homonym of *Atrachynyemis sharpi* Blackburn, 1878a: 120).


*Baryneus sharpi*: Sharp, 1903: 209.

*Colpodes octoocellatus* Karsch, 1881: 3 (synonymy, Blackburn, 1882: 63).

**Diagnosis.** A large piceous beetle, standardized body length 11.1-13.6 mm, with fully developed flight wings and broad humeri (Fig. 33A), tarsomere 4 triangular, expanded apically, but not bilobed, and tarsomere 5 with elongate ventral setae, longer than depth of tarsomere at their point of insertion. The pronotum lacks indication of hind angles (Fig. 33A), except in some specimens there is a slight change in curvature of the laterobasal margins behind the basal pronatal setae.

*Pterothorax.* The metepisternum is elongate, lateral margin 2.1× length of anterior margin; flight wings fully developed, wing area 5.0× area of elytra in single specimen measured.

*Male genitalia.* Aedeagal median lobe with medioventral expansion, shaft nearly straight in middle portion, apex abruptly downturned to tightly rounded tip (Fig. 34A); apex laterally constricted near tip, attenuate (Fig. 34B).

*Female reproductive tract.* Gonocoxa with 5-6 larger setae restricted to medial angle of gonocoxite 1, about 5 very small setae laterad (Fig. 34C); gonocoxite 2 elongate, subparallel, apex tightly rounded, with 2-3 very small lateral ensiform setae, and 1-2 very small dorsal ensiform setae, each about 0.04× length of gonocoxite 2; apical nematiform setae elongate, about 0.33× length of gonocoxite 2; bursa copulatrix elongate, about 1.9× length of common oviduct, with a large left-directed expansion, and obvious ring of spikelike lumenal microtrichia (Fig. 34D); spermatheca elongate, without evidence of basal projections, exhibiting numerous fine constrictions.

**Lectotypes.** For *Anchomenus sharpi*, ♂ lectotype hereby designated, labeled with three parallel lines and a diagonal ink slash, signifying Maui among Blackburn’s labels (Zimmerman 1957), with “B. sharpi” handwritten on reverse side (BMNH). For *Colpodes octoocellatus*, ♂ lectotype labeled “Type No: 60819 // Olinda, Finsch 8-oceellatus Karsch” (MNHU) hereby designated. Karsch’s type series is mixed; the ♂ lectotype and a ♂ paratype represent this species, whereas the ♀ paratype represents *B. rupicola*.

**Etymology.** The species epithet *octoocellatus* does not fit well with the habitus of this species, as nearly all specimens have 6 dorsal elytral setae located in depressions less than half the width of the third elytral interval.

**Distribution.** This species is known only from material collected by Finsch in 1872, and by Perkins in the 1890s, on the lower slopes of the Haleakala volcano near Olinda (Fig. 35).

**Habits.** One collection with accompanying ecological information was made by Perkins: “under koa bark,” date and year unknown. Perkins included this species in his lots 364 and 384, with those lots recorded as Olinda, 4000 ft., 31-III-1894, and Haleakala, 4500 to 5000 ft., III-1894. His lot 384 included 69 *Blackburnia erro*, 4 *B. sphodriformis*, 1 *B. putealis*, and 1 *B. octoocellata*. Of these, “The large spec. [was] beaten from dead tree” (Anonymous n.d.). This single large specimen was no doubt *B. octoocellata*. Perkins notes in Sharp (1903) that *B. octoocellata* is “truly arboreal, and especially fond of Koa, and is found
Fig. 34. B. (Blackburnia) octoocellata. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view. D. Female bursa copulatrix, ventral view, showing medial band of spikelike microtrichia, left lateral expansion, and fusiform spermatheca with gland, attaching to common oviduct.
under the bark, or in hollows in branches, sometimes in the top-most twigs. Female seen ovipositing in the daytime in chinks of the bark of Koa.” Later on he notes this species “may be obtained high up in trees from beneath bark, usually of Acacia koa; but it is not restricted to that tree” (Perkins 1913, cxli). Thus, like its patristically closest relative—the brachypterous Hawaii Island species B. ewingi—the fully winged B. octoocellata occurs on large trees in mesic forest.

**Phylogenetic relationships.** Based on the cladistic analysis, this species is the putative adelphotaxon of the species triplet: B. ewingi, B. rupicola, and B. incendiaria. All four of these species live on either Maui or Hawaii Island.

**Blackburnia (Blackburnia) ewingi** Liebherr, new species
(Figs. 33B, 36A, 37)

**DIAGNOSIS.** As with B. rupicola and B. incendiaria, a large piceous beetle—standardized body length 14.2 mm—with reduced, rounded humeri (Fig. 33B), but with more coarsely granulate isodiametric microsculpture on frons, pronotal disc and elytra, pronotal lateral margins broad to front angles without upturned edge in anterior half of pronotum, and evident rounded punctulæ in all elytral striae.

**DESCRIPTION.** **Head** gracile, neck elongate with broad, shallow dorsal impression; labrum broadly, moderately emarginate apically; frontoclypeal grooves broad, shallow; two supraorbital setae each side, vertex with fine wrinkles radiating medioanteriorly from area
Fig. 36A. B. (Blackburnia) ewingi, new species, left female gonocoxa, ventral view. Fig. 36B-E. B. (Blackburnia) rupicola. B. Male aedeagal median lobe, right lateral view. C. Male aedeagal median lobe, euventral view. D. Left female gonocoxa, ventral view. E. Female bursa copulatrix, spermathecal assembly, and common oviduct, ventral view, showing right-directed bursal expansion.
Fig. 37. Distributional records for B. (Blackburnia) ewingi, new species (■), and B. (Blackburnia) incendiaria (●).

near hind seta; antennal pedicel with longer outer seta plus 1 very short inner apical seta; mentum with a single seta each side, mentum tooth triangular with a finely rounded apex.

Prothorax broad, maximum width 1.28× median length, lateral marginal depressions broad in anterior half without an upturned edge; hind angles rounded, basolateral setae situated cephalad of hind angles 0.12× distance to broadly rounded front angles; lateral pronotal seta absent; median base expanded posteriorly, the hind margin sinuate laterally,
basal bead continuous across entire base, median base with fine rugose wrinkles; laterobasal depressions with flat bottom, bordered laterally by upraised basolateral margin; median longitudinal impression finely incised, intersected with fine transverse wrinkles; anterior transverse impression nearly obsolete, indicated by a series of short longitudinal wrinkles; anterior marginal bead obsolete medially, present laterally but obsolete on flat, rounded front angles. Prosternal process flat medially, with fine vertical wrinkles on posterior surface.

Elytra oviform, humeri reduced, rounded; basal groove and lateral marginal depressions both narrow; elytral intervals broadly convex, striae deep and broad, with rounded punctulae lining their lengths, punctures slightly visible even near elytral apex; subapical sinuation reduced, the lateral margin straight near apex of eighth stria; sutural apex angulate, with a very small denticle; scutellar seta and 3 dorsal elytral setae present; 18 lateral elytral setae.

Pterothorax. Metepisternum elongate, lateral margin about 2.0× anterior width; flight wings extended as micropterous straps about 0.5× elytral length.

Legs. Profemur without anteroventral or posteroventral setae; mesocoxa with 1 ridge seta; mesofemur with 5 anteroventral setae; metacoxa trisetose, mesal seta present; metafemur with 1 anteroventral seta; tarsomeres gracile, elongate, basal metatarsomere 2.7× length of inner tibial spur; basal 3 tarsomeres without dorsolateral sulci; metatarsomere 4 emarginate apically, inner and outer lobes 0.5× mediobasal length; basal metatarsomeres with 3 dense rows of ventrolateral setae bordering a broad central space; tarsomere 5 with two ventrolateral rows of 8 setae, 1.5× as long as tarsomere depth at point of setal insertion.

Abdomen. Female with 2 setae each side of sternite VII.

Coloration. Body a unicolorous ferruginous brown; palpi, antennae, tibiae, and tarsi slightly paler, more flavous.

Microsculpture. Vertex with distinct granulate isodiametric microsculpture, the sculpticells forming only irregular transverse rows; pronotal disc with granulate isodiametric sculpticells arranged in transverse rows, microsculpture on median base and in laterobasal and lateral depressions similar in roughness to disc, but sculpticells more isodiametric; elytral striae with distinct isodiametric sculpticells arranged in irregular transverse rows; abdominal sternites with granulate isodiametric microsculpture on median areas of basal sternites, microsculpture smoother on apical two sternites.

Male genitalia. Only the female holotype is known.

Female reproductive tract. Gonocoxa with 3-4 setae along medioapical margin of gonocoxite 1, a single row of 6-8 very short peglike sensilla laterally separated from medial group (Fig. 36A); gonocoxite 2 elongate, subparallel, the apex tightly rounded, with 4 small lateral ensiform setae and 5 small dorsal ensiform setae, each about 0.07× length of gonocoxite 2; apical nematiform setae moderate, about 0.30× length of gonocoxite 2; bursa copulatrix elongate, about 1.6× length of common oviduct, with a large left-directed expansion and obvious ring of spikelike luminal microtrichia; spermatheca elongate, fusiform, without basal projections, with numerous fine constrictions (as in Fig. 39D).

Holotype ♀ labeled “HI: Hawaii Kohala Mts. Puu Pohoulaula, 0.5km E 12-X-1997 lot04 el. 1200 m pyrethrum fog mossy ohia J.Liebherr” (CUIC).

Etymology. This species honors Curtis P. Ewing, who was present at the time of the only collection of this species, and who has contributed to many other discoveries and rediscoveries of native Hawaiian carabids. 
**Distribution.** So far only known from the Kohala Mountains of Hawaii Island (Fig. 37).

**Habits.** The lone known female fell from between loose bark flaps on the underside of a horizontal ohia trunk about 2 m above the ground when pyrethrin fog was applied to the plant. The collection was made in closed-canopy forest along the south rim of Kohakohau Gulch.

**Phylogenetic relationships.** This species is the putative adelphotaxon of *B. rupicola* of East Maui and *B. incendiaria* of Mauna Loa and Mauna Kea, Hawaii Island (Fig. 9).

**Blackburnia (Blackburnia) rupicola** (Blackburn), new combination
(Figs. 29A-B, 31A, 33C, 36B-E, 38)

*Anchomenus rupicola* Blackburn, 1878a: 122.
*Barypristus rupicola*:
Blackburn & Sharp, 1885: 213.
*Colpodes octoocellatus* Karsch, 1881: 3 (in part, ♀ paratype misidentified).

**DIAGNOSIS.** As *B. incendiaria* and *B. ewingi*, a large piceous beetle—standardized body length 11.1-15.9 mm—with reduced, rounded humeri (Fig. 33C), flight wings reduced to micropterous flaps extended 1/3 length of elytra, but scutellar seta absent. The male aedeagus is more expanded medioventrally (Fig. 36B) than in *B. octoocellata* (Fig. 34A) and *B. incendiaria* (Fig. 39A). The female reproductive tract is bilaterally inverted from the plesiomorphic condition in these two species plus *B. ewingi*, with an expansion on right side of bursa (Fig. 36E).

**Pterothorax.** Metepisternum moderately elongate, with lateral margins ranging from 1.5 to 1.7× length of anterior margin.

**Male genitalia.** Aedeagal median lobe broadly recurved medioventrally, the lobe thereby very broad dorsoventrally (Fig. 36B), apex abruptly downturned to finely rounded tip; median lobe apex constricted laterally, from point of eversion of internal sac to tightly rounded tip (Fig. 36C).

**Female reproductive tract.** Gonocoxa with 5-7 setae along apical margin of gonocoxite 1 (Fig. 36D); gonocoxite 2 elongate, subparallel, apex rounded, with 3-4 very small lateral ensiform setae (Fig. 31A), and 2 very small dorsal ensiform setae, each about 0.06× length of gonocoxite 2; apical nematiform setae moderate, about 0.27× length of gonocoxite 2; bursa copulatrix elongate, about 2.2× length of common oviduct, with large right-directed expansion with accordion pleat, and obvious ring of spikelike luminal microtrichia (Fig. 36E); spermatheca elongate, without basal projections, with numerous fine constrictions.

**Lectotype** ♀ labeled with 3 parallel lines plus diagonal ink slash—i.e., Blackburn Maui label (Zimmerman 1957)—with “B. rupicola” handwritten on back (BMNH) hereby designated.

**Distribution.** This species is found on the higher elevations of Haleakala, East Maui, including leeward sites and within the crater (Fig. 38).

**Localities.** Across Haleakala’s drier portions, this species has been collected at Olinda, Waiapai Gulch, Leleiwi Overlook, White Hill, Kapalaoa, Puu Mamane, Kolekole Peak, and above timberline at Kuiki, located on the south rim of Kipahulu Valley. These sites range from 1210 to 3030 m elevation. Nonetheless, this species was last seen at the relatively low elevation sites of Olinda in 1918, and Waiopai Gulch in 1926. All other twentieth-century collections have been above 2000 m either in the volcano’s crater or on its upper flanks.
Habits. This species is most often observed on the ground. During winter it can be found under rocks. Perkins (1913) found his specimens almost always under rocks. In April and May it has been collected from Deschampsia tufts and leaf litter under Sophora plants. It has been observed actively foraging under Sophora plants at nighttime temperatures of 10° C. Nonetheless, individuals can climb on vegetation, and have been beaten from Coprosma montana after dark. One specimen was found at a diphacinone bait station in September.

Phylogenetic relationships. Based on cladistic analysis using adult characters (Fig. 9), this is the adelphotaxon to B. incendiaria, found on Mauna Kea and Mauna Loa, Hawaii Island. This hypothesis places the flightless B. rupicola on an island different from its flightless adelphotaxon. Moreover, it places the geographically intermediate B. ewingi of the Kohala Mountains, Hawaii Island, as the adelphotaxon to B. rupicola + B. incendiaria. This set of relationships is due in part to the greater reduction of humeri and wings shared by B. rupicola and B. incendiaria (Fig. 33B-D). Adding phylogenetic data from other sources would test the homology statements concerning flight apparatus reduction inherent in the relationships defined by the preferred cladogram.
Blackburnia (Blackburnia) incendiaria (Blackburn), new combination
(Figs. 33D, 37, 39)
Anchomenus incendiarius Blackburn, 1879: 105.
Barypristus incendiarius: Blackburn & Sharp, 1885: 213.

DIAGNOSIS. As preceding two species, large, piceous, standardized body length 12.2-15.7
mm, but pronotum more elongate, basolateral margins straighter before basal pronotal setae
(Fig. 33D); flight wings vestigial; scutellar seta present; basal pronotal setae present or
absent.

Pterothorax. The elytral humeri are not as reduced as in B. rupicola (Fig. 33C), and
metepisternum is slightly longer than in that species; lateral margin length ranging from 1.9
to 2.0× length of anterior margin.

Male genitalia. Median aedeagal lobe slightly expanded medioventrally, apex
downturned with tip as long as in B. rupicola, but not as abruptly angled (Figs. 36B, 39A);
median lobe apex constricted resulting in an attenuate tip (Fig. 39B).

Female reproductive tract. Gonocoxa with 4-6 setae in a partially doubled row along
apical margin of gonocoxite 1 (Fig. 39C); gonocoxite 2 elongate, subparallel, apex rounded,
with 2-3 very small lateral ensiform setae near base, and 2 very small dorsal ensiform setae,
each about 0.05× length of gonocoxite 2; apical nematiform setae moderate, about 0.30×
length of gonocoxite 2; bursa copulatrix elongate, about 1.7× length of common oviduct,
with a large left-directed expansion and obvious ring of spikelike lumenal microtrichia (Fig.
39D); spermatheca elongate, without evidence of basal projections, exhibiting numerous
fine constrictions.

Variation. This species is polymorphic for presence of the basal pronotal seta. Of 36
specimens examined for this feature, 10 lack both basal setae, 2 have one seta unilaterally
present, and 24 possess basal setae on both sides of the specimen.

Lectotype ♂ labeled with 2 parallel lines, 2 vertical ink lines to right of pin—Blackburn’s
coding for Hawaii Island (Zimmerman 1957)—(BMNH) hereby designated.

Distribution. This species appears restricted to Mauna Kea, Mauna Loa, and Kilauea on
the island of Hawaii (Fig. 37).

Localities. On Mauna Kea this species has been recorded from Humuula, Kalepeamoaa,
Kole, Mauna Kea Road, and Pohakuloa. On Mauna Loa records include Kilauea and
Volcano along the Hilo Road. Elevations of recorded localities range from 1210 to 2575
m.

Habits. This is a terrestrially active species like its sister, being recorded from litter under
mullein clumps, under rocks, and in pitfall traps. In the 1890s, it was most commonly found
under bark or logs of Acacia koa (Sharp 1903). Perkins (1913, cxli) notes it “occurs low
down under bark of Koa trees, sometimes even beneath the level of the soil.” It is also a
species of open bunchgrass and scrub habitats.

Phylogenetic relationships. As stated above, B. incendiaria is hypothesized to be the
adelphotaxon of B. rupicola of East Maui.
Blackburnia (Blackburnia) lucipetens (Blackburn), new combination
(Figs. 29C-D, 31B, 40A, 41, 42, 43)

*Anchomenus lucipetens* Blackburn, 1879: 105.
*Colpodiscus lahainensis* Sharp, 1903: 210 (new synonymy).

**DIAGNOSIS.** A large brunneous beetle with slightly darker head, standardized body length 11.0-12.7 mm, fully developed flight wings, and broad, bilobed tarsomere 4 (Fig. 29C-D); distinguished from adelphotaxon *B. kukui* by: 1, distinct isodiametric microsculpture on vertex; 2, transverse pronotum with maximum width 1.2 to 1.3× median length, and broader lateral marginal depressions (Fig. 40A-B); and 3, tightly rounded humeral angles.

**Pterothorax.** Metepisternum elongate, lateral margin 1.8 to 2.0× length of anterior margin; flight wings fully developed, wing area 3.0 to 3.5× area of elytron.
Fig. 41. *B. (Blackburnia) lucipetens*. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view.

**Male genitalia.** Aedeagal median lobe elongate, slightly expanded medioventrally, apex evenly downcurved, tip broadly rounded (Fig. 41A); median lobe evenly narrowed to tightly rounded tip in euventral view (Fig. 41B).

**Female reproductive tract.** Gonocoxa with single series of 6-8 apical setae on gonocoxite 1 (Fig. 41C); gonocoxite 2 elongate, subparallel, with apex narrowly rounded, 3 peglike lateral ensiform setae about 0.15× as long as gonocoxite 2, and 1-2 dorsal ensiform setae close to dorsolateral edge, dorsad lateral setae (Fig. 31B); apical nematiform setae elongate, about 0.4× length of gonocoxite 2; bursa copulatrix elongate, about 1.7× length of common oviduct, slightly asymmetrical with a leftward expansion; luminal surface of bursa with a band of cristate microtrichia, mostly 5-pointed cristae.

**Lectotypes.** For *Anchomenus lucipetens*, lectotype ♂, label with 2 parallel lines, inked circle on bottom thinner line, and “237 lucipetens” handwritten on reverse side (BMNH) hereby designated. For *Colpodiscus lahainensis*, lectotype ♀, label “♀ Colpodiscus lahainensis Type. D.S. West Maui Mts. Jao Valley. Perkins. VIII.1894.” (BMNH) hereby designated.
Distribution. This species is distributed across windward Mauna Kea and Mauna Loa (Fig. 42).

Localities. On Mauna Kea, this species has been recorded from Laupahoehoe Natural Area Reserve, above Honomu, Kawaiiki, and Nauhi Gulch. Mauna Loa localities include Amauulu above Hilo, Glenwood, Olaa, Kilauea, Volcano House, Kipuka Pauulu, and Kau.
Recorded habitats range from 425 to 1820 m on Hawaii Island, with collections most common during four months: June (56 specimens), July (18 specimens), August (23 specimens), and November (25 specimens).

*Blackburnia lucipetens* has also been found at a variety of sites on islands comprising Maui Nui (Fig. 43): Honomanu Gulch and Keanae, East Maui; Iao Valley, West Maui; Lanaihale, Lanai; Kainalu, Molokai; and Honolulu, Oahu. The Iao Valley records include collections in 05/1894, 09/1896, 03/1909, and 08/1918. The East Maui records include collections at Honomanu in 04/1911 and 06/1920. Haleakala recorded localities are between 150 and 910 m elevation. All Molokai records relate to collecting done at Kainalu by O. Swezey and E.H. Bryan during July of 1927 at elevations of 455 to 480 m. The lone Lanai specimen was collected by K. Sattler in September of 1976 at Lanaihale summit (1020 m). Of the two specimens collected on Oahu, one was taken at a shop window on Kuaumolu St., Honolulu. These off-Hawaii Island collections can be summed by month as follows: March, 5 specimens; April, 1 specimen; May, 2 specimens; June, 8 specimens; July, 19 specimens; August, 11 specimens; September, 3 specimens; December, 1 specimen.

From these data on phenology of collections, and elevational distribution across recorded localities, two aspects of this species’ distribution seem likely: 1, the species’ original habitation is Hawaii Island, as that island has had specimens recovered from the greatest diversity of seasons and elevations; and 2, collections on Maui Nui islands and Oahu have resulted from individuals dispersing by flight during warmer nights. Such flights would most likely occur during summer’s southerly Kona wind conditions, with beetles subsequently carried to northwesterly islands on reestablished northeasterly trade winds after a switch back to trade wind conditions. This would result in landfall in the larger eastward-facing valleys such as Keanae, Iao, and Kainalu.
Habits. Perkins found this species “In West Maui, under stones on bank of stream, but in Olaa, Hawaii, generally under logs or fallen fern-stems, or decayed vegetable matter” (Sharp 1903). Perkins (1913, cxli) notes its abundance at lights at night. Since then, this species has been recorded principally from plant surfaces, including within moss on large ohia trunks, at the top of a large Pritchardia tree, and from Tetraplasandra. One series of five specimens was collected at light in July, supporting occurrence of summer flight activity. A single April-collected specimen is recorded from under rocks.

Phylogenetic relationships. This species is sympatric with its adelphotaxon, B. kukui (Figs. 9, 42).

Blackburnia (Blackburnia) kukui Liebherr, new species
(Figs. 40B, 42, 44)

DIAGNOSIS. Large beetles, 11.7-13.5 mm standardized body length, with a shiny brunneous body and paler, rufotestaceous legs and antennae; flight wings fully developed, humeri broad (Fig. 40B); tarsomere 4 broadly and deeply bilobed. The species is externally diagnosed from its adelphotaxon, B. lucipetens, by the narrower pronotum (maximum width less than 1.1× median length), and narrower lateral marginal depressions almost obsolete along anterior half of pronotum.

DESCRIPTION. Head capsule elongate, dorsal impression of neck well developed, eyes moderately projected, ocular ratio 1.58, but not more convex than gena (Fig. 40B); frons smooth, shiny, frontoclypeal depressions shallow, only slightly extended toward margin of eye; vertex broadly depressed just inside posterior half of eye, depression extended ventrad behind eye; antennae moderately elongate, extended as far as basal 1/4 of elytra; labrum elongate, less than 1.5× as broad as long, front margin medially concave, medial pair of setae shortest; mentum tooth short, blunt to broadly rounded.

Prothorax. Pronotum quadrate with rounded basal angles, maximum width less than 1.1× median length; lateral marginal depressions very narrow toward rounded, nonprotuberant front angles; laterobasal depressions smooth, impunctate, bordered laterally by a raised margin, not beadlike, and posteriorly by a raised bead continuous with a median basal marginal bead; median base smooth, with only indistinct longitudinal irregularities; median longitudinal impression extremely fine; pronotal disc completely smooth or with slight transverse wrinkles; anterior transverse impression very shallow, indistinct; prosternal process convex ventrally, not margined, evenly rounded posteriorly; dorsal triangle above process with angulate margins, but not carinate.

Elytra. Humeri broad, evenly rounded; lateral margins subparallel, slightly expanded to apical 2/3 of length, subapical sinuation reduced, lateral margin straight to slightly convex throughout apical portion of elytra; elytral striae smooth, impunctate; elytral intervals slightly convex; 3 dorsal elytral setae each side in third interval, 16-19 lateral elytral setae outside eighth stria.

Pterothorax. Metepisternum elongate, lateral margin 2.0 to 2.4× length of anterior margin; flight wings fully developed, wing area 2.9× area of elytron.

Legs. Profemur without anterior setae, 2 posteroventral setae; mesoconyx with 1 ridge seta; mesofemur with 2 anteroventral setae; metacoxa bisetose, mesal seta absent; metafemur with 2 anteroventral setae; tarsomeres progressively broader apically from tarsomere 1 to
Fig. 44. B. (Blackburnia) kukui, new species. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, mesal view. D. Female bursa copulatrix, spermathecal assembly, and common oviduct, ventral view.

3, third protarsomere broader apically than median length, mesotarsomere 3 nearly an equilateral triangle in shape, and third metatarsomere $0.8\times$ as broad apically as median length; tarsomere 4 deeply bilobed, each lobe broad, on metaleg, outer lobe $1.15\times$ as long as inner lobe, and $3.8\times$ median basal length; tarsomeres with dense ventral setation, progressively finer and denser from tarsomere 1 to 4 (as in Fig. 29D), tarsomere 4 with approximately 6 flattened squamosetae (Stork 1980) at apex of each lobe; tarsomere 5 with 6-8 ventrolateral setae each side, the setae subequal to tarsomere depth at setal insertion.
**Abdomen.** Females with 4 setae each side of apex of sternite VII, males with 2 setae each side.

**Coloration.** Quite uniformly brunneous, though head of some immature specimens darker than pronotum and elytra; ventral surface of body and legs also almost concolorous, though legs of some individuals slightly paler; greatest contrast in color are the flavous setose portions of antennomeres 5-11.

**Microsculpture.** Vertex with reduced isodiametric microsculpture, depressed areas inside and behind eyes with distinct isodiametric mesh; pronotum with transverse mesh microsculpture on disc, laterobasal depressions with distinct, granulate isodiametric mesh; elytra with flat isodiametric sculpticells arranged in irregular transverse rows.

**Male genitalia.** Aedeagal median lobe remarkably narrow and long, evenly curved on medioventral surface (Fig. 44A), apex strongly downturned to tightly rounded tip, tip 2.33× as long as deep; median lobe tip laterally constricted apicad opening of internal sac, tip therefore attenuate (Fig. 44B).

**Female reproductive tract.** Gonocoxa with single series of 6-8 apical setae on gonocoxite I, 4-5 on mesal angle, 2-3 laterad (Fig. 44C); gonocoxite 2 elongate, subparallel, with apex rounded, 2-3 peglike lateral ensiform setae about 0.12× as long as gonocoxite 2, and 1 dorsal ensiform seta close to dorsolateral edge, dorsad lateral setae; apical nematiform setae elongate, about 0.4× length of gonocoxite 2; bursa copulatrix elongate, about 3.25× length of common oviduct, slightly asymmetrical with a leftward expansion (Fig. 44D); lumenal surface of bursa with a band of cristate microtrichia, mostly 5-pointed cristae.


**Paratypes.** HAWAII: 1881 Flow at Tree Planting Road, 1200 m, 1-VI-1998, Gruner (BPBM, 1); Hilo, black light trap, 12-X-1979, Preston (BPBM, 1); Kilauea, light trap, 12-VIII-1958, Beardsley (BPBM, 1), 15-VIII-1958, Beardsley (BPBM, 3); Kilauea-Hilo Rd., 29 miles, 22-VI-1966, Yoshimoto (BPBM, 1); Volcano, Jiwi Street, 1177 m, IV-1989, Gambino (CUIC, 1), local post office, at light, 09-VII-1991, Perreira (CUIC, 1).

**Etymology.** The species epithet *kukui* signifies the tree whose nutlike fruits were used by native Hawaiians to extract lamp oil. The Hawaiian word *kukui* also means light.

**Distribution.** This species is currently known from windward Mauna Loa, at sea level near Hilo, to Kilauea (Fig. 42).

**Habits.** This species, like its adelphotaxon *B. lucipetens*, is known to fly to lights at night. Specimens have been recorded at UV lights or light traps during June, August, and October. Presumably it will be recorded from arboreal situations as more collections are made.

**Phylogenetic relationships.** This species is the adelphotaxon of *B. lucipetens* (Figs. 9, 42), and exhibits a distribution that overlaps the eastern portion of the distribution of that species. If these species diverged through allopatric speciation, it is most parsimonious to hypothesize vicariance between Mauna Kea as the ancestral range of *B. lucipetens*, and Mauna Loa as the original range of *B. kukui*. 
Blackburnia (Blackburnia) maculata (Sharp), new combination
(Figs. 40C, 45, 46)

Apteromesus maculatus Sharp, 1903: 211.

Diagnosis. One of three species—also including B. mystica and B. tibialis of Oahu—exhibiting irregular fletching of the elytra, the melanin laid down in patches that are not bilaterally symmetrical (Fig. 40C); distinguishable from those species by slightly angulate carinae on elytral intervals 1, 3, 5, and 7; humeri slightly reduced, shoulders narrowed to pronotal hind angles and humeri tightly rounded, flight wings micropterous (Fig. 45A), extended only ½ length of elytra; profemur with 2 anteroventral setae; mesofemur with 6 anteroventral setae; tarsomere 4 bilobed, inner and outer lobes subequal in length, with outer lobe of fourth metatarsomere 2.5 to 2.6× length of median base of segment. Standardized body length 5.8-7.0 mm.

Pterothorax. The flight wings are partially reduced, present only as micropterous straps 1/3 the width of each elytron, and extend to ½ elytral length (Fig. 45A); metepisternum short, lateral margin 1.3 to 1.6× length of anterior margin; humeri are narrowed resulting in humeral angle being tightly rounded to slightly angulate.

Male genitalia. Aedeagal median lobe evenly curved on ventral surface, apex tightly rounded, extended about 2× depth at point of eversion of internal sac (Fig. 45B); median lobe evenly tapered to tightly rounded apex (Fig. 45C).

Female reproductive tract. Gonocoxa with 1-2 larger setae at medial angle of gonocoxite 1, 4 shorter setae laterad (Fig. 45D); gonocoxite 2 elongate, narrowed to tightly rounded apex, with 3 peglike lateral ensiform setae and 1 dorsal ensiform seta, each about 0.06× length of gonocoxite 2; apical nematiform setae elongate, each about 0.45× length of gonocoxite 2; bursa copulatrix short, about as long as common oviduct, asymmetrical, with leftward expansion; bursal wall with medial band of cristate microtrichia, mostly elongate 5-pointed cristae; spermatheca elongate, reservoir covered with numerous fine constrictions (Fig. 45E).

Variation. The basal pronotal setae are usually absent in this species, but in one specimen of 23 examined for these setae, basal setae were present. One other specimen had a seta unilaterally present.

Lectotype ? labeled “A. maculatus Type D.S. Koholuaman, Kauai, 1400 ft. Perkins iv. 1895,” with lot number “529” handwritten on reverse of card (BMNH) hereby designated. This lot number corresponds to beetles collected on 13.IV.1895 (Anonymous n.d.). On this day Perkins was collecting on the plateau above Waialae Cabin (Perkins 1895a), along the present-day Mohihi-Waialae Trail. The lectotype is part of a series of 12 of this species. Accompanying species collected that day included B. alternans, B. aterrima, B. erythropa, B. micantipennis, B. opaca, and B. pavida.

Distribution. This species exhibits a relatively leeward distribution in the upper reaches of Waimea Canyon and the Olokele River, Kauai (Fig. 46).

Localities. Perkins collected this species from Koholuaman upward onto the high plateau at elevations of about 1200 m. It has more recently been collected from the Alakai Swamp Trail and Kawaikoi Stream at 1120 to 1180 m elevations. Other localities include Halemanu and Makaweli, 1200 m.
Fig. 45. *B. (Blackburnia) maculata*. A. Right metathoracic flight wing, dorsal view, showing reduced venation associated with micropterous condition. B. Male aedeagal median lobe, right lateral view. C. Male aedeagal median lobe, euventral view. D. Left female gonocoxa, ventral view. E. Female spermatheca, and spermathecal duct entering onto common oviduct, ventral view.
**Habits.** This species has been collected on the forest floor in pitfall traps, and on trunks of *Metrosideros* (ohia lehua), where adults rest during day under bark flaps and moss.

**Phylogenetic relationships.** The Oahu species pair, *B. mystica + B. tibialis*, comprise the adelphotaxon to this species.

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**Blackburnia (Blackburnia) mystica (Blackburn), new combination**

(Figs. 40D, 47, 48)

*Anchomenus mysticus* Blackburn, 1877: 147.

*Metromenus mysticus*: Blackburn & Sharp, 1885: 213.


**DIAGNOSIS.** Darkest of the three species with flecked elytra, head brunneous, concolorous with median base of elytra (Fig. 40D); pronotum lacking both lateral and basal setae; elytral intervals slightly convex; subapical sinuation of elytra reduced, lateral margin straight before apex; profemur without anteroventral setae; mesofemur with 2 anteroventral setae;
Fig. 47. *B. (Blackburnia) mystica*. A. Male aedeagal median lobe, internal sac everted, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view. D. Female bursa copulatrix with band of cristate microtrichia, spermatheca, and common oviduct, ventral view.

tarsomere 4 bilobed, lobes subequal but shorter than in *B. maculata* and *B. tibialis*, outer lobe of fourth metatarsomere 1.5× median basal length. Standardized body length 7.0-7.3 mm.

**Pterothorax.** Metepisternum elongate, lateral margin 1.8× length of anterior margin; flight wings fully developed, wing area 3.0× area of elytron.
Male genitalia. Aedeagal median lobe with medioventral expansion, therefore thicker at midlength (Fig. 47A), apex tightly downturned to an acuminate tip; median lobe with slight right-lateral constriction near tightly rounded tip (Fig. 47B).

Female reproductive tract. Gonocoxite 2 longer than gonocoxite 1 (Fig. 47C); a single seta at medioapical angle of gonocoxite 1, laterally glabrous or with only very short sensilla; gonocoxite 2 parallel-sided, tightly rounded apex only slightly curved laterally; 4-5 peglike lateral ensiform setae, and 1-2 peglike dorsal ensiform setae, each about 0.10× length of gonocoxite 2; apical nematiform setae moderately elongate, about 1/3 length of gonocoxite 2; bursa copulatrix elongate, about 1.3× length of common oviduct, with broad leftward expansion (Fig. 47D); lumenal wall of bursa with band of cristate setae, a mixture of 3-pointed, 5-pointed, and 7-pointed cristae; spermatheca elongate, reservoir about 2.0× as long as spermathecal duct, numerous fine constrictions on reservoir surface.

Lectotype ♀ labeled with 2 parallel lines and 2 ink slashes perpendicular to the parallel lines to left of pin—indicating Waianae Mountains in Blackburn’s code (Zimmerman 1957)—“mysticus” handwritten on reverse (BMNH) hereby designated.

Distribution. Blackburn (1877) in his first paper on Hawaiian Carabidae, described this species from the Waianae Mountains (Fig. 48), calling it “Very local.” It has not been re-collected.
Habits. We know little about this species’ biology, its localized distribution or its current status as part of the present-day Oahu biota. Based on Blackburn’s limited time spent in the Waianae Mountains in 1877 (Blackburn & Sharp 1885), it is likely he collected this species in Haleauau Gulch below Mt. Kaala, probably at elevations near 700 m (Fig. 48). Blackburn records it as “Under stones, &c., at an elevation of about 2000 ft. on the Waianae mountains. July. Very local, but not rare” (Blackburn & Sharp 1885, 213).

Phylogenetic relationships. This species is the adelphotaxon to the sympatric species, B. tibialis (Fig. 9).

*Blackburnia (Blackburnia) tibialis* (Sharp), new combination

(Figs. 48, 49A, 50)

*Mysticomenus tibialis* Sharp, 1903: 212.

DIAGNOSIS. Largest and palest of the species with flecked elytra (Fig. 49A), glabrous pronotum evenly flavous, dark flecks of elytra brunneous, more extensive light areas testaceous, standardized body length 6.9-8.2 mm; flight wings fully developed (Fig. 50A); elytra with evident subapical sinuation, elytral margin concave just before apex; metatarsomere 4 bilobed, lobes subequal, outer lobe of fourth metatarsomere 2.6× median basal length of segment; male metatibia slightly angled near middle, outer half directed toward midline of body.

Pterothorax. Metepisternum elongate, lateral margin 2.0 to 2.2× length of anterior margin; flight wings fully developed (Fig. 50A), wing area 3.1 to 3.4× area of elytron.

Male genitalia. Aedeagal median lobe medioventrally expanded, ventral surface recurved (Fig. 50B); apex straight ventrally, narrowed to triangular tip, lateral view; median lobe with right-lateral constriction at point where it tapers to acuminate tip, euventral view (Fig. 50C).

Female reproductive tract. Gonocoxite 2 longer than gonocoxite 1 (Fig. 50D); 4–6 setae at apex of gonocoxite 1, 1-2 near medioapical angle, 3-4 laterad; gonocoxite 2 elongate relative to shorter gonocoxite 1; gonocoxite 2 subparallel, tapered to tightly rounded apex, with 3-4 peglike lateral ensiform setae and 1-2 dorsal ensiform setae, each about 0.07× length of gonocoxite 2; apical nematiform setae moderately elongate, 0.37× length of gonocoxite 2; bursa copulatrix length subequal to common oviduct, with a left lateral expansion; lumenal surface of bursa with a patch of sparsely distributed 3- and 5-pointed cristate microtrichia; spermatheca elongate, reservoir about 1.5× as long as spermathecal duct, numerous fine constrictions on reservoir surface.

Lectotype ♂ labeled “Oahu Perkins” (BMNH) hereby designated.

Distribution. This species is restricted to the Waianae Mountain range of Oahu, where it has been collected on the slopes of the Mt. Kaala massif (Fig. 48).

Localities. Collected from Mt. Kaala and neighboring Haleauau, Puu Kalena, and Perkins’ localities of Waianae Mountains lee side, and windward side. Though specimens of *B. tibialis* lack lot numbers, the three specimens from “Waianae lee side” otherwise match labeling of lots 542 and 544. These were collected II-1896, at elevations of 2000+ ft. During this month Perkins camped in the lee side of the Waianae Stream. Presumably, specimens of *B. tibialis* were found while he was based at this camp.
Fig. 49. Blackburnia species habitus, dorsal view. A. B. (Blackburnia) tibialis. B. B. (Blackburnia) costata. C. B. (Blackburnia) corrusca. D. B. (Blackburnia) molokaiensis.
**Habits.** The only record of this species being associated with a plant species is one record from *Cibotium chamissoi*. Perkins first noted it from under bark (Sharp 1903), later stating it “is common under bark in both mountain ranges” (Perkins 1913, cxli). However, no Koolau-labeled specimens have been seen for this revision.

**Phylogenetic relationships.** This species is the adelphotaxon of the sympatric *B. mystica* (Fig. 48).
Blackburnia (Blackburnia) costata Sharp, new combination
(Figs. 14E, 49B, 51, 52, 53)

Chalcomenus costatus Sharp, 1903: 207.

DIAGNOSIS. Typical of many Kauai species in the possession of costate elytral intervals (Fig. 49B), in this species rounded costae in intervals 1, 3, 5, 6, 7, and 8; body piceous with metallic purplish sheen, legs and antennae rufous; flight wings fully developed (Fig. 51); pronotal base punctate, disc with deep transverse wrinkles; elytral striae basally punctate, punctures absent in apical half of elytra. Standardized body length 6.9-9.5 mm.

Pterothorax. Metepisternum elongate, lateral margin 1.7 to 2.0× length of anterior margin; flight wings fully developed (Fig. 51), but shorter relative to body length than in winged species treated above, flight wing area 1.4 to 2.1× area of elytron.

Male genitalia. Aedeagal median lobe with broad medioventral expansion and elongate ventral excavation, apex straight on ventral side, little extended beyond attachment of internal sac (Fig. 52A); median lobe constricted laterally about 2/3 distance toward apex, apex broadly rounded (Fig. 52B).

Female reproductive tract. Gonocoxites 1 and 2 subequal in length (Fig. 52C); gonocoxite 1 with 2-3 setae near medioapical angle, 2-5 laterally; gonocoxite 2 subparallel, apex broadly rounded, 2-3 peglike lateral ensiform setae and 1 dorsal ensiform seta, each about 0.18× length of gonocoxite 2; apical nematifom setae elongate, about 0.55× length of gonocoxite 2; bursa copulatrix elongate, 1.9× as long as common oviduct, with crescent-shaped dorsal pouch in vagina (for reception of apex of male aedeagal median lobe), 2 lateral glands, a ringlike band of 5-pointed cristate microtrichia, and a large leftward expansion just basal to spermathecal duct entrance (Fig. 52D); spermatheca ovoid, reservoir about 0.7× length of spermathecal duct, reservoir with less than 20 fine constrictions.

Lectotype ♂ labeled “♂ Chalcomenus costatus Type D.S. Kauai 4000 ft. VI.94 Perkins. 267.” (BMNH) hereby designated. During this time Perkins collected in the Hanapepe Valley (Perkins 1894b).

Distribution. This species is restricted to mountain streamside habitats across Waimea Canyon and its tributaries, and up the Makaweli, Kauai (Fig. 53).
Fig. 52. *B. (Blackburnia)* costata. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view. D. Female bursa copulatrix, ventral view, with dorsal pouch (dp) near base, bursal glands (bg), band of cristate microtrichia (cmt), leftward expansion (ex), and ovoid spermatheca (sp).
Localities. Distributed across the Waialeale plateau, from Kalalau, Ka Uno o Hua, Halemanu, and Kumewela in Kokee State Park, to Kilohana, the high plateau along the Mohihi-Waialae Trail, Kaholuamano, and Makaweli. Known localities range in elevation from 910 to 1515 m.

Habits. Records with ecological data are available only for captures in May, July and October. Most commonly this species has been found along stream beds under rocks or logs. It has also been found on moss mats at night in wetter forest situations, as well as under moss mats on Metrosideros (ohia lehua).

As with the following two species, *B. costata* exhibits fully venated, yet relatively small flight wings, suggesting that adults are not as prone to flight as are those of species recorded from lights.

Phylogenetic relationships. This species is the hypothesized adelphotaxon to the species pair *B. corrusca* + *B. molokaiensis* (Fig. 9), distributed on Oahu and Maui Nui + Hawaii, respectively. As such, this species triplet supports a progressive colonization and speciation pattern much like that supported by species of the subgenus *Colpocaccus*. 

Fig. 53. Distributional records for *B. (Blackburnia) costata*. 
Blackburnia (Blackburnia) corrusca (Erichson), new combination
(Figs. 29E, 31C, 49C, 54, 55)

Anchomenus corruscus Erichson, 1834: 223.
Metromenius corruscus: Blackburn & Sharp, 1885: 211.

DIAGNOSIS. Like B. costata in possessing fully developed flight wings and dark piceous cuticle with a metallic reflection and basally punctate elytral striae, but pronotum more constricted basally (Fig. 49C), basolateral margins straight behind posterior pronotal setae positioned 1/10 median length before hind angles; vertex and pronotal disc with strong isodiametric microsculpture, therefore with greenish to aenescen metallic reflection; pronotal lateral marginal depressions very narrow in apical half, barely wider at nonprotuberant front angles; pronotal median base impunctate, basal marginal bead very strong mediadly; inner 3 elytral striae punctate in basal 1/4, outer striae for up to half of length; elytral intervals convex, without carinae. Standardized body length 8.3-10.2 mm.

Pterothorax. Metepisternum elongate, lateral margin 1.8 to 2.0× length of anterior margin; flight wings fully developed (Fig. 54A) but of similar relative length as observed in B. costata—i.e., wing area 1.4 to 2.1× area of elytron.

Male genitalia. Aedeagal median lobe with broad medioventral expansion and elongate ventral excavation, apex elongate and slightly downturned, tip 3.0× as long as depth at attachment to internal sac (Fig. 54B); sagittal crest of basal bulb well developed; median lobe constricted on right lateral surface before tapered to a tightly rounded tip (Fig. 54C).

Female reproductive tract. Gonocoxite 2 shorter than gonocoxite 1 (Fig. 54D); gonocoxite 1 with 2-3 setae at medioapical angle, glabrous laterally; gonocoxite 2 subparallel, apex broadly rounded, 2 peglike lateral ensiform setae and 1 peglike dorsal ensiform seta, each about 0.12× length of gonocoxite 2 (Fig. 31C); apical nematiform setae elongate, about 0.50× length of gonocoxite 2; bursa copulatrix elongate, about 2× length of common oviduct; a crescent-shaped dorsal bursal pouch present near apex of vagina, pouch lined with strong microsculpture, appearing yellow, leathery in a cleared dissection; a field of 3- to 6-pointed cristate microtrichia on ventral lumenal surface of bursa just apical dorsal pouch; bursa with large leftward expansion extended to spermathecal duct; spermatheca ovoid, reservoir about 0.4× as long as duct (Fig. 54E).

Lectotype. For Anchomenus corruscus, ♀ lectotype hereby designated, labeled “3216” on white paper //“Ins. Sand. Meyer” handwritten on blue paper // “corruscus N.” handwritten on blue paper/Hist. Col. (Coleoptera) Nr. 3216 (1 Ex.) Anchomenus corruscus N. Ins. Sand. Meyer Zool. Mus. Berlin (MNHU). In addition, there are three paralectotypes—2 ♂♂ and 1 ♀—that are unlabeled except for the fourth label listed above. Meyen collected near Honolulu from 25 June to 22 July, 1830, when the Princess Louise called upon the islands during her voyage around the world (Ratzeburg 1843).

Distribution. This species is widespread on the island of Oahu (Fig. 55).

Localities. Found in both the Koolau and Waianae Ranges. In the Waianaeas, recorded from Mt. Kaala 600 m to the summit bog area, as well as along the Waialua coast (1901 collection by Perkins, BMNH). Found along the length of the Koolaus, including Kawailoa Gulch, Castle Trail and Kaluanui Stream, Wahiawa, Puu Kaumakua, Lanihuli, Nuuanu Valley, Konahunui, Tantalus, and Waialale Iki. Historical Koolau Range records include
Fig. 54. B. (Blackburnia) corrusca. A. Right metathoracic flight wing, dorsal view. B. Male aedeagal median lobe, right lateral view. C. Male aedeagal median lobe, euventral view. D. Left female gonocoxa, ventral view. E. Female bursa copulatrix, ventral view, with dorsal pouch near base, field of cristate microtrichia, leftward expansion, and ovoid spermatheca.
365 m elevation in Nuuanu Valley (1892 to 1908). In recent years this species has been most commonly encountered above 1000 m on Mt. Kaala. The lone exceptions are captures in the north Koolaus, including those at 600 m elevation in Kaluanui Valley in 1971 (Hardy, UHEM), and near Wahiawa in 1979 (Nagai, UHEM).

**Habits.** Mostly observed on the ground, under rocks, plantain rosettes, rotten logs, and along stream banks. Specimens of the type series were found under rotten bark (Erichson 1834). A single specimen has been collected on *Freycinetia* in May (Tsuda, BPBM). This species possesses fully venated wings; however there is no evidence that individuals can fly.

**Phylogenetic relationships.** This species is the adelphotaxon of *B. molokaiensis* (Fig. 9), widespread on Maui Nui and Hawaii Island.
Blackburnia (Blackburnia) molokaiensis (Sharp), new combination
(Figs. 30A, 49D, 56, 57, 58, 59)

Chalcomenus molokaiensis Sharp, 1903: 207.

DIAGNOSIS. Sharing with B. corrusca the distinct isodiametric microsculpture on vertex and pronotal disc, the impunctate median pronotal base, convex, noncarinate elytral intervals, and basally punctate elytral striae, but pronotum broader (ratio of maximum pronotal width to median length 1.18-1.25, versus 1.10-1.15 in B. corrusca), basolateral margins of pronotum only slightly sinuate (Fig. 49D), the strongest point of sinuation at basal pronotal setae, positioned 0.03× median length before obtuse-rounded hind angles. Standardized body length 8.1-10.5 mm.

Pterothorax. Metepistemum elongate, but slightly shorter than in preceding two species, lateral margin 1.7 to 2.0× length of anterior margin; flight wings fully developed (Fig. 56A), flight wing area 1.7 to 2.3× area of elytron.

Male genitalia. Aedeagal median lobe very similar to that of B. corrusca (Fig. 54B), with elongate ventral excavaation and elongate, slightly downturned apex, but with tip more acuminate in lateral view (Fig. 56B, D); median lobe with slightly protuberant right lateral surface tapered to a tightly rounded tip (Fig. 56C, E).

Female reproductive tract. Gonocoxite 2 slightly shorter than gonocoxite 1 (Fig. 57A); gonocoxite 1 with 2-3 setae at medioapical angle, 1-2 setae laterally; gonocoxite 2 subparallel, apex broadly rounded, with 2 peglike lateral ensiform setae and 1 peglike dorsal ensiform seta, each about 0.14× length of gonocoxite 2; apical nematiform setae elongate, about 0.50× length of gonocoxite 2; bursa copulatrix elongate, about 2× length of common oviduct; a horseshoe-shaped dorsal bursal pouch present near apex of vagina, pouch lined with strong microsculpture, appearing yellow, leathery in a cleared dissection; a field of mostly 5-pointed cristate microtrichia on ventral luminal surface of bursa just apicad dorsal pouch; bursa with large leftward expansion extended to spermathecal duct; spermatheca ovoid, reservoir about 0.35× as long as duct (Fig. 57B).

Lectotype ♂ labeled "♂ Chalcomenus molokaiensis. Type D.S. Molokai. 4000 ft. VI.96. Perkins. 595." (BMNH) hereby designated. Perkins’ lot 595 is described as “Molokai Mtns., Carabidae mostly on side of stream in bottom of Gulch, about 4000 ft. VI ‘96” (Anonymous n.d.). This Gulch is most likely Kawela Gulch, near other Perkins collecting localities on Molokai.

Distribution. This species is known from the Maui Nui fragments of Molokai and Maui (Fig. 58), and the older windward portions of Hawaii Island (Fig. 59).

Localities. On Molokai, this species was collected by Perkins at Kalae and Kalawao, as well as in the Molokai mountains. Perkins’ Molokai mountains localities are now within the TNCH Kamakou Preserve, where this species is found along the Hanalilolilo Trail, and in both East and West Forks of Kawela Gulch from 900 to 1100 m elevation. In West Maui, this species has been found only in Iao Valley. On Haleakala, it is known from many of the windward valleys, including Waikamoi, Puohokamoa, Haipuaena, Honomanu, Keanae, Kuhiwa, Waihoi, and Kipahulu, at elevations ranging from 600 to 1575 m. On Hawaii Island, it is known principally from the Kohala Mountains, and is common along the Upper Hamakua Ditch at Kawaihui and Alakahi Streams. On Mauna Kea it has been collected at 750 m elevation along Saddle Road (Gressitt, BPBM), and on the Humula Trail along
Fig. 56. *B. (Blackburnia) molokaiensis*. A. Right metathoracic flight wing, dorsal view. B. Male aedeagal median lobe, right lateral view; Kawela Gulch, Molokai. C. Male aedeagal median lobe, evventral view; Kawela Gulch, Molokai. D. Male aedeagal median lobe, right lateral view; Kohala Mountains, Hawaii. E. Male aedeagal median lobe, evventral view; Kohala Mountains, Hawaii.
Kaula Gulch at 2880 m elevation (Hosaka, BPBM). This last site is well above other recorded elevation for the species, but occurs at the elevation where an upper extension of Humuula Trail crosses Kaula Gulch, with the collecting year of 1936 suggesting that the specimens’ capture was associated with botanical collections (Wagner et al. 1990) made possible by the Civilian Conservation Corps’ trail building around that time.

**Habits.** This species is almost always found on the ground, either under rocks, in moss, or along stream banks. Perkins (1893, 11-VI) noted that adults walk along stream banks in daytime as do those of *B. corrusca* on Oahu. Such behavior has also been observed in *B. munroii*, another riparian species, suggesting diurnal activity is an attribute of such
streamside species, or perhaps individuals of such species are compelled to move by changes in stream flow. Of 50 specimens with ecological information, 2 were collected on plants: 1 on *Cyanea* and 1 on *Melicope*. Though *B. molokaiensis* possesses fully venated flight wings, no individual has been collected in flight.

**Phylogenetic relationships.** This species is most closely related to *B. corrusca* of Oahu (Fig. 9).

**Blackburnia (Blackburnia) sulcipennis** (Sharp), new combination
(Figs. 14D, 29F, 31D, 60A, 61, 62)

*Disenochus sulcipennis* Sharp, 1903: 204.

**DIAGNOSIS.** Immediately diagnosed by the elytral microsculpture of fine parallel lines producing an iridescent lustre (Fig. 14D), in combination with the smooth elytral striae, pronotum with greatly constricted, punctate base and straight basolateral margin in front of basal pronotal seta (Fig. 60A); elytral intervals convex, but of equal development, thereby lacking elytral costae so characteristic of other Kauaian species. Standardized body length 7.9-9.4 mm.

**Pterothorax.** Metepistemum nearly quadrate, lateral margin from 1.3 to 1.4× length of anterior margin; flight wings vestigial, not extended beyond metanotum.

**Male genitalia.** Aedeagal median lobe stout, slightly expanded medioventrally, ventral excavation extended onto elongate apex narrowed to a tightly rounded, evenly downcurved tip (Fig. 61A); basal sagittal crest moderately developed; median lobe broad, evenly tapered to a tightly rounded apex (Fig. 61B).
Female reproductive tract. Gonocoxa with apical fringe of 5-7 setae on gonocoxite 1, 2-3 near medioapical angle, 3-4 laterally (Fig. 61C); gonocoxite 2 parallel-sided, apex rounded (Fig. 31D), 3-4 long, peglike lateral ensiform setae and 2 long peglike dorsal ensiform setae, lateral setae about 0.15× length of gonocoxite 2; apical nematiform setae moderately elongate, about 0.35× length of gonocoxite 2; bursa copulatrix elongate, about 2.1× length of common oviduct, with leftward expansion but no dorsal pouch; bursal lumen lined with medial band of 3-pointed cristate microtrichia; spermatheca ovoid, reservoir about 0.5× length of spermathecal duct, with a basal lobe present at base of reservoir.

Fig. 59. Hawaii Island distributional records for B. (Blackburnia) molokaiensis.
Fig. 60. Blackburnia species habitus, dorsal view. A. B. (Blackburnia) sulcipennis. B. B. (Blackburnia) atra, new species. C. B. (Blackburnia) erythopus. D. B. (Blackburnia) aterrina.
Fig. 61. *Blackburnia* sulcipennis. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view.
Lectotype ♀ labeled "♀ Disenochus sulcipennis Type D.S. Makaweli, 2500 ft. II 97. Perkins 668" (BMNH) hereby designated. On this trip to Kauai, Perkins collected in the Makaweli area with logistic support from Mr. Francis Gay, who had a tent set up for Perkins' use. He collected at 2000 to 3000 ft. (605 to 910 m) elevation between the Makaweli and Hanapepe Rivers, not venturing to higher-elevation habitats (Perkins 1897).

Distribution. Exhibiting a leeward distribution across the higher elevations above Waimea Canyon, Kauai (Fig. 62).

Localities. Distributed around Waimea Canyon, from Makaweli, to Kaholuamano, Koalie Stream, Alakai Swamp Trail near Kawaikoi Stream, Halemanu, and Ka Uno o Hua Ridge. Known localities range from 605 to 1260 m elevation, with Perkins’ January 1897 collections along Makaweli River representing the lowest elevation.

Habits. This species appears to restrict its activities to the ground, where it has been found on moss mats and trail surfaces at night, under logs and rocks, and collected via pitfall trap.

Phylogenetic relationships. This species is the adelphotaxon to a large complex of species from Kauai, Oahu, and Maui Nui (Fig. 9). It is broadly sympatric with six of these: B. aterrima, B. bryophila, B. curtipes, B. elegans, B. erythropus, and B. micantipennis.
Blackburnia (Blackburnia) atra Liebherr, new species 
(Figs. 60B, 62, 63)

DIAGNOSIS. A markedly distinctive species due to its coal black body and legs, large body size, standardized body length 11.6 mm, pronotum with evenly rounded hind angles and complete basal marginal bead, and elytra with very narrow humeri, and 3 very short dorsal elytral setae, each seta about as long as the convex elytral intervals (Fig. 60B).

DESCRIPTION. Head elongate, eyes slightly protruded beyond curvature of gena, ocular ratio 1.42, neck elongate with slight dorsal impression; labrum broadly emarginate, single known specimen has median pair of setae reduced to a single median seta, therefore 5 apical labral setae; mandibles moderately elongate, left mandible extended 0.70× length beyond labral front margin; frontoclypeal grooves shallow, but extended to anterior supraorbital setae; vertex broadly convex between 4 supraorbital setae, smooth; antennomeres 1-3 shiny, pedicel with only 1 longer outer seta near apex, otherwise glabrous; mentum tooth narrow truncate apically, with slight median nick in margin.

Prothorax. Pronotum ovoid, narrow lateral margins depressed relative to broadly convex disc (Fig. 60B); lateral marginal depressions obsolete for most of their length, reduced to a lateral marginal bead, slightly widened just inside basal pronotal setae, continuous with pronotal basal marginal bead, basal marginal bead traceable medially, slightly effaced at base of median longitudinal impression; anterior pronotal setae absent; laterobasal depressions almost obsolete, their surface nearly planar with disc, their presence indicated by sparse punctulae; median longitudinal impression punctate on pronotal median base, finely inscribed on disc, intersecting numerous fine wrinkles on pronotal disc; anterior transverse impression obsolete, indicated only by slight expansion of median longitudinal impression; anterior marginal bead obsolete medially, present near slightly protruded, tightly rounded front angles. Prosternal process flat ventrally, with slightly developed posterior marginal bead, a single seta on left side of rounded marginal bead. Proepisternum punctate near hind margin.

Elytra convex with greatly depressed lateral margins and apex, boatlike; humeri very narrow, basal groove only slightly irregular near base of fifth stria, otherwise smoothly curved posteriorly; lateral margins evenly curved from humeri to apex, subapical sinuation obsolete; elytral intervals convex; medial 2 elytral striae smooth, striae 3-8 with progressively longer basal portions punctate, eighth striae punctate for about 2/3 their length, punctures separated by about 5× their diameter; ninth elytral stria punctate for about half of length; scutellar seta and three dorsal elytral setae each side, all setae shorter than typical, about as long as width of an elytral interval; 14-15 lateral elytral setae.

Pterothorax. Metepisternum moderately elongate, lateral margin 1.5× length of anterior margin; flight wings vestigial, not extended beyond metanotum; mesosternum punctate ventrally and laterally.

Legs. Profemur without anteroventral setae, with 1 posteroventral seta; mesocoxa with 2 ridge setae; mesofemur with 4 anteroventral setae; metacoxa bisetose, mesal seta absent; metafemur with 2 anteroventral setae, glabrous dorsoapically; tarsi robust, slightly widened apically; tarsomeres 1-4 with dense ventral vestiture of elongate setae bordering a median space; metatarsomere 4 with short, subequal inner and outer apical lobes, lobes about 0.5× median basal length of segment; tarsomere 5 with ventrolateral rows of 6 setae, their length subequal to tarsomere depth at point of setal insertion.
Abdomen. Two setae each side of female sternite VII.

Coloration. Head capsule, mandibles, thorax, abdomen, femora, and tibiae shiny coal black; palpi, antennae, and tarsi shiny rufobrunneous.

Microsculpture. Vertex with distinct isodiametric microsculpture; pronotal disc with distinct transverse mesh microsculpture, sculpticells slightly more isodiametric near base and in laterobasal depressions; elytra covered with dense transverse lines loosely connected into an irregular mesh, sculpticells 3 to 4× as broad as long.

Male genitalia. This species is known from a single female.
Female reproductive tract. Gonocoxa with apical fringe of 5-6 setae on gonocoxite 1 (Fig. 63A); gonocoxite 2 subparallel with tightly rounded apex, 3-5 peglike lateral ensiform setae, 2 peglike dorsal ensiform setae, setae about 0.14× length of gonocoxite 2; apical nematiform setae moderately elongate, 0.40× length of gonocoxite 2; bursa copulatrix elongate, about 1.6× length of common oviduct, with an indistinct dorsal pouch near vagina, a luminal band of mixed spikelike and 2-pointed cristate microtrichia, and a leftward expansion narrowed toward entry of spermathecal duct; spermatheca ovoid, reservoir about 0.50× length of spermathecal duct, with a small basal lobe (Fig. 63B).

Holotype ♂ labeled “HI: Kauai Mt. Kahili N 21°58′56″ W 159°29′45″ 21-V-1995 lot 01 895 m on mossy ohia trunks and roots J.K. Liebherr” (CUIC).

Etymology. The species epithet *atra* denotes the intense black coloration of this beetle.

Distribution. The single specimen was collected on a flanking ridge to the north and west of Mt. Kahili summit, Kauai (Fig. 62).

Habits. Through the flying expertise of Mr. Steve Chilton, Dan Polhemus and JKL were dropped onto a steep ridge adjoining the main ridge extended north from Mt. Kahili summit. The ridge top was not more than 1 m wide, with precipitous sides, and was covered with dense, shoulder-high vegetation of *Metrosideros* (ohia lehua) and *Freycinetta* (ieie). The holotype was found by scraping moss from exposed ohia roots onto a beating sheet. Because of the steepness of the terrain, we could move no more than 20 m along the ridge. Nonetheless, 6 carabid species were found on top of this ridge: 1, *B. atra*; 2, *B. (Colpocaccus) posticata*; 3, *B. (Metromenus) kahili*, new species; 4, *B. (Metromenus) limbata*; 5, *Bembidion mnuroi* (Sharp); and 6, the adventively introduced Asian platynine, *Metacolpodes buchanani*. Both new species are known only from Mt. Kahili.

The elevation of this site is low relative to habitats in which related species are found today. Nonetheless, Perkins found the closely related *B. sulcipennis* below 910 m in 1897. Finding *B. atra* nearly 100 years later at similar low elevations attests to the undisturbed nature of Mt. Kahili. The existence of the adventive *M. buchanani* on Mt. Kahili is of recent occurrence, as first records for this species on Kauai are from 1992. The possibility of competitive displacement of Mt. Kahili endemics by *M. buchanani* should not be dismissed. Nonetheless, current knowledge of 2 carabid beetle species unique to Mt. Kahili supports recognition of this mountain as a distinct area of endemism.

Asquith (1995) recognized the Wahiawa Swamp, lying at the western foot of the Mt. Kahili ridge, as a distinct habitat supporting ecologically restricted species. If that area supports precinetic species and can therefore be defined as an area of endemism, it is probably distinct from the Mt. Kahili area. The Kahili ridge is best interpreted as a relictual, and nearly completely eroded satellite of the Waialeale massif. Cosmopolitan distributions including both Waialeale and Kahili would be dated to the time before extensive erosion, when Mt. Waialeale was much more massive: 2600 m elevation (Carson & Clague 1995). This area relationship between Kahili and Waialeale is attested to by the widespread distributional pattern exhibited by *B. bryophila* (Fig. 83).

Phylogenetic relationships. This species is the basal adelphotaxon to a complex of 13 species distributed on Kauai, Oahu, and Maui Nui (Fig. 9). Even though the origin of this species is relatively early in the diversification of the Kauai fauna, it is sympatric only with one species of its adelphotaxon: *B. bryophila*.
Blackburnia (Blackburnia) erythropus (Sharp), new combination
(Figs. 60C, 64, 65)

Disenochus erythropus Sharp, 1903: 204.

DIAGNOSIS. Dorsum shiny piceous, microsculpture reduced, elytral microsculpture of dense transverse lines visible laterally and apically, disc without microsculpture; legs and antennae shiny brunneous; pronotum narrowed posteriorly, with obsolete lateral marginal depressions composed of 1-3 indistinct punctures (Fig. 60C); elytral disc flat, intervals moderately convex, all striae basally punctate, punctures diminished posteriorly until absent in apical 1/4 of length; mesepisterna shallowly punctate, metepisterna impunctate; metafemur with single small dorsoapical seta. Standardized body length 8.5-10.9 mm.

Pterothorax. Metepistemum moderately elongate, lateral margin 1.6 to 1.8× anterior margin; flight wings vestigial, not extended beyond metanotum.

Male genitalia. Aedeagal median lobe stout, straight medioventrally, ventral excavation extended to short, blunt tip (Fig. 64A); basal sagittal crest small; median lobe broad, tip rounded, ventral excavation evident (Fig. 64B).

Female reproductive tract. Gonocoxa with apical fringe of 8-12 setae on gonocoxite 1 (Fig. 64C); gonocoxite 2 subparallel with rounded apex, 2-3 peglike lateral ensiform setae, 1 peglike dorsal ensiform seta, setae about 0.13× length of gonocoxite 2; apical nematiform setae moderately elongate, 0.40× length of gonocoxite 2; bursa copulatrix elongate, about 2.0× length of common oviduct, with a narrow, indistinctly delimited dorsal pouch near vagina, a lumenal band of 3- to 5-pointed cristate microtrichia, and a leftward expansion narrowed toward entry of spermathecal duct; spermatheca ovoid, reservoir about 0.40× length of spermathecal duct, with a small basal lobe.

Lectotypeipe labeled “Disenochus erythropus. Type. D.S. (517). Koholuamano. Kauai, 4000 ft. Perkins. iv.1895.” (BMNH) hereby designated. Perkins’ lot 517 was collected on 13-IV-1895 (Anonymous n.d.). On that day, Perkins went out to hunt both birds and insects, but seeing no birds worth shooting, spent the day collecting carabids. He states “In addition to some numbers of the black one obtained yesterday [Blackburnia aterrima], I got another, less elongate and more shining beneath, with it under bark of a dead tree” (Perkins 1895a). This second species was B. erythropus. During this period Perkins was collecting from Kaholuamano to the high plateau, an expanse of the Mohihi-Waialae Trail that passes Waialae Cabin and climbs into the high plateau of the A`lakai Swamp.

Distribution. This species is known from upland Waimea Canyon, as well as the high Alakai, Kauai (Fig. 65).


Habits. The only information on microhabitat for this species come from collections made by JKL (CUIC) along the Mohihi-Waialae Trail above Waialae Cabin: 1, three specimens under moist moss mats on trunks of Metrosideros (ohia), 19-V-1995; 2, one specimen under bark flaps of a large dead ohia covered with vines, 20-V-1995. These collections demonstrate that this species can climb trees, but conditions during this collecting trip were very dry, and based on the habits of related species; this species should also be sought in ground-level mossy situations.

Phylogenetic relationships. This species is the adelphotaxon to a clade subtended by the sympatric species B. aterrima, plus seven other species from Oahu and Maui Nui (Fig. 9).
Fig. 64. *B. (Blackburnia) erythropus*. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view.
Fig. 65. Distributional records for *B. (Blackburnia) erythropus*.

*Blackburnia* (Blackburnia) *atterrima* (Sharp), new combination
(Figs. 60D, 66, 67)

*Disenochus aterrimus* Sharp, 1903: 203.

DIAGNOSIS. This moderately large, black, shiny beetle is among the most apparent on Kauai, occurring in various situations. It is readily distinguished by: 1, broad, smooth pronotum with rounded basolateral margins; 2, parallel-sided elytra with marked humeri, distinct subapical sinuation, punctate elytral striae, and moderately convex, non-costate intervals (Fig. 60D); in combination with 3, vestigial flight wings. Standardized body length 7.9-10.7 mm. The pronotal lateral marginal depressions are broader, and elytra more elongate than in *B. erythropus* (Fig. 60C). The pronotum is more transverse than in that species, *B. sulcipennis* (Fig. 60A), *B. atra* (Fig. 60B), or *B. bryophila* (Fig. 77D).

**Pterothorax.** Metepisternum moderately short, lateral margin 1.4 to 1.6× length of anterior margin; flight wings vestigial, not extended beyond metanotum. (This species exhibits a reduced metepisternum, associated with loss of flight wings, but lateral reduction of the humeri often seen in vestigially winged species has not accompanied longitudinal reduction of the metathorax.)
Fig. 66. B. (Blackburnia) aterrima. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, evuentral view. C. Left female gonocoxa, ventral view. D. Female spermatheca, ventral view.
Male genitalia. Aedeagal median lobe gracile, elongate, medioventral margin with elongate expansion, therefore recurved (Fig. 66A); ventral excavation associated with abrupt apical downturn of the lobe, apex tapered to a short, tightly rounded tip; basal sagittal crest short, broad; median lobe melanized on ventral surface, of moderate breadth, gradually tapered to a finely rounded apex (Fig. 66B).

Female reproductive tract. Gonocoxite 1 with sparse apical setal fringe, 2 setae at medioapical angle, 4-5 laterally (Fig. 66C); gonocoxite 2 with markedly falcate lateral margin, base broadly attached to gonocoxite 1; gonocoxite 2 with 2 peglike lateral ensiform setae and 1 peglike dorsal ensiform seta, each about 0.12× length of gonocoxite 2; apical nematiform setae elongate, about 0.45× length of gonocoxite 2, set in elongate apical furrow; bursa copulatrix elongate, about 2.0× length of common oviduct, with a narrow dorsal pouch on right side, a lumenal band of 3- and 5-pointed cristate microtrichia, and a leftward expansion narrowed to entrance of spermathecal duct; spermatheca ovoid, reservoir about 0.6× length of spermathecal duct, with a well-developed basal lobe (Fig. 66D).
Lectotype ♀ labeled “♀ Disenochus aterrimus Type D.S. Koholuamano, Kauai, 4000 ft. Perkins. iv. 1895,” with “517” handwritten on reverse of card (BMNH) hereby designated. Perkins’ lot 517 also contained the specimen designated lectotype for *B. erythropus*.

**Distribution.** This species is found across the higher-elevation, mesic forests of Waimea Canyon and Kalalau, Kauai (Fig. 67).

**Localities.** This species is broadly distributed across surveyed portions of mountainous Kauai. Records span from Makaweli, Kaholuamano, Waialae River and Cabin, Mohihi-Waialae Trail, Koalie Stream, Alakai Swamp Trail near Kawaikoi Stream and Lehua Makanoe Bog, Pihea Trail, Kumuwela Ridge, Halemanu, Ka UNo o Hua Ridge, Honopu Trail, and above Kalalau Valley. Known localities range from 600 m elevation (Perkins’ collections in Makaweli) to 1280 m.

**Habits.** Beetles of this species are avid climbers, and have been found on a variety of plants, including *Cibotium* (tree fern), low ferns, *Metrosideros* (ohia lehua) trunks and branches, *Acacia koa*, *Alphitonia*, *Broussaisia*, *Cryptocarya*, *Ilex anomala*, *Pouteria*, and *Tetraplasandra*. They can be commonly encountered running over plant surfaces at night, but can also be found by scraping ohia bark and associated moss during day.

**Phylogenetic relationships.** This species is the adelphotaxon to seven arboreal species from Oahu and Maui Nui (Fig. 9). The species that is the outgroup of this clade, *B. erythropus*, also occurs predominately in arboreal situations.

*Blackburnia* (*Blackburnia*) micans (Sharp), new combination

(Figs. 68A, 69, 70)

*Derobroscus micans* Sharp, 1903: 197.

*Derobroscus politus* Sharp, 1903: 198 (new synonymy).

*Derobroscus solitarius* Sharp, 1903: 198 (new synonymy).

**Diagnosis.** Immediately diagnosed by the unique configuration of prothorax, with lateral and basal marginal beads effaced, except for possible trace of carina near hind angle, and basal pronotal seta absent (Fig. 68A); elytral striae a series of deep round pits, only shallowly connected by linear strial segments. *Blackburnia micans* shares with the following two species (Fig. 68B-C) the following characteristics: I, tubular prothorax with greatly reduced lateral marginal depressions; 2, elytral striae reduced both laterally and apically; and 3, elytral microsculpture reduced, disc shiny with bluish to greenish reflection, indistinct transverse microlines laterally. Standardized body length 6.8-9.2 mm.

**Pterothorax.** Metepisternum moderately elongate, lateral margin 1.6 to 1.7× length of anterior margin; flight wings vestigial, not extended beyond metanotum.

**Male genitalia.** Aedeagal median lobe stout, straight to slightly curved medioventrally, apical 1/3 of length evenly downcurved to finely rounded tip (Fig. 69A); sagittal crest various, short and broad to absent; median lobe broad, evenly tapered to finely rounded tip (Fig. 69B).

**Female reproductive tract.** Gonocoxite 1 longer than gonocoxite 2 (Fig. 69C); gonocoxite 1 with apical fringe of 2-5 setae, 2-3 setae near medioapical angle, 0-2 setae laterally; gonocoxite 2 with falcate lateral margin, base expanded laterally, 2-3 peglike lateral ensiform setae positioned close to laterally expanded base, and 1 peglike dorsal
Fig. 68. Blackburnia species habitus, dorsal view. A. B. (Blackburnia) micans. B. B. (Blackburnia) optata. C. B. (Blackburnia) hihia, new species. D. B. (Blackburnia) agonoides.
ensiform seta, setae about 0.12× length of gonocoxite 2; apical nematiform setae elongate, 0.48 to 0.50× length of gonocoxite 2; bursa copulatrix elongate, about 1.7× length of common oviduct, only slightly asymmetrical, with small crescent-shaped dorsal pouch near vagina, and a medial band of 3- to 5-pointed cristate microtrichia; spermatheca ovoid, reservoir about 0.50× length of spermathecal duct, with small basal lobe (Fig. 69D).
Fig. 70. Distributional records for B. (Blackburnia) micans.

Types. For Derobroscus micans, lectotype ♂ labeled "♂ Derobroscus micans Ind. typ. D.S. Waianae II.96. Perkins (542)" (BMNH) hereby designated. For Derobroscus politus, ♂ lectotype (dissected) labeled "♂ Derobroscus politus Ind. typ. D.S. Lanihuli, Honolulu 3000 ft. 27.X.92. Perkins. 42." (BMNH) hereby designated. For Derobroscus solitarius, ♀ holotype labeled "♀ Derobroscus solitarius Type. D.S. Oahu, Halemano. 3000 ft., XII.1892. Perkins." (BMNH). Perkins’ lot 542 was collected on the lee side of the Waianae Mountains. Lot 42 included only the two specimens considered Derobroscus politus by Sharp, and were collected on “Lanihuli ridge, nr. Honolulu, from leaves of trees nearly 3000 ft. (pair of Disenochus)” (Anonymous n.d.).

Distribution. This species is known from Mt. Kaala in the Waianae Range, and from the mid- to northern Koolau Range of Oahu (Fig. 70).

Localities. Within the Waianae Mountains, specifically recorded only from Mt. Kaala. In the Koolaus, recorded localities include Castle Trail (665 m elevation), Waihoi Ridge, Helemano (910 m), Wahiawa, Waimalu Stream (515 m), Halawa Ridge (605 m), Kalihi, and Puu Lanihuli (910 m). This species was last seen in 1952: 2 specimens from Koolau Mountains (Ford, BPBM), and 1 from Halawa Ridge (Hardy, BPBM). The preponderance of low-elevation sites makes this species a high risk candidate for extinction due to the presence of exotic arthropod pests and invasive plants.
Habits. This and the following two species have been found exclusively on plants, under bark or moss. Genera of plants from which this species has been collected include Cheirodendron, Hesperomannia, and Melicope. Perkins (1913, cxl) notes that he found specimens within twigs or branches.

Phylogenetic relationships. This species is the adelphotaxon of the Oahu species pair B. optata + B. hihia (Fig. 9). Blackburnia micans is broadly sympatric with the former species, as specimens have been found at similar elevations in the Koolau Mountains. However, in the Waianae Mountains, B. micans is allopatric with B. hihia; the former has been collected only from 600 m elevation, whereas B. hihia is known only from elevations above 900 m.

Blackburnia (Blackburnia) optata (Sharp), new combination

(Figs. 68B, 71, 72)

Brosconymus optatus Sharp, 1903: 198.

Diagnosis. This species and the following can be reliably separated only by dissection of male genitalia, as the aedagi are markedly distinctive. Based on external characters, B. optata shares the tubular prothorax, laterally and apically reduced elytral striae (Fig. 68A-C), and shiny cuticle with metallic green reflection observed in B. micans and B. hihia, but, differs by exhibiting very reduced microsculpture on the frons, with the isodiametric sculpticells seen in related species almost impossible to trace in this species; pronotal laterobasal depressions are punctate, and depressed in the middle of the field of 8-18 punctures (though some B. hihia have as many punctures as the least punctate B. optata); male aedeagal median lobe with medioventral surface straight or only slightly expanded basal ventral excavation (Fig. 71A, C). From B. micans, this species can be told by the complete lateral marginal bead extended around the hind angles onto base of prothorax, and the shorter metepisternum (see Pterothorax). Hind pronotal setae vary in B. optata, either present, unilaterally absent, or absent on both sides. Standardized body length 6.4-7.9 mm.

Pterothorax. Metepisternum short, lateral margin 1.3 to 1.5× length of anterior margin; flight wings vestigial, not extended beyond metanotum.

Male genitalia. Aedeagal median lobe robust, straight, or only slightly expanded medioventrally basal ventral excavation (Fig. 71A, B); apex evenly curved downward, with tip finely rounded, slightly more downturned; median lobe broad, lateral margins slightly concave near finely rounded tip (Fig. 71B, D).

Female reproductive tract. Gonocoxite 2 basally broad, shorter than gonocoxite 1 (Fig. 71E); gonocoxite 1 with apical fringe of 5-7 setae, 3-4 near medioapical angle, 2-3 laterally; gonocoxite 2 with sheer lateral cutting margin, 2 peglike lateral ensiform setae near base, and 1-2 peglike dorsal ensiform setae, lateral setae 0.11 to 0.12× length of gonocoxite 2; apical nematiform setae elongate, 0.60× length of gonocoxite 2; bursa copulatrix elongate, 1.6× length of common oviduct, nearly symmetrical, with a narrow, parallel-sided dorsal pouch near vagina, and a broad lumenal ring of 5-pointed cristate microtrichia (Fig. 71F); spermatheca ovoid, reservoir 0.6× length of spermathecal duct, with small basal lobe.

Lectotype ♂ labeled "♂ Brosconymus optatus Type D.S. Halemano, Oahu, 1.1893. Perkins." (BMNH) hereby designated. The lectotype also bears the label "#1215 examined by Prof. Thaxter for Laboulbeniaceae."
Fig. 71. *B. (Blackburnia) optata*. A. Male aedeagal median lobe, right lateral view; Poamoho Trail. B. Male aedeagal median lobe, euventral view; Poamoho Trail. C. Male aedeagal median lobe, right lateral view; Kahana. D. Male aedeagal median lobe, euventral view; Kahana. E. Left female gonocoxa, ventral view. F. Female bursa copulatrix and spermatheca, ventral view, showing narrow triangular dorsal pouch, lumenal field of cristate microtrichia, and spermathecal reservoir with basal lobe.
**Distribution.** This species is restricted to the northern Koolau Range of Oahu (Fig. 72), allowing it to be distinguished from *B. hihia* by geographic provenance.

**Localities.** Found along the length of the northern Koolaus, including Kawailoa Trail, Kaipapau Valley, Castle Trail and Kaluanui Valley, Marsh Trail, Helemano and Poamoho Trail, Punaluu Valley, Kahana Valley, Wahiawa, Puu Kaaumakua, and Schofield-Waikane Trail. Recorded elevations range from 515 to 810 m at the Koolau crest.

**Habits.** Best found on plants, with a variety of plant substrates recorded, including under moss on *Metrosideros* (ohia lehua), under bark of *Acacia koa*, and from *Broussaisia*, *Cheirodendron*, *Cibotium*, and *Melicope*. One specimen collected in March was recorded from “ground.” Otherwise, this species has been found by beating vegetation during day or night.

**Phylogenetic relationships.** Each species of the sister-species pair of *B. optata* and *B. hihia* is isolated on a mountain range within easy view of the other (Fig. 72). Nonetheless, conditions in the saddle region of Oahu have been inhospitable to arboreal montane carabids long enough for speciation associated with substantial morphological change in male genitalia (Figs. 71, 73) to have taken place.
Blackburnia (Blackburnia) hihia Liebherr, new species
(Figs. 29G, 32A, 68C, 72, 73, 74)

DIAGNOSIS. As the preceding 2 species (Fig. 68A-C) in: 1, tubular prothorax, but with complete lateral marginal bead and generally smooth or sparse punctate laterobasal depressions; and 2, laterally and apically reduced elytral striae; but, separable from B. optata by vertex covered with reduced though traceable isodiametric sculpticells; male aedeagal median lobe markedly recurved medioventrally (Fig. 73A, C, E, G). Standardized body length 5.9-7.5 mm.

DESCRIPTION. Head pedunculate, with eyes moderately projected and with narrow neck with distinct dorsal impression, ocular ratio 1.46; labrum broadly and shallowly emarginate apically; frontoclypeal grooves deepest just behind frontoclypeal suture, extended toward anterior supraorbital seta as diagonal wrinkles; antennal pedicel with 1 outer seta and 2 shorter apical setae; mentum tooth triangular, with rounded apex.

Prothorax. Pronotum with complete lateral marginal bead, disc extended to bead (Fig. 68C); lateral bead slightly thickened inside basal pronotal seta, and continuing around base; anterior pronotal seta absent in most specimens, unilaterally present in a few specimens, basal setae present; laterobasal depressions circular, surface pitted with usually less than 12 small punctures; median base smooth, elevated relative to basal marginal bead; median longitudinal impression obsolete basally, deeper and broader at basal 1/5 of length, finely inscribed on disc; anterior transverse impression marked by a broad depression on midline, then narrowly and shallowly extended almost to slightly protruded, obtuse-angulate front angles; anterior marginal bead effaced medially, but evident in lateral 1/4 of width.

Elytra. Humeri very narrow, elytra widest behind middle, sides and apex depressed relative to disc; humeral groove evenly arcuate posteriorly; subapical sinuation obsolete, elytral margin convex near apex; disc flat medially; intervals slightly convex; striae a series of round pits connected by shallow grooves, striae reduced laterally to a series of small pits, reduced apically to smooth striae without pits; scutellar setae variously present or absent; 3 dorsal elytral setae present in third interval, each seta short, shorter than width of elytral interval; 10-11 lateral elytral setae.

Pterothorax. Metepisternum short, lateral margin 1.4 to 1.5× length of anterior margin; flight wings vestigial, not extended beyond metanotum.

Legs. Profemur without anteroventral setae, with 2 posteroventral setae; mesocoxa with 1 ridge seta; mesofemur with 2 anteroventral setae; metacoxa bisetose, mesal seta absent; metafemur with 2 anteroventral setae; tarsi robust, first 4 tarsomeres ventrally with sparsely distributed lateral brushes of elongate setae and a glabrous median space; metatarsomere 4 with subequal outer and inner lobes (Fig. 29G), lobes 0.5× median basal length of segment; tarsomere 5 ventrolaterally with 6 setae each side subequal to depth of tarsomere at point of setal insertion.

Abdomen. Males with 1 apical seta each side sternite VII, females with 2 setae each side; sternites II and III depressed along anterior margins, depressed areas wrinkled or punctate.

Coloration. Head and pronotum shiny piceous with slight metallic bluish reflection; elytra piceous with more distinct greenish or purplish metallic reflection; ventral surface of body and elytral epipleura rufopiceous, without metallic reflection; antennae and legs paler than ventral surface of body, brunneous; trochanters, femoral-tibial joint, and tarsi slightly paler or not.
Fig. 73. B. (Blackburnia) hitia, new species. A. Male aedeagal median lobe, right lateral view; Palikea. B. Male aedeagal median lobe, euventral view; Palikea. C. Male aedeagal median lobe, right lateral view; Puu Kaua. D. Male aedeagal median lobe, euventral view; Puu Kaua. E. Male aedeagal median lobe, right lateral view; Puu Kalena. F. Male aedeagal median lobe, euventral view; Puu Kalena. G. Male aedeagal median lobe, right lateral view; Mt. Kaala. H. Male aedeagal median lobe, euventral view; Mt. Kaala.
Fig. 74. *B. (Blackburnia) hihia*, new species. A. Left female gonocoxa, ventral view. B. Female bursa copulatrix and spermatheca, ventral view, showing narrow triangular dorsal pouch, lumenal field of cristate microtrichia, and spermathecal reservoir with basal lobe.

**Microsculpture.** Head with distinct isodiametric microsculpture on vertex in females, microlines more reduced but still traceable in males; pronotum with reduced transverse mesh microsculpture, but sculpticells still traceable in transverse wrinkles; elytra with transversely stretched sculpticells in transverse rows, most visible on elytral apex.

**Male genitalia.** Aedeagal median lobe stout, consistently with a broadly and markedly recurved medioventral margin and an angularly downturned apex (Fig. 73A, C, E, G); apex variously extended beyond opening of internal sac, from quite short and barely extended
(Fig. 73G), to elongate with a finely rounded apex (Fig. 73A); basal sagittal crest of various length, but quite broad; median lobe of moderate breadth, tapered to a broadly rounded tip (Fig. 73B, D, F, H).

**Female reproductive tract.** Gonocoxite 2 basally broad, shorter than gonocoxite 1 (Fig. 74A); gonocoxite 1 with apical fringe of 6-10 setae in a single row; gonocoxite 2 with sheer lateral cutting margin (Fig. 32A), 1-3 peglike lateral ensiform setae near base, and 1 peglike dorsal ensiform seta, lateral setae 0.11× length of gonocoxite 2; apical nematiform setae elongate, 0.60 to 0.75× length of gonocoxite 2; bursa copulatrix elongate, 1.6× length of common oviduct, nearly symmetrical, with a narrow, parallel-sided dorsal pouch near vagina, and a broad lumenal ring of 5-pointed cristate microtrichia (Fig. 74B); spermatheca ovoid, reservoir about 0.5× length of spermathecal duct, with small basal lobe.

**Holotype** 

tree ferns, dead petioles, 1175 m, 08-VI-1991, Newton & Thayer (FMNH, 1), under rocks, road debris, 1210 m, 18-V-1991, Liebherr (CUIC, 2), summit bog, 1210 m, 08-VI-1991, Ivie (MTSU, 6); Palikea, 18-VI-1938, Zimmerman (BPBM, 4), Broussaisia 30-VI-1935, Swezey (HDAC, 1), 18-VI-1938, Swezey (HDAC, 1), beating Cheirodendron, night, 925-935 m, 03-V-1995, Liebherr (CUIC, 5), beating Freycinetia, night, 925-935 m, 03-V-1995, Liebherr (CUIC, 2), beating branches w/moss, 910 m, 15-VIII-1957, Mockford (UVM, 4), beating ohia at night, 925-935 m, 03-V-1995, Liebherr (CUIC, 24), beating ohia in day, 925-935 m, 03-V-1995, Liebherr (CUIC, 5), Polhemus (BPBM, I), beating tree ferns in day, 925-935 m, 03-V-1995, Liebherr (CUIC, 1), moss on trees, 06-X-1940, Anderson (BPBM, 2), under moss on Cheirodendron, 925-935 m, 03-V-1995, Liebherr (CUIC, 11); Pohakuloa, 26-III-1948, Bianchi (BPBM, 1); Puu Kalena, Cibotium chamissoi, 29-XII-1929, Swezey (HDAC, 1), 19-IV-1931, Swezey (BPBM, 2); Puu Kaua, VIII-1954, Ford (BPBM, 3), beating ohia at night, 940-948 m, 04-V-1995, Liebherr (CUIC, 21), beating ohia in day, 940-948 m, 04-V-1995, Liebherr (CUIC, 22), scrape moss, ohia, day, 940-948 m, 04-V-1995, Liebherr (CUIC, 13); Waianae Mts., VI-1953, Ford (BPBM, 1), X-1953 (NMNH, 8).

**Etymology.** The species epithet *hihia* is the Hawaiian word for problem, snarl, or trouble, and indicates the difficulty in separating this species from *B. optata* using external characters.

**Distribution.** Beetles of this species live at the highest elevations throughout the length of the Waianae Range, Oahu (Fig. 72). That the collecting locality Pohakuloa is the one of Oahu, not that of Hawaii Island, is attested by the co-occurrence of two other Oahu species—*B. hilaris* and *B. muscicola*—in the same collection sample.

**Habits.** Like its sister species, *B. hihia* is usually encountered by beating plants, including Broussaisia, Cheirodendron (olapa), Cibotium (hapuu), Freycinetia (ieie), Melicope, and Metrosideros (ohia lehua). In such situations it can be secreted under moss or in dead plant material. Additionally it has been found in terrestrial situations on Mt. Kaala, where this species is particularly abundant, in rotten logs, and moss mats on the ground. *Blackburnia hihia* has been recorded only from elevations above 900 m along the Waianae crest.

**Phylogenetic relationships.** *Blackburnia hihia* is restricted to the Waianae Mountains, and its adelphotaxon, *B. optata* (Fig. 9), is distributed in the Koolau Mountains.

*Blackburnia* (*Blackburnia*) *agonoides* (Sharp), new combination
(Figs. 68D, 75, 76)

*Anchonymus agonoides* Sharp, 1903: 199.

**Diagnosis.** Recognizable based on the reduced setation, with pronotum glabrous and scutellar seta absent, otherwise pronotum with obsolete lateral marginal depressions and punctate base would agree with the preceding 3 species and the following 3 species; pronotum appearing elongate, maximum width about 1.1× median length, basolateral margins slightly sinuate before obtuse-angulate hind angles (Fig. 68D); elytral striae 1-4 with small punctures basally, striae impunctate in apical 3/4 of length, striae 5-8 increasingly punctate, outermost striae consisting of a series of isolated punctures; vertex with evident isodiametric microsculpture, pronotal disc with evident transverse mesh,
elytral disc with isodiametric sculpticells in transverse rows. Standardized body length 8.9-9.0 mm.

Pterothorax. Metepistemum broad, lateral margin 1.4 to 1.5× length of anterior margin; flight wings vestigial, not extended beyond metanotum.

Male genitalia. Aedeagal median lobe stout, in lateral aspect medioventral margin slightly recurved, nearly straight, apex angulate with median shaft, ventral excavation extended onto apex, latter tapered to a finely rounded tip (Fig. 75A); in euventral aspect sagittal crest narrow; median lobe moderately broad, evenly tapered to a finely rounded tip (Fig. 75B).

Female reproductive tract. Gonocoxite 1 with apical fringe of 7-8 setae, 5 near medioapical angle, 3 laterally (Fig. 75C); gonocoxite 2 shaped like a scimitar, apex
Fig. 76. Distributional records for *B. (Blackburnia) agonoides* (□), *B. (Blackburnia) pukalaina*, new species (■), and *B. (Blackburnia) fracta* (●).

acuminate, with lateral and dorsal ensiform setae both on lateral, concave cutting edge, 5-6 peglike lateral ensiform setae along ventrolateral margin, 4 peglike dorsal ensiform setae along dorsolateral margin, setae about 0.12× length of gonocoxite 2; apical nematiform setae elongate, 0.55× length of gonocoxite 2 (unilaterally 3 setae present in dissected individual) (Fig. 75C); bursa copulatrix elongate, 1.5× length of common oviduct, with small crescent-shaped dorsal pouch near vagina, a band of 3- and 4-pointed cristate microtrichia, and a large leftward expansion; spermatheca ovoid, reservoir 0.65× length of spermathecal duct, with a basal lobe.

**Lectotype** ♀ labeled “Disenochus agonoides, Type, D.S., Haleakala 5000 ft. IV 1894 Perkins 250” (BMNH) hereby designated. Perkins’ lot 250 consisted of a series of this species collected under bark of *Acacia koa* at 1515 m elevation, 1-IV-1894 (Perkins 1894a).

**Distribution.** Living along the leeward edge of the mesic forest on Haleakala, East Maui (Fig. 76). The degradation and loss of this forest due to logging, cattle, and adventive introductions of exotic arthropods and grasses makes the continued existence of this species suspect.

**Localities.** Perkins is the only one to collect this species, and all localities are in the vicinity of his 1894 camp above Olinda at 1210 m (Perkins 1894a), and his 1896 camp at about 1515 m (Perkins 1896b). Therefore the range of this species can be defined to the west by the limit of forest above Olinda, to the east by Waikamoi Gulch or possibly Koolau Gap, and in elevation by the 1200 and 1500 m contours.
Habits. We know where this beetle lives through Perkins' mention of its capture under bark of a smooth-barked Koa (Perkins 1894a). "Anchonymus agonoides was found very locally on Haleakala, inhabiting cavities in the trunk or branches of the Koa. When found, a considerable number of individuals is liable to occur" (Perkins 1913, cxl). Recent searches of such microhabitats have produced only large aggregations of adventive isopods—e.g., Porcellio scaber Latreille (Taiti & Howarth 1996)—suggesting involvement of this biotic agent in the decline of B. agonoides.

Phylogenetic relationships. Blackburnia agonoides is the adelphotaxon to the Maui Nui species triplet B. longipes (B. pukalaina + B. fracta). Of those, it is sympatric with B. fracta along the extreme western edge of that species' distributional range.

Blackburnia (Blackburnia) longipes (Sharp), new combination
(Figs. 32B, 77A, 78, 79)

Disenochus longipes Sharp, 1903: 205.

DIAGNOSIS. This and the following two species—B. pukalaina and B. fracta—are characterized by the antennal pedicel with increased setation—6 apical setae present in addition to the longer outer seta—in combination with dorsal surface bronzy metallic with distinct microsculpture, elytral striae punctate throughout their length, and metafemur with several short dorsoapical setae. Like B. agonoides, these species all lack the scutellar seta. B. longipes is diagnosed by the more markedly punctate pronotal laterobasal depressions, more deeply punctate elytral striae, and granulate isodiametric elytral microsculpture that results in an alutaceous sheen (Fig. 77A). Standardized body length 8.4-10.2 mm.

Pterothorax. Metepisternum moderately elongate, lateral margin 1.5 to 1.8× length of anterior margin; flight wings vestigial, not extended beyond metanotum.

Male genitalia. Aedeagal median lobe stout, recurved medioventrally, apex angulate to median shaft, ventral excavation extended onto apex tapered to a finely rounded tip (Fig. 78A); basal sagittal crest short and moderately broad; median lobe constricted laterally just beyond midlength, tapered to finely rounded tip (Fig. 78B).

Female reproductive tract. Gonocoxite I with apical fringe of 6-8 setae, 3-4 near medioapical angle, and 3-4 laterally (Fig. 78C); gonocoxite 2 elongate with acuminate apex, 3 peglike lateral ensiform setae restricted to basal portion of lateral cutting margin, each 0.11× length of gonocoxite 2; 1 dorsal ensiform seta; apical nematiform setae elongate, 0.6× length of gonocoxite 2; bursa copulatrix not elongate, subequal in length to common oviduct, with small crescent-shaped dorsal pouch near vagina, leftward expansion 1/2 distance from base to spermatheca, and a medial band of 3- to 5-pointed cristate microtrichia; spermatheca elongate, reservoir about 0.75× length of spermathecal duct, with a basal lobe (Fig. 78D).

Holotype ♀ labeled "♂ Diseachsen longipes Type D.S. Molokai 4000 ft. 8.VI.1893. Perkins" (BMNH).

Distribution. Known from the mountains of Molokai along the canyon rims above Waikolu and Pelekunu (Fig. 79).

Localities. Found in the highest forest above Waikolu and Pelekunu Valleys. Within TNCH Kamakou Preserve, known from Puu Kolekole and vicinity, Hanalilolilo Trail, and Kaunuohua. The elevational range of known localities is 1150 to 1380 m.
Fig. 77. Blackburnia species habitus, dorsal view. A. B. (Blackburnia) longipes. B. B. (Blackburnia) pukalaina, new species. C. B. (Blackburnia) fracta. D. B. (Blackburnia) bryophila, new species.
**Habits.** As with *B. pukalaina* and *B. fracta*, specimens of this species are most often found associated with moss mats off the ground, on trunks, or in crotches of ohia lehua trees (*Metrosideros*). Adults actively forage on plant surfaces at night, including those of low ferns and tree ferns (*Cibotium*).

**Phylogenetic relationships.** This Molokai species is the adelphotaxon to the Maui species pair, *B. pukalaina* and *B. fracta* (Fig. 9). As such, the phylogenetic relationships define a biogeographic pattern congruent with isolation of Molokai prior to vicariance of montane habitats on Puu Kukui (West Maui) and Haleakala (East Maui). This hypothesis differs from that proposed based on phylogenetic and distributional data for three other species triplets in Division 1 (see discussions under *B. frigida*, *B. sharpi*, and *B. anomala*), but is congruent with relationships of the *B. constricta* species triplet.
DIAGNOSIS. Like *B. longipes*, with pedicel bearing 6 or more apical setae, completely punctate elytral striae, obsolete pronotal lateral marginal depressions (Fig. 77B), and distinct isodiametric microsculpture of the elytral intervals, but, in this species isodiametric sculpticells are smooth, shiny, so that alutaceous sheen is not so pronounced. *Blackburnia fracta* differs by having less punctate elytral striae, the discal striae irregularly interrupted, without pitlike punctures observed in *B. pukalaina*. Standardized body length 7.3-9.5 mm.

DESCRIPTION. **Head** narrow, eyes moderately convex, ocular ratio 1.54; frontoclypeal grooves shallow, extended to anterior supraorbital seta, vertex with 3-4 diagonal wrinkles inside seta; neck with distinct dorsal impression; antennal pedicel with ring of 8 apical setae plus longer outer seta; labrum broadly, shallowly emarginate with median pair of setae barely shorter than lateral pair; mentum tooth triangular with finely rounded apex.

**Prothorax.** Pronotal lateral marginal depressions obsolete, the lateral bead slightly wider at slightly protruded, finely rounded front angles; anterior pronotal setae absent; basolateral margins straight to slightly concave near basal pronotal setae, hind angles obtuse-angulate; basal marginal bead continuous with lateral bead; laterobasal depressions deeply punctate, punctures close enough to cause deep, irregular wrinkles; median base punctate, punctures densest near laterobasal depressions, sparsely distributed medially; median longitudinal impression finely inscribed throughout length, many intersecting transverse wrinkles across disc; anterior transverse impression shallow, difficult to trace. Proepistemum with shallow punctures, the surface looking hammered; pronotal process concave ventromedially.

**Elytra** ovoid, widest at midlength; humeri moderately reduced, basal groove recurved cephalad of scutellum to tightly rounded humeral angles; subapical sinuation reduced, lateral margin straight before apex; elytral intervals slightly convex, striae punctate throughout their length, though punctures fine near apex; strial punctures pitlike on disc, their diameter about twice the width of linear strial elements; strial punctures more isolated on striae 7 and 8, the striae interrupted by cuticle coplanar with the intervals; scutellar setae absent in most specimens, unilaterally or bilaterally present in few specimens; three dorsal elytral setae; 9-11 lateral elytral setae.
Fig. 80. *B. (Blackburnia) pukalaina*, new species. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view. D. Female bursa copulatrix and spermatheca, ventral view, showing sclerotized quadrate dorsal pouch (dp), band of crista microtrichia, large leftward expansion, and spermathecal reservoir with basal lobe.

Pterothorax. Mes- and metepisternum punctate; metepisternum of various length, lateral margin 1.3 to 1.7 x length of anterior margin; flight wings vestigial, not extended beyond metanotum.

Legs. Profemur with 0-1 anteroventral setae, 2 posteroventral setae; mesocoxa with 1 ridge seta; mesofemur with 2-4 anteroventral setae; metacoxa bisetose, mesal seta absent; metafemur with 2-3 anteroventral setae, and 1 dorsoapical seta near apical 3/5 to 3/4 of
length; basal tarsomeres gracile, barely broadened apically, metatarsomere 4 with subequal inner and outer lobes, lobes 0.45× median basal length of segment; tarsomeres 1-4 with sparsely distributed ventrolateral rows of elongate setae; tarsomere 5 with ventrolateral rows of 6 setae, each subequal in length to tarsomere depth at point of setal insertion.

Abdomen. Lateral reaches of sternites II and III irregularly depressed, wrinkled, along anterior margins; sternite VII with 1 seta each in males, 2 setae in females.

Coloration. Dorsal surface of head and prothorax shiny piceous, with metallic green reflection; elytra piceous with metallic purplish reflection and alutaceous sheen; ventral body surface rufopiceous without metallic reflection, legs including pro- and mesocoxae slightly paler, rufobrunneous.

Microsculpture. Vertex with evident isodiametric mesh microsculpture, sculpticells shiny; pronotal disc with reduced transverse mesh microsculpture, surface shiny, laterobasal depressions with irregularly swirled isodiametric mesh; elytra with isodiametric sculpticells in transverse rows, sculpticells flat, shiny.

Male genitalia. Aedeagal median lobe elongate, gracile, in lateral aspect with medioventral margin markedly recurved, ventral excavation extended onto angulately downturned apex, the tip of which is tightly rounded, slightly deflected (Fig. 80A); basal sagittal crest short, narrow; median lobe in euventral aspect moderately broad, slightly expanded on right side, convexly tapered to a rounded tip (Fig. 80B).

Female reproductive tract. Gonocoxite 1 with apical fringe of 6-8 setae, 4-5 near medioapical angle, and 2-3 laterally (Fig. 80C); gonocoxite 2 elongate, triangular, with finely rounded apex, 3 peglike lateral ensiform setae restricted to basal portion of lateral cutting margin, each 0.11× length of gonocoxite 2; 1 dorsal ensiform seta; apical nematiform setae elongate, 0.65× length of gonocoxite 2; bursa copulatrix elongate, about 1.5× length to common oviduct, with small quadrates dorsal pouch on right side near vagina, large leftward expansion ½ distance from base to spermatheca, a ventral field of 3- and 4-pointed cristate microtrichia; spermatheca ovoid, reservoir about 0.50× length of spermathecal duct, with a basal lobe (Fig. 80D).

Holotype ♀ labeled “HI: West Maui Is. Pu’u Kukui summit 11-V-1992 1725 to 1750m J.K. Liebherr / beating and scraping ohia during day” (CUIC).

Paratypes. MAUl: West Maui: Hanaula, Hanaula Springs, ridgetop forest, ohia, beating, 1300 m, 11-V-1993, Liebherr (CUIC, 1); Lihau N.A.R., 1060-1275 m, Medeiros (BPBM, 2), Lihau summit, Puka Camp, ohia, moss, 1240 m, 08-V-1993, Liebherr (CUIC, 10), 09-V-1993, Liebherr (CUIC, 2); vegetation at night, 1240 m, 08-V-1993, Liebherr (CUIC, 2), summit forest, ohia, moss, 1270 m, 09-V-1993, Liebherr (CUIC, 8); Puu Kukui, 0.7 km E summit, trail to bog, beating Melicope, 1700-1750 m, 21-V-1997, Liebherr (CUIC, 1), beating mossy ohia/day, 1700-1750 m, 21-V-1997, Liebherr (CUIC, 2), sifting moss ex ohia, 1700-1750 m, 21-V-1997, Liebherr (CUIC, 1), summit, beating and scraping ohia, 1725-1755 m, 11-V-1992, Liebherr (CUIC, 39), 20-V-1997, Liebherr (CUIC, 7), beating ohia at night, 1750 m, 20-V-1997, Liebherr (CUIC, 6), beating ohia during day, 1750 m, 20-V-1997, Liebherr (CUIC, 15), beating vegetation at night, 1725-1750 m, 11-V-1992, Liebherr (CUIC, 4), Polhemus (CUIC, 1), on ohia at night, 1750 m, 20-V-1997, Liebherr (CUIC, 3); Puu Kukui Tr., Violet Lake, ohia, beating at night, 1485 m, 12-V-1992, Liebherr (CUIC, 1), ohia, beating/scraping, 1485 m, 12-V-1992, Liebherr (CUIC, 6), unnamed Puu 4503 ft., beating and scraping ohia, 1335 m, 22-V-1997, Liebherr (CUIC, 4), beating ohia at night, 1330 m, 13-V-1992, Liebherr (CUIC, 12), 22-V-1997, Liebherr (CUIC, 2), beating
CARABIDAE PART I: PLATYNINI

ohia during day, 1330 m, 13-V-1992, Liebherr (CUIC, 1), scraping moss ex ohia, 1360 m, 22-V-1997, Liebherr (CUIC, 1), sifting moss on ohia, 1330 m, 22-V-1997, Liebherr (CUIC, 5).

**Etymology.** The species epithet *pukalaina* joins the Hawaiian words for pit or hole (*puka*) and line (*laina*), denoting the punctate elytral striae.

**Distribution.** This species is distributed throughout higher elevations across much of West Maui (Fig. 76).

**Habits.** All specimens of this species have been collected from arboreal situations. Adults have been found by beating on *Metrosideros* (ohia lehua) during day or night, by scraping moss mats on ohia, and by beating *Melicope*.

**Phylogenetic relationships.** This species is the adelphotaxon of *B. fracta* of Haleakala (Fig. 9). Vicariance between habitats on the Puu Kukui and Haleakala massifs facilitated speciation of these two forms.

*Disenochus fractus* Sharp, 1903: 205.

**Blackburnia (Blackburnia) fracta** (Sharp), new combination

(Figs. 76, 77C, 81)

**Diagnosis.** Sharing with *B. longipes* and *B. pukalaina*: 1, narrow pronotum with rugosely punctate laterobasal depressions (Fig. 77A-C); 2, punctate elytral striae; 3, apically multisetose antennal pedicel; 4, lack of a scutellar seta; and 5, dorsoapically setose metafemur. But: 1, elytral striae more interrupted than distinctly punctate, the punctures elongate on striae 1-5 and closely joined one to the next; 2, striae 6-8 with punctures more distinct and separated by cuticle coplanar with the elytral intervals; 3, head and pronotum piceous with metallic green to purple reflection; 4, elytra shining black with alutaceous sheen due to distinct isodiametric microsculpture in transverse rows. This species is most similar to *B. pukalaina*, but, appears to be distinguishable by constant differences in the elytral striae. Standardized body length 8.6-9.9 mm.

**Pterothorax.** Mes- and metepistemum slightly punctate; metepistemum lateral margin from 1.4 to 1.7× length of anterior margin; flight wings vestigial, not extended beyond metanotum.

**Male genitalia.** Aedeagus very similar to that of individuals of *B. pukalaina*; aedeagal median lobe elongate, gracile, with medioventral margin markedly recurved, ventral excavation extended onto angulately downturned apex, the tip of which is tightly rounded, slightly deflected (Fig. 81A); basal sagittal crest short, broad; median lobe moderately broad, slightly expanded on right side, convexly tapered to a finely rounded tip (Fig. 81B).

**Female reproductive tract.** Gonocoxite 1 with apical fringe of 7-9 setae, 5 near medioapical angle in double series, and 2-4 laterally (Fig. 81C); gonocoxite 2 elongate, triangular, with finely rounded apex, 4 peglike lateral ensiform setae restricted to basal portion of lateral cutting margin, each 0.11× length of gonocoxite 2; 1 dorsal ensiform seta; apical nematiform setae elongate, 0.67× length of gonocoxite 2; bursa copulatrix elongate, about 1.7× length to common oviduct, with small quadrate dorsal pouch on right side near vagina, large leftward expansion ½ distance from base to spermatheca, a ventral field of 3-, 4-, and 5-pointed cristate microtrichia; spermatheca elongate-ovoid, reservoir about 1.0× length of spermathecal duct, with a basal lobe.

Distribution. This species is found throughout windward forest on Haleakala, East Maui (Fig. 76).

Localities. Widespread across the windward forests of Haleakala, with recorded localities including Waikamoi Flume (Waikamoi to Haipuaena Gulches), TNCH Waikamoi Preserve (Honomanu Gulch), Hanawi Natural Area Reserve (Hanawi Gulch and Kuhiwa Gulch), Midcamp and New Greensword Bogs in Upper Hana Forest of Haleakala National Park, Kipahulu Valley, Kipahulu south rim below Kuiki, and Kekuewa Hill 0.7 km N Puu Ahulili. Habitats for this species range from 1060 to 2120 m elevation.

Habits. This species almost always has been encountered on vegetation, either actively foraging at night, or secreted during day in moss mats. In Waikamoi, adults and pupae were found together in moss mats, suggesting that the entire life cycle takes place in trees. Recorded host substrates include Dubautia, Metrosideros (ohia lehua), and Styphelia.

Phylogenetic relationships. This species is the adelphotaxon of B. pukalaina of West Maui (Fig. 9).

Fig. 81. B. (Blackburnia) fracta. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view.
DIAGNOSIS. As *B. erythropus* in: 1, reduction of microsculpture resulting in shiny dorsal body surface; 2, bruneous legs contrasting against shiny piceous body; 3, reduced pronotal laterobasal depressions mesally margined by less than 10 sparsely distributed punctulae; 4, convex, basally punctate elytral striae; and 5, presence of 1 small mesofemoral dorsoapical seta; but, differing in: 1, body size and shape, standardized body length 7.3-9.3 mm; 2, pronotum narrower, quadrate with rounded corners (Fig. 77D); 3, elytra without vestige of microsculpture laterally or apically; and 4, metepisternum punctate near its anterior margin.

DESCRIPTION. Head elongate due to elongate neck with distinct dorsal impression; frontoclypeal grooves shallow, extended to anterior supraorbital setae; eyes small, of same convexity as genae, ocular ratio 1.51; antennae short, third antennomere shorter than horizontal diameter of eye; pedicel with 1 longer outer seta and 2 shorter apical setae; labrum broadly and shallowly emarginate; mentum tooth triangular, apex rounded.

Prothorax. Pronotum quadrate, maximum width 1.05× median length, hind angles broadly rounded but as wide apart as slightly protruded, obtuse-angulate front angles; lateral marginal depressions obsolete for most of length, lateral marginal bead thickened in vicinity of basal pronotal seta, continuous with basal marginal bead; anterior pronotal seta absent, posterior seta located in lateral marginal bead at 1/5 distance from median base to apex; laterobasal depressions smooth, with from 1 to 10 sparsely distributed punctulae from mesal edge of depression to largely smooth median base; median longitudinal impression obsolete basally, deeply incised on disc, traversed by a few large transverse wrinkles; anterior transverse impression deep medially, shallow to obsolete away from median impression; anterior marginal bead obsolete medially, apparent only just inside front angles.

Elytra convex, basal, lateral, and apical margins depressed relative to inflated disc; basal groove evenly rounded on moderately narrow humeri; elytra widest just behind midlength, subapical sinuation reduced, margin straight before rounded elytral apex; elytral intervals broadly convex; all elytral striae punctate over basal 4/5 of length, the punctures distinct pits connected by shallow, clearly incised striae; scutellar seta and 3 dorsal elytral setae; 13 lateral elytral setae.

Pterothorax. Metepisternum moderately elongate, lateral margin 1.5 to 1.7× length of anterior margin; flight wings vestigial, not extended beyond metanotum.

Legs. Profemur without anteroventral setae and with 2 posteroventral setae; mesocoxa with 1 ridge seta; mesofemur with 2 anteroventral setae; metacoxa bisetose, mesal seta absent; metafemur with 2 anteroventral setae, 1 dorsoapical seta.

Abdomen. Males with 1 apical seta each side of sternite VII, females with 2 each side.

Coloration. Body shiny piceous, elytra with a slight purplish reflection; palpi, antennae, and legs including pro- and mesocoxae shiny rufobrunneous.

Microsculpture reduced over all of body, vertex smooth with only vague wrinkles and small pits indicating the underlying epidermal cells; pronotal and elytral discs without microsculpture, indistinct parallel lines visible in pronotal laterobasal depressions and along elytral lateral margins.
Fig. 82. *B. (Blackburnia) bryophila*, new species. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view. D. Female bursa copulatrix and spermatheca, ventral view, showing narrow crescent-shaped dorsal pouch, leftward expansion of bursa, and spermathecal reservoir without any basal expansion.

**Male genitalia.** Aedeagal median lobe gracile, straight medioventrally, apex markedly, downwardly curved, tapered to a finely rounded tip (Fig. 82A); basal sagittal crest moderately developed; median lobe broad, with slight boss on right side before tapered to a rounded tip (Fig. 82B).

**Female reproductive tract.** Gonocoxite 1 with apical setal fringe of 9-10 setae accompanied by several more, shorter setae (Fig. 82C); gonocoxite 2 parallel-sided, apex rounded, 1-2 peglike lateral ensiform setae, 1 peglike dorsal ensiform seta, each seta about 0.10× length of gonocoxite 2; apical nematiform setae very elongate, 1.03 to 1.15× length of gonocoxite 2; bursa copulatrix elongate, 2.1× length of common oviduct, with a small
crescent-shaped dorsal pouch, a broad medial lumenal band of 2- and 3-pointed cristate microtrichia, a broad leftward expansion narrowed to entrance of spermathecal duct; spermathecal reservoir elongate, spermathecal duct short, reservoir 1.2× length of duct, reservoir without indication of basal expansion (Fig. 82D).


**Paratypes.** KAUAI: Alakai Swamp, 2.5 mi. W Waialeale, sift moss ex tree trunk, 1365 m, 30-XII-1970, Gagné (BPBM, 1); Alakai Swamp Tr., 11-X-1981, Lynch (UHEM, 1), ground at night, 1150 m, 11-V-1991, Liebherr (CUIC, 1), trees at night, 1150 m, 11-V-1991, Liebherr (CUIC, 1), scraping bark of ohia, 1150 m, 11-V-1991, Liebherr (CUIC, 3), moss mats/trail at night, 1150 m, 12-V-1991, Liebherr (CUIC, 4), trail at night, 1150 m, 15-V-1991, Liebherr (CUIC, 1), W of Kawaikoi Str., scraping dry ohia moss, 1120-1180 m, 16-V-1991, Liebherr (CUIC, 13), Lehua Makanoe Bog, 1270 m, 21-III-1964, Rice (BPBM, 2), Pihea Tr. junction, beating vegetation at night, 1180 m, 12-V-1991, Liebherr (CUIC, 4); Central Plateau, 1210 m, 05-I-1970, Rice (BPBM, 1); Mohihi-Alakai Tr., moss mats on ohia trunks, 1275 m, 19-V-1995, Liebherr (CUIC, 3), 1320 m, 19-V-1995, Liebherr (CUIC, 1); Mt. Kahili, liverwort on tree, 850 m, 18-I-1973, Howarth (BPBM, 1), *Tetraplasandra,*
870 m, 22-VI-1972 (BPBM, 1), mossy ohia trunks & roots, 895 m, 21-V-1995, Liebherr (CUIC, 1), beating ohia at night, 895 m, 21-V-1995, Liebherr (CUIC, 3), Polhemus (BPBM, 1); Pihea Tr., under logs along trail, 1180 m, 16-V-1991, Liebherr (CUIC, 12); Waialeale, 1515 m, 21-XII-1969, Rice (BPBM, 1), summit, beating vegetation at night, 1515-1530 m, 16-V-1995, Asquith (CUIC, 3), mossy creekbank at night, 1515-1530 m, 16-V-1995, Liebherr (CUIC, 12), 17-V-1995, Liebherr (CUIC, 15).

Etymology. Adults of this species can often be found standing, exposed on ground-level moss mats at night. The epithet bryophila refers to this as yet unexplained behavior.

Distribution. This species is found in the highest, wettest forests of Kauai, from Mt. Kahili on the south, to Waialeale, northwest across the Alakai to Pihea (Fig. 83).

Habits. Consistent with its broad elevational and geographical distributions, this species lives in a variety of ecological situations. On the ground it has been found under logs, walking on open trails, and standing on mossy creekbanks or pin-cushion moss mats at night. This species also climbs trees, and has been repeatedly found by beating ohia branches at night, by sifting moss mats on ohia trunks, as well as by searching under liverworts on branches. In addition to Metrosideros, one series is from Tetraplasandra.

Phylogenetic relationships. This Kauai species is geographically isolated from its adelphotaxon, which comprises the Maui Nui species triplet of B. frigida (B. munroi + B. viridis) (Fig. 9).

Blackburnia (Blackburnia) frigida Blackburn
(Figs. 32C, 84A, 85, 86)

Blackburnia frigida Blackburn, 1878b: 157; Blackburn & Sharp, 1885: 214.
Mauna frigida: Blackburn, 1884: 25; Sharp, 1903: 200.

DIAGNOSIS. Pronotum small, orbicular, with obsolete lateral marginal depressions and rounded hind angles as in B. optata and B. hihia, but with punctate median base (Fig. 84A); vertex shiny, with reduced isodiametric mesh microsculpture barely traceable; humeri reduced, basal elytral groove barely recurved on humerus; elytral striae punctate except in apical 1/6, the pitlike punctures connected by continuous striae; scutellar seta present; mesofemur with 3-4, and metafemur with 3 anteroventral setae; tarsomere 5 with elongate ventral setae, each 1.5× depth of tarsomere at point of setal insertion. Standardized body length 7.9-9.6 mm.

Pterothorax. Metepisternum elongate, lateral margin 1.7 to 1.9× length of anterior margin; flight wings vestigial, not extended beyond metanotum.

Male genitalia. Aedeagal median lobe stout, slightly expanded medioventrally, ventral excavation extended onto elongate, downturned apex, tapered to an acuminate tip, apical portion 3× depth of apex at opening of internal sac (Fig. 85A); basal sagittal crest very broad; median lobe of moderate breadth, tapered to a finely rounded tip, with sides slightly constricted before tip (Fig. 85B).

Female reproductive tract. Gonocoxite 1 with apical fringe of 8-9 setae, inner two a double series (Fig. 85C); gonocoxite 2 parallel, with broadly rounded apex (Fig. 32C), 2 peglike lateral ensiform setae and 1 peglike dorsal ensiform seta, each about 0.11× length of gonocoxite 2; apical nematiform setae elongate, 0.60× length of gonocoxite 2; bursa
Fig. 84. *Blackburnia* species habitus, dorsal view. A. *B. (Blackburnia) frigida*. B. *B. (Blackburnia) munroi*. C. *B. (Blackburnia) viridis*, new species. D. *B. (Blackburnia) aaaa.
Fig. 85. B. (Blackburnia) frigida. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view. D. Female bursa copulatrix and spermatheca, ventral view, showing triangular dorsal pouch with sclerotized surface, reduced field of cristate microtrichia, small apical lobe, leftward expansion, and spermathecal reservoir with basal lobe.

copulatrix elongate, 1.6× length of common oviduct, with a sclerotized dorsal pouch with rounded apex, sparsely distributed field of 3- and 5-pointed cristate microtrichia, a small apical lobe, a leftward expansion tapered to spermathecal duct entrance; spermatheca ovoid, reservoir about 0.7× length of spermathecal duct, with a small basal lobe (Fig. 85D).

Holotype ♂ labeled with 3 parallel lines, the uppermost broader, and one vertical ink slash at pin—indicative of Blackburn Maui code (Zimmerman 1957)—with “Blackb. frigida” handwritten on reverse side of card (BMNH). Blackburn (1878b) stated that the type was collected on Haleakala, Maui at an elevation of 10,000 ft., meaning the summit.
Fig. 86. Distributional localities for B. (Blackburnia) frigida: records from 1870 to 1900 (○), records from 1900 to present (●), localities sampled during both periods (□). Distributional records for B. (Blackburnia) viridis, new species (■).

**Distribution.** This species is known from Haleakala, both from leeward elevations of 1500 m to the summit and caldera, and from windward habitats above timberline on the windward side (Fig. 86). The range has diminished progressively due to conversion of leeward habitats to pasture, restricting recent records to higher elevations.

**Localities.** Known from Haleakala Crater, White Hill, Halemauu trail, Leleiwa overlook, Kuiki to the crater rim, Kipahulu Valley (2260 m), and Manawaiui Stream (1635 m).

**Habits.** This species occurs mostly in terrestrial situations above timberline and in dry leeward scrub habitats of Haleakala. Beetles are found under rocks or among roots of *Deschampsia* bunchgrass during day, and actively walking on open rocky surfaces at night. Near the summit of Haleakala they have been observed standing still on small rocky prominences while antennating the night breeze. Along Halemauu Trail, of 33 individuals observed on 5-V-1991 (time 2200-2400 h, T = 10° C), 4 pairs were in copula.

Fidelity to open habitats may not be absolute, as Perkins noted for lot 661: “Maui Haleakala 5000 ft. X ‘96. contains amongst others a unique Carabid (nr. Mauna) found under lichen on stem of Pelea” [Melicope] (Anonymous n.d.). This unique carabid is a specimen of *B. frigida*, and as Perkins field identified this specimen as close to Blackburn’s *Mauna frigida*, his collection information is no doubt genuine. Other species represented in lot 661 include *B. rupicola, B. fracta, B. derodera,* and *B. erro*. The first is known from open country, the latter three from forested habitat. Thus, this lot appears to represent collections made at the ecotone between closed-canopy forest and savannah scrub.
Phylogenetic relationships. This species is the adelphotaxon to the allopatric species pair *B. munroi* of Molokai plus *B. viridis* of West Maui (Fig. 9). The biogeographic pattern associated with phylogenetic divergence in this triplet—i.e., the basal divergence of East Maui relative to Molokai + West Maui—is not congruent with the vicariant history of Maui Nui. This incongruence, coupled with *B. frigida*'s occupation of leeward and aeolian habitats on Haleakala, led Liebherr (1997) to propose a mechanism whereby populations evolving into present-day *B. frigida* became isolated from genetically connected populations on the other two massifs. This is hypothesized to have occurred when populations leading to *B. frigida* gained access to, and became isolated in, the substantial areas of habitat above timberline as Haleakala attained its maximum elevation of 5000 m (Carson & Clague 1995). Speciation of *B. frigida* may have been facilitated by isolation of one or more small, isolated populations among the large dry expanses of Haleakala. If so, the genetic variation in this species may be less than in either of the more recently divergent species. This interpretation is supported by similarly geographically incongruent patterns in the species triplets *B. sharpi* (*B. perkinsi* + *B. koebelei*), and *B. anomala* (*B. brevipes* + *B. cephalotes*) (see species treatments for *B. sharpi* and *B. anomala* for discussion of patterns in these species triplets).

*Blackburnia (Blackburnia) munroi* (Perkins), new combination
(Figs. 84B, 87, 88)

*Disenochus munroi* Perkins, 1936: 177.

**DIAGNOSIS.** Like *B. frigida* and *B. viridis*, that follow, in punctate pronotal median base, presence of scutellar seta, and punctate, continuous elytral striae but, differing by: 1, pronotal lateral marginal depressions broader, quite evidently punctate inside basal pronotal seta (Fig. 84B); 2, basolateral pronotal margins broadly sinuate before basal seta; 3, pronotal basal margin straight medially, pronotum not orbicular; 4, lateral elytral striae reduced to a discontinuous series of pitlike punctures; 5, elytral disc without discernible microsculpture; 6, metepisternum punctate, and 7, larger body size, standardized body length 9.3-10.3 mm.

**Pterothorax.** Metepisternum lateral margin 1.4 to 1.9× length of anterior margin, its median surface irregular due to indistinct punctures that may join to form wrinkles; flight wings vestigial, not extended beyond metanotum.

**Male genitalia.** Aedeagal median lobe stout, broadly expanded medioventrally, with ventral excavation extended to elongate apex tapered to a finely rounded tip, apex extended 2.4× depth of apex at opening of internal sac (Fig. 87A); basal sagittal crest short, small; median lobe basally broad, evenly tapered to finely rounded tip (Fig. 87B).

**Female reproductive tract.** Gonocoxa broad, gonocoxite 1 with apical fringe of 11-12 setae, inner 6 in double series (Fig. 87C); gonocoxite 2 parallel-sided, apex broadly rounded, with 4 peglike lateral ensiform setae and 1 peglike dorsal ensiform seta, lateral setae 0.11× length of gonocoxite 2; apical nematiform setae elongate, 0.58× length of gonocoxite 2; bursa copulatrix elongate, 1.6× length of common oviduct, with small parallel-sided dorsal pouch near vagina, reduced field of 3-, 4-, 5-, and 6-pointed microtrichia (Fig. 87D); leftward expansion of bursal wall large; spermatheca ovoid, reservoir 0.6× length of spermathecal duct, with a small basal lobe.
Fig. 87. B. (Blackburnia) munroi. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view. D. Female bursa copulatrix and spermatheca, ventral view, showing parallel-sided dorsal pouch, field of cristate microtrichia, large leftward expansion, and spermathecal reservoir with basal lobe.

**Holotype** δ labeled “Molokai about 4000 ft. G.C. Munro // Disenochus munroi Type Molokai, above head of Wailau Valley // #1320” (yellow label) (BPBM). Left antenna is broken off beyond scape, right has 5 segments, genitalia dissected.

**Distribution.** This species is known only from higher reaches of streams draining the mountains of Molokai (Fig. 88).

**Localities.** Recorded from woods E and W of Pepeopae Bog, East and West Forks of Kawela Gulch, and Puu Kolekole in TNCH Kamakou Preserve. Also known from Waikolu Valley. Elevations of known localities range from 1040 to 1290 m.
Habits. Adults have been seen mostly in riparian stream bed habitat, either under rocks or logs, or in moss mats on the rocks. They are active and exposed during daytime and at night. If one assumes that the ancestral habitat of this species was similar to that of the closely related *B. frigida* of Haleakala, these habitats may constitute a relictual distribution for this species, with ancestral populations of *B. munroi* having been able to occupy a much more extensive array of open, riparian localities when Kamakou volcano attained a height of 3300 m at the end of its shield-building phase (Carson & Clague 1995).

Phylogenetic relationships. This species is the adelphotaxon of *B. viridis* of West Maui, supporting the sister-area relationship of West Maui and Molokai.

**Blackburnia (Blackburnia) viridis** Liebherr, new species  
(Figs. 84C, 86, 89)

**DIAGNOSIS.** Pronotum combining the narrow lateral marginal depressions of *B. frigida* and straighter pronotal base of *B. munroi* (Fig. 84C); head with isodiametric mesh microsculpture and greenish metallic reflection, pronotum with transverse mesh microsculpture and greenish metallic reflection on disc; elytra with isodiametric sculpticells in transverse rows producing alutaceous, greenish lustre; femora piceous, contrasted with flavous tibiae; lateral elytral striae continuous, punctures connected by distinct striae. Standardized body length 8.6-9.1 mm.

**DESCRIPTION.** Head elongate, neck with distinct dorsal impression; eyes small, outer surface slightly more convex than genal surface, ocular ratio 1.40; antennal pedicel with 1 long outer seta and 3 more setae around apex, each seta as long as basal diameter of third antennomere; labrum broadly, shallowly emarginate; frontoclypeal grooves broad, shallow, continued behind eyes as diagonal wrinkles; apex of mentum tooth broadly rounded.

**Prothorax.** Pronotum with narrow lateral marginal depressions, isodiametric microsculpture visible in bottom of depression to slightly protruded, rounded front angles; anterior pronotal seta absent; lateral marginal bead widened at basal pronotal seta, narrowly continued onto pronotal base, basal marginal bead complete; lateral marginal depression broadest just behind basal pronotal seta, where it is covered with distinct isodiametric
microsculpture, pronotal base more or less evenly punctate between lateral depressions; median longitudinal impression traceable to basal marginal bead, deepest near basal 1/5 of length, irregularly wavering on disc due to transverse wrinkles extended onto disc; anterior transverse impression linearly joined to apex of median impression, extended anterolaterally about ½ distance to front angles; anterior marginal bead indicated by short longitudinal wrinkles in median 1/3 of width, well defined in lateral thirds.

Elytra. Basally narrow, basal groove slightly recurved anteriorly on humerus; elytra widest just before midlength, subapical sinuation reduced, lateral margin straight near apex; intervals moderately convex, striae punctate in basal 5/6 of length, punctures set in pits connected by deep, continuous striae, lateral striae also continuous; scutellar seta and 3 dorsal elytral setae present; 12-13 lateral elytral setae.

Pterothorax. Metepisternum impunctate, moderately elongate, lateral margin 1.5 to 1.7× length of anterior margin; flight wings vestigial, not extended beyond metanotum.

Legs. Profemur without anteroventral setae, with 2 posteroventral setae; mesocoxa with 1 ridge seta; mesofemur with 2-3 anteroventral setae; metacoxa bisetose, mesal seta absent; metafemur with 2-3 anteroventral setae; tarsomeres 1-4 with sparse ventrolateral rows of elongate setae; metatarsomere 4 with outer and inner lobes subequal, lobes 0.4× median basal length of segment; tarsomere 5 with ventrolateral rows of 6 setae subequal to tarsal depth at point of setal insertion.

Abdomen. Males with 1 apical seta each side of sternite VII, females with 2 each side.

Coloration. See diagnosis.

Microsculpture. See diagnosis.

Male genitalia. Aedeagal median lobe stout, medioventral margin slightly recurved, expansion broad, ventral excavation extended onto elongate apex, apex tapered to an acuminate tip, 2.5× as long as depth of apex at opening of internal sac (Fig. 89A); moderately broad sagittal crest; median lobe moderately broad, apex tapered to triangular tip (Fig. 89B).

Female reproductive tract. Gonocoxa broad, gonocoxite 1 with apical fringe of 8-9 setae, 3-4 at medioapical angle, 1 medially, and 3-4 laterally (Fig. 89C); gonocoxite 2 parallel-sided, apex broadly rounded, with 3 peglike lateral ensiform setae and 1 peglike dorsal ensiform seta, lateral setae 0.14× length of gonocoxite 2; apical nematiform setae elongate, 0.56× length of gonocoxite 2; bursa copulatrix elongate, 1.6× length of common oviduct, with small parallel-sided dorsal pouch near vagina, reduced field of 5-pointed microtrichia (Fig. 89D); leftward expansion of bursal wall large; spermatheca ovoid, reservoir 0.7× length of spermathecal duct, with a small basal lobe.


Paratypes. MAUI, West Maui: Hanaula, Hanaula Springs, 1270 m, 01-VIII-1984, Medeiros (BPBM, 1), reservoirs, ohia, beating/scraping, 1210 m, 10-V-1993, Liebherr (CUIC, 1); Mt. Eke N.A.R., on mud creekbank, 1330 m, 24-V-1997, Ewing (CUIC, 1); Puu Kukui, 0.7 km E summit, bog, under log in creekbed, 1705 m, 21-V-1997, Liebherr (CUIC, 1), Puu Kukui summit, ohia, beating/scraping, 1725-1750 m, 11-V-1992, Liebherr (CUIC, 1); Puu Kukui Tr., on boardwalk at night, 1635 m, 22-V-1997, Miedell (CUIC, 1), unnamed Puu 4503 ft., ohia, beating at night, 1330 m, 13-V-1992, Liebherr (CUIC, 1), ohia, beating during day, 1330 m, 13-V-1992, Liebherr (CUIC, 1), above Puu 4503 ft., ground/boards at night, 1330-1365 m, 13-V-1992, Liebherr (CUIC, 2).
Fig. 89. B. (Blackburnia) viridis, new species. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view. D. Female bursa copulatrix and spermatheca, dorsal view, showing parallel-sided dorsal pouch, field of cristate microtrichia, large leftward expansion, and spermathecal reservoir with basal lobe.

**Etymology.** The bronzy greenish pronotum and elytra suggest the species epithet *viridis*, a Latin adjective meaning green.

**Distribution.** This species occurs across all major blocks of the West Maui mountains except Lihau (Fig. 86).

**Habits.** Adults live on the ground, but also climb vegetation. They are active at night on muddy open ground such as along bog edges or small streamlets. Individuals have also been found repeatedly by beating ohia lehua (*Metrosideros*) branches or scraping moss mats and loose bark on ohia lehua trunks.

Like *B. munroi*, this species would have had access to a greater variety and expanse of open habitats when the Puu Kukui volcano achieved its greatest stature, some 3400 m (Carson & Clague 1995).

**Phylogenetic relationships.** This West Maui species is the adelphotaxon to the Molokai species, *B. munroi* (Fig. 9).
Blackburnia (Blackburnia) aaaa (Samuelson & Liebherr), new combination
(Figs. 84D, 90, 91)


DIAGNOSIS. A remarkably apomorphic cave species, with eyes composed of only 4 ommatidia, cuticle lightly melanized, body color rufotestaceous to flavous, antennal pedicel with up to 20 setae in its apical half, prosternal process apically setose, humeri very narrow (Fig. 84D), three dorsal elytral setae, mesofemur with 7 anteroventral setae, metafemur multisetose dorsoapically, tarsomeres setose dorsally with indistinct dorsolateral sulci, tarsomere 5 with elongate ventral setae, the setae longer than depth of tarsomere at point of setal insertion. Standardized body length 7.4 mm.

Pterothorax. Metepisternum reduced, lateral margin 1.8× length of anterior margin; flight wings vestigial, not extended beyond mesonotum.

Male genitalia. This species is known only from one female specimen.

Female reproductive tract. Gonocoxite 1 glabrous except for 2-4 very small setae near medioapical angle and 2 short setae laterally (Fig. 90A); gonocoxite 2 elongate, parallel-sided, with 1-2 lateral and 1-2 dorsal ensiform setae; apical nematiform setae elongate, 0.55× length of gonocoxite 2; bursa copulatrix elongate, about 1.6× length of common oviduct, lightly sclerotized, vagina broad, dorsal pouch indistinctly delimited but evident as a broad truncate fold (Fig. 90B); 5- to 7-pointed cristate microtrichia broadly lining lumenal wall; bursa broadly expanded laterally on left side; spermatheca ovoid, with small basal expansion, reservoir about as long as spermathecal duct, finely constricted.


Distribution. This species is known only from the Pukamoa Lava Tube in Kipahulu Valley, Haleakala, East Maui (Fig. 91).

Habits. The single known specimen was collected from under a stone on a muddy stream bank in the dark zone of the lava tube.

Phylogenetic relationships. Based on our preferred cladogram, the adelphotaxon to B. aaaa comprises B. polhemusi + B. pilikua (Fig. 9). These latter two species inhabit moss mats on the ground and in trees. The adelphotaxon to these three species is the clade of five species subtended by the terrestrial, epigean species, B. curtipes, of Kauai. This pattern of phylogenetic relationships defines an ecological path to cave habitation in B. aaaa that led from epigean terrestrial life, to a secretive life in moss mats both arboreal and terrestrial, and ultimately to a totally subterranean existence. B. polhemusi and B. pilikua exhibit extreme fidelity to dense moss mats (see below), suggesting that beetles of these species spend most of their life occupying moss or small voids between rocks beneath moss. Thus, the moss habitat may serve as a botanical “cave” —i.e., the habitat is dark, moist, and stable. Colonization of lava tube caves by the ancestors of B. aaaa could have occurred via networks of small subterranean voids.

The Kipahulu cave species B. aaaa is isolated geographically from species of its adelphotaxon: B. pilikua from the western edge of the montane forest on Haleakala, and B. polhemusi from the forest of Kamakou volcano, East Molokai.
Fig. 90. *Blackburnia* *aaae*. A. Left female gonocoxa, ventral view. B. Female bursa copulatrix, ventral view, with dorsal pouch, ventral field of cristate microtrichia, leftward expansion, and ovoid spermatheca with small basal lobe.
CARABIDAE PART I: PLATYNINI

Fig. 91. Distributional records for B. (Blackburnia) aaeae (●), B. (Blackburnia) pilikua, new species (○), B. (Blackburnia) polipoli, new species (□), B. (Blackburnia) sharpi (●), and B. (Blackburnia) koebelei (■).

Even noting the many evolutionary derivations of this species, a relationship with B. polhemusi and B. pilikua is supported by the elongate neck with distinct dorsal impression, pronotum with basal seta before hind angles, reduced number of lateral elytral setae (in this specimen 9), and female reproductive tract traits described above. Many autapomorphies of this species involve modification through increased body setation on the antennal scape and pedicel, prosternal process, femora, and tarsomeres. The presence of 3 dorsal elytral setae represents retention of the plesiomorphic condition observed among the basal species of Division 1 (Liebherr & Zimmerman 1998).

**Blackburnia (Blackburnia) polhemusi** Liebherr, new species
(Figs. 92A, 93, 94)

**DIAGNOSIS.** A large, narrow-bodied, rufopiceous beetle (Fig. 92A), standardized body length 12.7 mm, with elongate mandibles, 1 long outer seta and 6-8 long apical setae on antennal pedicel, pronotal disc with distinct transverse mesh microsculpture and laterobasal depressions with shallow, diffuse punctures, elytral dorsal setae absent, 11 lateral elytral setae laterad eighth interval, elytral subapical sinuation obsolete, apicolateral elytral margin convex, metacoxa trisetose, 2 lateral setae and 1 mesal seta. This species can only be confused with B. pilikua from East Maui (Fig. 92B). From it, B. polhemusi can be
Fig. 92. *Blackburnia* species habitus, dorsal view. A. *B. (Blackburnia) polhemusi, new species*. B. *B. (Blackburnia) pilikua, new species*. C. *B. (Blackburnia) curtipes*. D. *B. (Blackburnia) polipoli, new species*. 

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diagnosed by the wider humeri, and pronotal lateral marginal depressions wide all the way to the front angles.

**DESCRIPTION.** Head elongate due to long neck with distinct dorsal impression; eyes small, slightly convex, ocular ratio 1.47; antennal pedicel setose, with 6-8 setae apically around segment in addition to longer outer apical seta; labrum markedly emarginate, angulate medially; mandibles elongate, extended as far beyond labral apical margin as distance from dorsal condyle to labral margin; mentum tooth truncate apically, only slightly rounded.

**Prothorax.** Pronotum with basolateral margins straight before basal setae; lateral marginal depressions broad to front angles; anterior pronotal setae lacking, posterior setae present, very short, appearing stunted in the holotype, normal in the allotype; lateral margins beaded in front half of pronotum, less distinct basally, where they are gradually elevated from diffusely punctate laterobasal depressions; median base longitudinally wrinkled, the wrinkles grading into punctures toward laterobasal depressions; hind margin trisinuate, expanded posteriorly both in the middle and at rounded hind angles; basal marginal bead traceable if narrower medially; median longitudinal impression deep, with numerous transverse wrinkles; anterior transverse impression very shallow, almost obsolete; anterior marginal bead obsolete medially, evident only near slightly protruded front angles. Prosternal process concave ventrally, medially depressed; area between procoxae expanded posteriorly.

**Elytra** elongate, humeri only slightly reduced, lateral margins expanded to midlength, then evenly tapered to pointed apex, subapical sinuation obsolete (Fig. 92A); elytral intervals moderately convex; elytral striae basal and laterally punctate, punctures extended only about 1/3 of length on inner striae, extended to midlength on outer striae, apical portions of striae smooth, with only hints of indistinct punctulae; dorsal elytral setae absent; 11 lateral elytral setae.

**Pterothorax.** Metepisternum elongate, lateral margin 1.9× length of anterior margin; wings vestigial, not extended beyond metanotum.

**Legs.** Profemur without anterior setae, with 1 posteroventral seta; mesocoxa with 1 ridge seta; mesofemur with 2 anteroventral setae; metacoxa trisetose, 2 lateral setae and 1 mesal seta; metafemur with 1 anteroventral seta; tarsi robust, broadened apically, metatarsomere 4 about as broad apically as median length of segment, with subequal inner and outer lobes, outer lobe about 0.5× as long as median length; tarsomeres 1-4 with sparse lateral fields of setae ventrally, about 3 setae in breadth, with a glabrous median space; tarsomere 5 ventrally setose, with two lateral rows of 6 setae, each about as long as depth of tarsomere at point of insertion.

**Abdomen.** Males with 1 apical seta each side of stemite VII, females with 2 each side.

**Coloration.** Body uniformly rufopiceous, legs and antennae slightly paler but still dark rufous.

**Microsculpture** quite distinct over all of body; vertex of head with granulate isodiametric mesh, slightly transverse on neck; pronotal disc with distinct transverse mesh, median base, laterobasal and lateral marginal depressions with granulate isodiametric mesh; elytral intervals with distinct isodiametric to transverse sculpticells intermixed in transverse rows; slight iridescent lustre, but without metallic reflections.
Fig. 93. *B. (Blackburnia) polhemusi*, new species. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view. D. Female bursa copulatrix, ventral view, with dorsal pouch near vagina, field of cristate microtrichia, leftward expansion, and ovoid spermatheca with small basal lobe.
Male genitalia. Aedeagal median lobe straight medioventrally basad distinct ventral depression that is continued onto narrow downturned apex, tip slightly more downturned, tightly rounded (Fig. 93A); basal sagittal crest long and broad; median lobe tapered to a finely rounded tip, lateral margins slightly constricted laterally near tip (Fig. 93B).

Female reproductive tract. Gonocoxites 1 and 2 subequal in length (Fig. 93C); gonocoxite 1 with partially doubled apical fringe of 10-11 setae; gonocoxite 2 parallel-sided, apex rounded, with 2-3 short lateral ensiform setae and 1-2 dorsal ensiform setae, each about 0.14× length of gonocoxite 2; apical nematiform setae elongate, from 0.45 to 0.50× length of gonocoxite 2; bursa copulatrix elongate, about 1.67× as long as common oviduct, with a triangular dorsal pouch at apex of vagina, a broad field of 5- and 6-pointed cristate microtrichia, and broad leftward expansion narrowed toward spermathecal duct entrance (Fig. 93D); spermatheca ovoid, with a small outer basal expansion at junction of reservoir and duct, reservoir about 0.5× as long as spermathecal duct.

Holotype ♀ labeled “HI: Molokai Kamakou Res. ridge 0.8 km W Kolekole Cabin 27-IV-1991 el. 1180 m swimming in forest pool / D. A. Polhemus collector” (BPBM).

Allotype ♂ labeled “HI: Molokai Kamakou NCP ridge 0.8 km W Kolekole Cabin 31-V-1997 lot01 1180 m el. pyrethrum fog mossy stream bank J. Liebherr” (CUIC).

Paratype. HI: Molokai, Kolekole Cabin, 1180 m el., pyrethrum fog mossy ohia, 22-X-1997, Polhemus (NMNH, 1).

Etymology. We are happy to name this species, previously known by the colloquial name “The Molokai Monster,” to honor Dan A. Polhemus’ innumerable contributions to the study of Hawaiian insects.

Distribution. The holotype and allotype were collected from the identical moss mat on a ridge W of Puu Kolekole Cabin in TNCH Kamakou Preserve, Molokai (Fig. 94), over six years apart. The second paratype was found in forest adjacent to Kolekole Cabin.

Habits. The female holotype specimen was found inelegantly swimming on the surface of a small forest pool in a moss-covered ravine during the afternoon hours, along the headwaters of a tiny creek that empties over a 20-m precipice into Kawela Gulch. A second, male specimen was collected from an adjacent moss-covered stream bank six years later when the bank was sprayed with a pyrethrin outdoor insect fogger. The immediate area had been visited numerous times in the intervening years, both during day and at night, without
observation of specimens of this species. These findings, both positive and negative, suggest that the initial collection was fortuitous, with the first specimen knocked out of the moss by activities aimed at collecting aquatic insects. The third specimen was found by fogging a large ohia tree sporting a dense covering of moss mats, a microhabitat identical to that in which the sister species, *B. pilikua*, has been found on Haleakala, Maui.

**Phylogenetic relationships.** This species is geographically isolated on Molokai from its adelphotaxon, *B. pilikua*, of Haleakala, East Maui (Fig. 9).

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**Blackburnia (Blackburnia) pilikua Liebherr, new species**

(Figs. 91, 92B, 95)

**DIAGNOSIS.** Like *B. polhemusi* in being a large rufopiceous beetle—standardized body length 10.9-11.6 mm—without metallic reflection, and with 1 long outer seta and 6-8 long apical setae on antennal pedicel, head with distinct isodiametric mesh microsculpture, pronotal disc with pronounced transverse mesh microsculpture, elytral dorsal setae absent, a reduced number of lateral elytral setae laterad eighth interval, in this species 10, elytral subapical sinuation obsolete, apicolateral elytral margin convex, metacoxa trisetose, 2 lateral setae and 1 mesal seta. Differing from *B. polhemusi* in the less convex eyes, narrower pronotal lateral depressions in apical half of pronotum, slightly concave basolateral pronotal margins, more ovoid elytra and narrower elytral humeri (Fig. 92B), and fully developed basal pronotal setae as long as the supraorbital setae. The elytral configuration reflects a greater reduction of the metathoracic flight apparatus in this species compared to *B. polhemusi*.

**DESCRIPTION.** **Head** elongate due to long neck with distinct dorsal impression; eyes small, convex outer surface barely deviating from convexity of gena, ocular ratio 1.38; antennal pedicel setose, with 6-8 setae apically around segment in addition to longer outer apical seta; labrum markedly emarginate, angulate medially, middle pair of apical setae reduced to a single median seta in some specimens; mandibles elongate, extended as far beyond labral apical margin as distance from dorsal condyle to labral margin; mentum tooth truncate apically, only slightly rounded.

**Prothorax.** Pronotum with basolateral margins slightly concave before basal setae, the lateral margins therefore slightly sinuate; lateral marginal depressions narrowed in apical half, obsolete near front angles, the lateral margin reduced to a marginal bead; anterior pronotal setae lacking, posterior setae present, fully developed; laterobasal depressions sparsely covered with indistinct punctures medially; median base slightly punctate to smooth, not wrinkled; hind margin trisinuate, expanded posteriorly both in middle and at rounded hind angles; basal marginal bead almost effaced medially; median longitudinal impression extended to basal margin of pronotum, finely inscribed on disc; anterior transverse impression linear, evident medially, shallower toward front angles; anterior marginal bead obsolete medially, evident only near tightly rounded front angles. Prosternal process concave ventrally, medially depressed; median area of prosternum between procoxae broadly rounded posteriorly.

**Elytra** ovoid, humeri narrowed, humeral groove only slightly recurved anteriorly on humerus, elytral widest behind middle (Fig. 92B); subapical sinuation obsolete, lateral
margin convex in apical half; elytral intervals moderately convex; elytral striae 3-8 punctate basally, punctures of striae 7 and 8 extended to midlength of elytra, striae 1 and 2 and posterior portions of other striae smooth; dorsal elytral setae absent; 10 lateral elytral setae.

**Pterothorax.** Metepisternum somewhat elongate, lateral margin 1.6× length of anterior margin; wings vestigial, not extended beyond metanotum.

**Legs.** Profemur without anterior setae, with 1 posteroventral seta; mesocoxa with 1 ridge seta; mesofemur with 2 anteroventral setae; metacoxa trisetose, 2 lateral setae and 1 mesal seta; metafemur with 2 anteroventral setae; tarsi robust, broadened apically, metatarsomere 4 about as broad apically as median length of segment, with subequal inner and outer lobes, outer lobe about 0.4× as long as median length; tarsomeres 1-4 with sparse lateral fields of setae ventrally, about 3 setae in breadth, with a glabrous median space; tarsomere 5 ventrally setose, with two lateral rows of 6 setae, each about as long as depth of tarsomere at point of insertion.

**Abdomen.** Male with 1 apical seta each side of sternite VII.

**Coloration.** Body uniformly piceous, legs and antennae slightly paler rufopiceous; dorsal surface with alutaceous lustre due to microsculpture.

**Microsculpture** quite distinct over all of body; vertex of head with granulate isodiametric mesh, slightly transverse on neck; pronotal disc and median base with distinct transverse mesh, laterobasal depressions with granulate isodiametric mesh; elytral intervals with distinct isodiametric to transverse sculpticells intermixed in transverse rows.

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Fig. 95. *B. (Blackburnia) pilikua*, new species. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view.
Male genitalia. Aedeagal median lobe with broad medioventral expansion and elongate ventral excavation continued onto narrow, downturned apex, tip slightly more downturned, tightly rounded (Fig. 95A); basal sagittal crest distinct; median lobe tapered to a finely rounded tip, slight lateral constrictions each side of apex near tip (Fig. 95B).

Female reproductive tract. Only two males are known for this species, though the female of its adelphotaxon, *B. polhemusi*, is described above.

Holotype ♂ labeled “ HI: Maui Haleakala NW slope, Waikamoi Pres. trans. 3 @ 1700 m el. 8-V-1991 scraping ohia bark J.K. Liebherr // beating/sifting moss on ohia” (CUIC).

Paratype. MAUl, Haleakala: NW Slope, Waikamoi Flume, Waikamoi to Haipuaena Gulch, under boards in wet ohia rain forest, 1300 m, 11-IV-1991, Liebherr (CUIC, 1).

Etymology. The species epithet *pilikua* is the Hawaiian word for monster, signifying the large body size of this species, a feature shared with its adelphotaxon, *B. polhemusi* of Molokai.

Distribution. This species is known from the northwest slope of Haleakala, near the northwest end of the windward forest belt (Fig. 91). The Waikamoi Flume site is east of Perkins' favored collecting sites near Olinda (i.e., “Haleakala 4000 ft.”), and the type locality is east across Waikamoi Gulch from Ukulele Camp, which corresponds approximately to Perkins' “Haleakala 5000 ft.” locality.

Habits. The holotype of this species was collected by scraping bark on a moss-covered trunk of a large ohia lehua, *Metrosideros polymorpha*. The paratype was found under boards along Waikamoi Flume, those boards lying on moss-covered ground, and themselves covered with moss. Thus, like its adelphotaxon, *B. pilikua* is associated with moss, but for this species an arboreal mossy microhabitat is also indicated.

Phylogenetic relationships. This species is the adelphotaxon of *B. polhemusi* of Kamakou volcano, East Molokai (Fig. 9).

*Blackburnia (Blackburnia) curtipes* (Sharp), new combination

(Figs. 92C, 96, 97)


DIAGNOSIS. A small, shiny beetle with broad head and small eyes, ocular ratio 1.30, standardized body length 5.5-6.0 mm, and rounded costate elytral intervals peculiar to the Kauaian fauna, the costae most angulate on elytral intervals 5 and 7, sutural interval also elevated (Fig. 92C); pronotal basolateral margins not expanded nor sinuate, basal angles rounded; elytral scutellar seta absent; elytral striae slightly wavering, irregular basally, but not punctate or interrupted; tarsi short, basal metatarsomere less than 2.0× length of inner tibial spur; tarsomeres 1-4 with dense, ventral vesture of elongate setae; frons with reduced isodiametric mesh microsculpture, pronotal disc with reduced transverse mesh, and elytra with transverse mesh, the elongate sculpticells tending toward parallel lines.

Pterothorax. Metepisternum short, lateral margin 1.4 to 1.5× length of anterior margin; flight wings vestigial, not extended beyond metanotum.

Male genitalia. Aedeagal median lobe moderately stout, greatest depth 0.20× distance from tip to base of dorsal opening associated with internal sac, ventral surface evenly curved, apex evenly curved to finely rounded tip (Fig. 96A); median lobe broad, left side more convex, apex broadly rounded (Fig. 96B).
**Female reproductive tract.** Gonocoxite 1 longer than gonocoxite 2, gonocoxite 1 with apical fringe of 4-6 short setae, 2-3 at medioapical angle and 2-4 laterally (Fig. 96C); gonocoxite 2 triangular, with a finely rounded apex, 3 elongate lateral ensiform setae, and 2 dorsal ensiform setae, lateral setae up to 0.28× length of gonocoxite 2; apical nematiform setae elongate, about 0.55× length of gonocoxite 2; bursa copulatrix of moderate size, length subequal to that of common oviduct, with a leftward expansion narrowed toward spermathecal duct insertion, a small crescent-shaped dorsal pouch near vagina and a second broad, apical lobe (position as in *B. perkinsi* [see Fig. 100D]); spermatheca elongate, with basal expansion on reservoir, reservoir about as long as spermathecal duct, covered with fine constrictions (Fig. 96D).
Fig. 97. Distributional records for *B. (Blackburnia) curtipes*.

**Lectotype** ♀ labeled “♀ Disenochus curtipes Type D.S. Waimea, Kauai May 1894. Perkins” (BMNH) hereby designated.

**Distribution.** This species is known only from mesic, leeward forests in Waimea Canyon, and above Kakalau Valley, south to Nualolo, Kauai (Fig. 97).

**Localities.** Perkins found this species in the southern reaches of Waimea Valley during a walk from Waimea to Kaholuamano, as well as near Kaholuamano. More recently it has been found in the Kokee area: Ka Uno o Hua Ridge, Kalalau Lookout, Honopu Trail, and Pihea Trail. All known localities range from 1210 to 1280 m elevation.

**Habits.** The nine known specimens of *B. curtipes* have been collected from February through October. The one record with associated ecological data was a July collection “under logs and rocks.” Perkins correctly predicts the phylogenetic position of this species based on anatomy and ecology: “*D. curtipes* in general form greatly resembles *Atrachycnemis* [*B. sharpi*, *B. perkinsi*, and *B. koebelei*], to which genus I supposed it to belong. It also has the same habits” (Perkins 1913, cxxl). These habits are occurrence on the ground, “beneath prostrate stems of tree-ferns or under logs” (cxxxix).

**Phylogenetic relationships.** Sharp (1903) was the first to note the similarity of this species to *B. sharpi*: though he and Perkins were in close communication throughout their
work on Hawaiian insects. Both authors, then, correctly predicted results of the cladistic analysis that confirm the close relationship of *B. curtipes* to the Maui Nui species allied to *B. sharpi*. The monophyly of these five species—*B. curtipes*, *B. polipoli*, *B. sharpi*, *B. perkinsi*, *B. koebelii* (Fig. 9)—is supported by the broad head relative to pronotal width, absence of scutellar seta, the foreshortened tarsi, increased ventral tarsal vestiture, and presence of a second dorsal pouch in the female bursa copulatrix. *Blackburnia curtipes* is an isolated lineage on Kauai, the most closely related Kauai species to it being the costate species *B. elegans*, *B. micantipennis*, and *B. waialeale*. That *B. curtipes* is a forest floor species, and the other three are often associated with streams or extremely wet open areas, attests to the long separation of these two clades.

**Blackburnia (Blackburnia) polipoli** Liebherr, new species
(Figs. 91, 92D, 99A)

**DIAGNOSIS.** Exhibiting the broad head, quadrate pronotum, and small body size—standardized body length 7.8 mm—of the following three species, but eyes more developed, ocular ratio 1.46, pronotal disc impunctate, elytral striae basally punctate and apically smooth (Fig. 92D); antennal pedicel with 1 outer apical seta and 3 other apical setae; third antennomere glabrous except for apical ring of setae; mesofemur with 3 anteroventral setae.

**DESCRIPTION.** Head broad but eyes moderately convex, neck with slight dorsal impression; single specimen with anterior supraorbital seta lacking on left side, both setae present on right; labrum broadly and shallowly emarginate; mandibles moderately elongate, distance from dorsal condyle to labral apical margin about 1.2× distance from labral margin to mandibular apex; mentum tooth broadly rounded apically.

**Prothorax.** Pronotum with protruded front and hind angles, front angles tightly rounded, hind angles angulate, almost acute (Fig. 92D); basolateral margin sinuate before setose hind angles; anterior lateral seta present on right side, absent from left (single specimen known); lateral marginal depressions obsolete medially, slightly widened near front angles; laterobasal depressions quadrate, with large diffuse punctures, lateral margins raised around basal setae, basal margin definite and continuous caudad impunctate median base; median longitudinal impression obsolete basally, distinctly impressed on disc; anterior transverse impression obsolete.

**Elytra** quadrate, humeri moderately reduced, basal groove rounded on humerus; elytra widest near midlength; subapical sinuation reduced, lateral margin straight to slightly concave near apex; elytral intervals slightly convex; elytral striae partially interrupted basally, longitudinal depressed areas of striae connected by shallower areas, or separated altogether; striae more continuous apically, with punctulae in the single teneral specimen indicated by wider melanized spots in the striae; scutellar seta absent, but pitlike punctures present at base of scutellar and second striae where they meet basal groove; 3 dorsal elytral setae; 9 lateral elytral setae laterad eighth stria.

**Pterothorax.** Metepistemum short, lateral margin 1.4× length of anterior margin; flight wings vestigial, not extended beyond metanotum.

**Legs.** Profemur with 2 posteroventral setae; mesocoxa with 1 ridge seta; mesofemur with 3 anteroventral setae; metacoxa bisetose, mesal seta absent; metafemur with 2 anteroventral
Fig. 98. *Blackburnia* species habitus, dorsal view. A. *B. (Blackburnia) sharpi*. B. *B. (Blackburnia) perkinsi*. C. *B. (Blackburnia) koebelei*. D. *B. (Blackburnia) agilis*. 
Fig. 99A. *B. (Blackburnia) polipoli*, new species, left female gonocoxa, ventral view. Fig. 99B-E. *B. (Blackburnia) sharpi*. B. Male aedeagal median lobe, right lateral view. C. Male aedeagal median lobe, cuventral view. D. Left female gonocoxa, ventral view. E. Female spermatheca with basal lobe on reservoir, ventral view.
setae; tarsi short, basal metatarsomere less than $2 \times$ length of inner tibial spur; tarsomere 5 with ventral setae subequal to depth of tarsomere at point of setal insertion.

**Abdomen.** The lone female has 2 setae each side of apical margin on sternite VII.

**Coloration.** The single specimen is teneral—with head a dark rufous, pronotal disc brunneous and margins testaceous, elytra flavobrunneous; mature beetles no doubt darker.

**Microsculpture.** Head with distinct, leathery isodiametric mesh microsculpture; pronotal disc with distinct transverse mesh microsculpture, median base and laterobasal depressions with a mixture of transverse and isodiametric sculpticells; elytra with distinct isodiametric sculpticells, facets arranged in diagonal or transverse rows.

**Male genitalia.** This species is known from only a single female specimen.

**Female reproductive tract.** Triangular gonocoxite 2 slightly shorter than gonocoxite 1 (Fig. 99A); gonocoxite 1 with apical fringe of 5-6 setae, 3 medial and 2-3 lateral; gonocoxite 2 with 2-3 broad lateral ensiform setae, 1 broad dorsal ensiform seta, lateral setae about 0.17× length of gonocoxite 2; apical nematiform setae elongate, length about 0.50× length of gonocoxite 2; bursa copulatrix moderately elongate, about 1.45× length of common oviduct, with a slightly developed, narrow dorsal pouch near vagina plus a small, more apical pouch near leftward expansion of bursal wall; lumenal wall of bursa with a median ring of microtrichia, ventral portion comprised of 5- and 6-pointed cristate microtrichia; spermatheca moderately elongate, with a small basal lobe on reservoir, length of reservoir about 0.8× length of spermathecal duct.

**Holotype** ♀ labeled “Polipoli Haleakala 5200 ft. Maui / W. M. Giffard VII. 13” (BPBM). The single known specimen is teneral, and badly damaged. Only basal 4 left and basal 2 right antennomeres remain. The left prothoracic leg is lost, the right has the tarsi glued to a card; left mesothoracic leg is intact; right mesothoracic leg has the tarsomeres 3-5 glued to the same card; left metatrochanter and femur are glued to the date locality label, and tibial apex and tarsi are glued to the card with the other tarsomeres.

**Etymology.** The species epithet is taken from the type locality, Polipoli, used as a noun in apposition. Poli is the Hawaiian word for breast, heart, or arms.

**Distribution.** The only known locality is Polipoli, on the southwest rift of Haleakala, East Maui (Fig. 91).

**Habits.** Nothing is known of this species’ way of life, but given the habits of related species, probably geophilic—i.e., restricted to the ground, under tree ferns, logs, rocks, etc.

**Phylogenetic relationships.** This species is adelphotaxon to the species triplet *B. sharpi* (*B. perkinsi + B. koebelei*) (Fig. 9). These species all occupy forest situations on Haleakala, Molokai, and West Maui, respectively (Figs. 91, 94). The range of *B. polipoli* is closest to that of *B. sharpi*, but still distantly isolated on the southwest rift of Haleakala.

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**Blackburnia (Blackburnia) sharpi** (Blackburn), new combination
(Figs. 91, 98A, 99B-E)

*Attractechnemis sharpi* Blackburn, 1878a: 120; Sharp, 1903: 193.

*Anisodontylus cuneatus* Karsch, 1881: 3 (synonymy, Blackburn, 1882: 63).

**DIAGNOSIS.** This and the next 2 species are among the least likely looking members of the tribe Platynini (Fig. 98A-C), with their: 1, broad head with eyes not protruded beyond curvature of gena; 2, extremely short mandibles; 3, anteriorly narrowed, medially...
emarginate labrum; 4, punctate pronotal apex, base, and lateral margins; 5, elytral striae comprising a discontinuous mix of separated longitudinal depressions and more circular pits; 6, granulate isodiametric microsculpture; and 7, small body size. From *B. perkinsi* and *B. koebelei*, *B. sharpi* can be recognized by the almost right, setose pronotal hind angles, reflexed pronotal lateral margin, and more markedly punctate pronotal disk (Fig. 98A). Standardized body length 5.9-6.6 mm.

**Pterothorax.** Metepisternum short, lateral margin 1.5 to 1.6× length of anterior margin; flight wings vestigial, not extended beyond metanotum.

**Male genitalia.** Aedeagal median lobe stout, evenly curved medioventrally; ventral excavation extended to finely pointed, slightly recurved tip (Fig. 99B); basal sagittal crest very small; median lobe very broad, apex broadly rounded (Fig. 99C).

**Female reproductive tract.** Gonocoxa broad, gonocoxite 1 with 1-2 setae at medioapical angle, 2 larger setae laterally (Fig. 99D); gonocoxite 2 with broadly rounded apex, 2-3 broad lateral ensiform setae and 2 broad dorsal ensiform setae, lateral setae about 0.18× length of gonocoxite 2; apical nematiform setae elongate, about 0.6× length of gonocoxite 2; bursa copulatrix about 1.2× as long as common oviduct, with a narrow dorsal pouch with truncate apex near vagina, and a parallel-sided, truncate apical pouch near leftward expansion, extended to entrance of spermathecal duct; bursa with sparse lumenal band of 4- to 5-pointed cristate microtrichia; spermatheca ovoid, reservoir about 0.8× length of spermathecal duct, with a small basal lobe (Fig. 99E).

**Lectotypes.** For *Atrachycnemis sharpi*, lectotype ♂ labeled with 2 parallel lines and “Atrach sharpi” on reverse of card (BMNH) hereby designated. For *Anisodactylus cuneatus*, lectotype ♂ labeled “Type No.: 60820 // Olinda, Finsch Type cuneatus Karsch” (MNHU) hereby designated.

**Distribution.** This species is known only from the leeward mesic forest edge of Haleakala, East Maui (Fig. 91).

**Localities.** This species was last seen in 1902 when Perkins collected three specimens at “Haleakala 4500 ft.” Only Perkins, Blackburn, and Karsch’s collector Finsch ever saw this beetle alive. Recorded localities include Olinda and Perkins’ Haleakala 4000 to 5000 ft. localities ranging from Olinda upward to Ukulele Camp.

**Habits.** Nothing is known about the biology of this species except the generic statement “Atrachycnemis, . . . ‘Like Deropristus, never under stones.’” (Sharp 1903, 289), meaning this species was found under logs or fallen tree fern trunks. Perkins collected *B. sharpi* on 30 March 1894, when he “Collected a few beetles . . .” (Perkins 1894a), with no other mention of the microhabitat of this peculiarly appearing species.

**Phylogenetic relationships.** This species is the adelphotaxon of *B. perkinsi* of Molokai, and *B. koebelei* of West Maui (Fig. 9). This phylogenetic hypothesis supports the sister-area relationship of Molokai and West Maui, as discussed in the treatment of *B. frigida*.

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**Blackburnia (Blackburnia) perkinsi** (Sharp), new combination

(Figs. 94, 98B, 100)

*Atrachycnemis perkinsi* Sharp, 1903: 194.

**DIAGNOSIS.** As *B. sharpi* and *B. koebelei* in: 1, broad head and non-protuberant eyes; 2, extremely short mandibles; 3, anteriorly narrowed, medially emarginate labrum; 4, punctate
pronotal apex, base, and lateral margins; 5, discontinuous elytral striae; 6, granulate microsculpture; and 7, small body size. But differing from both in basolateral margins of pronotum sinuate and pronotal disc less punctate than margins, the cuticular irregularities of the disc tending toward indistinct transverse wrinkles (Fig. 98B). From *B. koebelei*, *B. perkinsi* is diagnosed by the more markedly sinuate pronotal basolateral margin. From *B. sharpi*, it is diagnosed by the glabrous, obtuse-angulate hind pronotal angles, and the generally larger standardized body length, 6.3-7.3 mm.

**Pterothorax.** Metepisternum short, lateral margin from 1.2 to 1.5× length of anterior margin; flight wings vestigial, not extended beyond metanotum.

**Male genitalia.** Aedeagal median lobe stout, medioventral surface nearly straight before markedly downturned apex and acuminate tip, apex 3× as long as depth of apex at point of eversion of internal sac (Fig. 100A); basal sagittal crest absent; median lobe broad, broadly rounded apically (Fig. 100B).

**Female reproductive tract.** Gonocoxa broad, gonocoxite 1 with 1 seta at medioapical angle, 4 larger setae laterally (Fig. 100C); gonocoxite 2 with broadly rounded apex, 3 broad lateral ensiform setae and 2 broad dorsal ensiform setae, lateral setae about 0.21× length of gonocoxite 2; apical nematiform setae elongate, about 0.66× length of gonocoxite 2; bursa copulatrix about 1.2× as long as common oviduct, with a narrow dorsal pouch with parallel sides and truncate apex near vagina, and a triangular apical pouch near leftward expansion extended to entrance of spermathecal duct (Fig. 100D); bursa with sparse lumenal band mostly composed of 3-pointed cristate microtrichia; spermatheca ovoid, reservoir about 1.0× length of spermathecal duct, with a small basal lobe.

**Lectotype** ♂ labeled "♂ Atrachynemis perkinsi. Type D.S. Molokai. 4000 ft. VI.1896. Perkins. 589" (BMNH) hereby designated. Perkins' lot number 589 is described as "Molokai Mts., about 4000 ft. VI '96. contains inter alia several Blackburnia and 1 Atrachynemis" (Anonymous n.d.). The several "Blackburnia" were probably *Blackburnia puncticeps*, which is very similar to *Blackburnia insignis*, but was assigned to *Deropristus* by Sharp (1903).

**Distribution.** This species is known only from the mountains of Molokai, in lands now part of TNCH Kamakou Preserve (Fig. 94).

**Localities.** The five specimens of this species have all been collected by Perkins and labeled as "Molokai 4000 ft." This corresponds roughly to the upper elevations of TNCH Kamakou Preserve in the vicinity of Hanalilolilo eastward across the upper reaches of the various forks of Kawela Gulch.

**Habits.** Perkins (1896c) mentions collecting this species with *B. puncticeps*, and later states "*Atrachynemis [B. perkinsi, etc.] is known only from Maui and Molokai, and has the habits of the *Deropristus [B. puncticeps, etc.] of those islands; in fact they are sometimes found in company, but individuals are not numerous" (Perkins 1913, cxl). Therefore, this species should be sought on the ground, under downed logs and tree ferns. *Blackburnia puncticeps* was noticed in abundance on moss mats during a heavy night rain (16-V-1992, JKL), and so one might predict seeing *B. perkinsi* in that situation.

**Phylogenetic relationships.** This is the adelphotaxon of West Maui's *B. koebelei* (Fig. 9).
Fig. 100. B. (Blackburnia) perkinsi. A. Male aedeagal median lobe with internal sac everted, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view. D. Female bursa copulatrix and spermatheca, dorsal view, showing narrow, truncate dorsal pouch, triangular apical pouch, leftward expansion of bursa, and spermathecal reservoir with a small basal lobe.
Blackburnia (Blackburnia) koebelei (Sharp), new combination
(Figs. 91, 98C, 101)

Atrachycnemis koebelei Sharp, 1903: 194.

DIAGNOSIS. Exhibiting a combination of states seen in the preceding two species (Fig. 98C), sharing the following: 1, head broad, eyes not protruded beyond outline of gena; 2, mandibles short; 3, labrum narrowed apically, medially emarginate; 4, elytral striae discontinuous; 5, microsculpture granulate isodiametric; and 6, body size small, standardized body length 6.6 mm. Differing from B. sharpi in the glabrous, obtuse pronotal hind angles and the more even punctation of the pronotal disc. Differing from B. perkinsi in the straight basolateral pronotal margins before the obtuse hind angles, only a slight sinuation of lateral margin near basal 1/3 of length.

Pterothorax. Metepisternum more elongate than in the preceding 2 species, lateral margin 1.7× length of anterior margin; flight wings vestigial, not extended beyond metanotum.

Male genitalia. Aedeagal median lobe stout, medioventral surface evenly curved, apex not markedly downturned, tapered to a finely acuminate, slightly recurved tip (Fig. 101A); basal sagittal crest absent; median lobe laterally broad at midlength, tapered to moderately broadly rounded apex (Fig. 101B).

Female reproductive tract. Unknown. The single specimen is a male.

Holotype ♂ labeled “♂ Atrachycnemis koebelei Type D.S. Hawaii Koebel” (BMNH). Sharp at first misinterpreted Koebel’s vague labeling to mean this species was from Hawaii Island (1903, 194). He later corrected the type locality (Sharp 1903, 289), after learning from Perkins that Koebel collected the insect in West Maui.

Distribution. The single known specimen was taken in the West Maui mountains, and judging from Koebel’s other, better-labeled collections, it was collected in elevations below 1200 m, somewhere on the west coast above Lahaina. Perkins wrote of his own
(1897) trip to West Maui, "As usual I worked entirely on foot mostly on ridges N. of Lahaina, and in very hot and dry weather found the climbing very laborious, before any fair collecting grounds were reached." These ridges would most likely be near Kanaha and Kahoma Streams, and represent the current best guess as to Koebele's West Maui approach to Puu Kukui (Fig. 91).

**Phylogenetic relationships.** This species is the adelphotaxon of *B. perkinsi* of Molokai (Fig. 9).

*Blackburnia (Blackburnia) agilis* (Sharp), new combination

(*Figs. 98D, 102A, 103, 104*)


**Diagnosis.** This and the following 6 species characterized by the broad head and narrow prothorax (*Figs. 98D, 105, 111A-B*), and absence of dorsal elytral setae in combination with generally reduced microsculpture on dorsal body surface; antennal pedicel with from 3 to 5 apical setae in addition to 1 outer seta; pronotum with nearly obsolete laterobasal and lateral marginal depressions (*Fig. 102*). *Blackburnia agilis* can be diagnosed from the rest of this group by the following combination: 1, basolateral pronotal margins slightly concave, pronotal base trisinuate (*Fig. 102A*); 2, pronotal laterobasal depression with up to 6 minute punctures over mesal surface; 3, discal elytral striae with round pitlike punctures, lateral striae evident, nearly continuous; 4, humeri moderately reduced, basal groove evenly curved on humerus. Standardized body length 8.3-9.4 mm.

**Pterothorax.** Metepisternum broad, lateral margin 1.4× length of anterior margin; flight wings vestigial, not extended beyond metanotum.

**Male genitalia.** Aedeagal median lobe stout, evenly curved medioventrally to short, thick apex abruptly downturned at finely rounded tip (*Fig. 103A*); basal sagittal crest obsolete; median lobe basally broad, tapered to a finely rounded tip, slightly constricted along each apicolateral margin (*Fig. 103B*).

**Female reproductive tract.** Gonocoxa broad, gonocoxite 1 with apical fringe of 3-4 setae, 2 at medioapical angle, 1-2 laterally (*Fig. 103C*); gonocoxite 2 broadly triangular with broadly rounded apex, 2-3 lateral enisiform setae and 2 dorsal enisiform setae, lateral setae 0.26× length of gonocoxite 2; apical nematiform setae elongate, 0.57× length of gonocoxite 2; bursa copulatrix elongate, about 1.6× length of common oviduct, with narrow, parallel-sided dorsal pouch with rounded apex near vagina, a medial band of 3- to 5-pointed cristate microtrichia, and moderate leftward expansion (*Fig. 103D*); spermatheca elongate, reservoir 1.0× length of spermathecal duct, with a large basal lobe.

**Lectotype** σ labeled "σ Disenochus agilis Type D.S. Haleakala 4-5000 ft. 28.3.1894. Perkins." (BMNH) hereby designated. During this trip, Perkins stayed in a mountain house owned by a Mr. Pogue, "considerably higher up than Olinda" (Perkins 1894a). On 28 March 1894, he collected beetles at elevations lower than the mountain house, finding *Mecyclothorax multipunctatus* (Blackburn) and *M. sobrinus* Sharp (Perkins 1894a), as well as *Blackburnia (Metromenus) erro*.

**Distribution.** This species is found from the western edge of the windward and mesic forest of Haleakala, East Maui, eastward at least as far as Kopiliula Stream, Hanawi Natural Area Reserve (*Fig. 104*).
Fig. 102A-G. Pronotum and elytral base, dorsal view, for species of the clade characterized by shiny dorsal surface and absence of dorsal elytral setae: the "big-headed carabids." A. B. (Blackburnia) agilis. B. B. (Blackburnia) medeirosi, new species. C. B. (Blackburnia) anomala.
Fig. 102 (cont.). D. *B. (Blackburnia) brevipes*. E. *B. (Blackburnia) cephalotes*. F. *B. (Blackburnia) lenta*. G. *B. (Blackburnia) terebrata*. 
**Localities.** Known from the western edges of the windward Haleakala rain forest, including Waiohiwi and Waikamoi Gulches, and Ukulele Pipeline; elevations range from 1120 to 1650 m.

**Habits.** During daytime, adults rest under loose bark and associated moss mats on large ohia lehua (*Metrosideros*) trunks, under loose bark of *Acacia koa*, and under logs on mesic soil. At night adults climb vegetation, and have been collected by beating 2-3 m tall native *Rubus* in Koolau Gap (1325 m el.), and *Cheirodendron*, tree fern, low ferns, and ohia lehua in lower TNCH Waikamoi Preserve (1310 to 1650 m el.)
**Phylogenetic relationships.** This species is the adelphotaxon to the remainder of what Sharp and Perkins called the “big-headed carabids” (e.g., Sharp 1900), *B. medeirosi* to *B. lenta* (Fig. 9). The ranges of *B. agilis* and *B. medeirosi* allopatrically span the windward faces of Haleakala, with the distributional border coincident with the recent Hana lava flows along the northeast rift zone (Langenheim & Clague 1987), suggesting that they may actually be recently evolved sister species, not a basal paraphyletic group relative to the other big-headed species. Previous cladistic analysis (Liebherr & Zimmerman 1998) using a slightly different set of taxa (see Cladistic Analysis) hypothesized adelphotaxon status for *B. agilis* and *B. medeirosi*. Additional phylogenetic data on relationships within the big-headed clade are required to resolve this issue.

**Blackburnia (Blackburnia) medeirosi** Liebherr, new species  
(Figs. 102B, 104, 105A, 106)

**DIAGNOSIS.** As *B. agilis*, with broad head and narrow prothorax (Fig. 105A), without dorsal elytral setae and shiny dorsal body surface, but, diagnosed by: 1, pronotal lateral margins slightly expanded outside basal pronotal setae and straight before them; 2, pronotal laterobasal depressions including a large central puncture, with only indistinct mesal punctures; and 3, evanescent lateral elytral setae (Fig. 102B), striae 6 and 7 absent on humerus, reduced to a series of pits in middle 1/3 of their length, and finely inscribed and interrupted in apical 1/3 of elytra. Standardized body length 7.7-9.2 mm.
Fig. 105. Blackburnia species habitus, dorsal view. A. B. (Blackburnia) medeirosi, new species. B. B. (Blackburnia) anomala. C. B. (Blackburnia) brevipes. D. B. (Blackburnia) cephalotes.
DESCRIPTION. Head broad (Fig. 105A), neck with only slight dorsal impression, ocular ratio 1.42; frontoclypeal grooves deepest just caudad frontoclypeal suture, then shallowly arced caudad to anterior supraorbital setae; antennal scape robust, maximum diameter 0.5× length from basal constriction to apex; pedicel with apical ring of 3 setae, plus longer outer seta; labrum with deep concave emargination; mandibles robust, extended 0.4× total length beyond labral apex; mentum tooth triangular with rounded apex.

Prothorax. Pronotum convex, lateral marginal depressions reduced to narrow lateral bead (Fig. 102B); laterobasal depressions evidenced only by single larger puncture and
surrounding depressed area, a few extremely indistinct punctures on mesal surface; hind angles obtusely rounded; median base smooth, basal marginal bead effaced medially; median longitudinal impression finely inscribed, disc depressed along length; anterior transverse impression shallow, broad, median impression continued nearly to anterior margin; anterior marginal bead effaced except toward extremely small, finely rounded front angles. Prosternal process markedly impressed medioventrally.

**Elytra.** Humeri narrow, basal groove recurved at humerus, widest at midlength, subapical sinuature reduced, lateral margin straight before sutural apex; elytral intervals moderately convex, striae continuous and punctate on disc, punctures barely expanding breadth of striae; scutellar striole reduced, impunctate; striae 6 and 7 reduced, seventh reduced to a series of punctures near midlength, nearly obsolete apically; scutellar seta present just mesad base of sutural stria; 10-11 lateral elytral setae.

**Pterothorax.** Metepistemum slightly elongate, lateral margin 1.5 to 1.6× length of anterior margin; flight wings a micropterous strap, without apparent venation, extended beyond metanotum to longitudinal position of third-most anterior lateral elytral seta.

**Legs.** Profemur without anteroventral setae, with 2 posteroventral setae; mesocoxa with 1 ridge seta; mesofemur with 2 anteroventral setae; metacoxa bisetose, mesal seta absent; metafemur with 2 anteroventral setae, dorsoapically glabrous; tarsomers robust, apical breadth of basal metatarsomere 0.4× length; metatarsomere 4 with subequal inner and outer lobes, each 0.4× median length of segment; tarsomers 1-4 ventrolaterally with sparsely distributed, elongate setae, each subequal to depth of tarsomere at point of setal insertion.

**Abdomen.** Stemites II and III with lateral reaches punctate on anterior margins; males with 1 seta each side of stemite VII, females with 2 setae each side.

**Coloration.** Body shiny rufopiceous, legs barely paler, brunneous with smoky infuscation; ventral body surface concolorous with legs; antennae and palpi contrastingly paler than rest of body, flavous.

**Microsculpture.** Vertex shiny, microsculpture obsolete; pronotum with slight traces of transverse microsculpture, median apex and base extremely smooth; pronotal laterobasal depressions with indistinct isodiametric mesh in central puncture and along marginal bead; elytral disc with only the slightest trace of transverse sculpticells under shiny surface, apex and depressions of lateral setae with more distinct parallel lines, but without distinct sculpticells.

**Male genitalia.** Median aedeagal lobe stout, medioventral margin evenly curved to thick apex and rounded, slightly downturned tip (Fig. 106A); basal sagittal crest long and broad; median lobe basally broad, sinuate apicolaterally, resulting in an attenuate apex with rounded tip (Fig. 106B).

**Female reproductive tract.** Gonocoxa broad, gonocoxite 1 with apical fringe of 4-8 setae, 2-4 at medioapical angle, 2-4 laterally (Fig. 106C); gonocoxite 2 broadly triangular with broadly rounded apex, 3-4 lateral ensiform setae and 1-2 dorsal ensiform setae, lateral setae 0.25× length of gonocoxite 2; apical nematiform setae elongate, 0.78× length of gonocoxite 2; bursa copulatrix elongate, about 1.6× length of common oviduct, with broad, indistinct dorsal pouch near vagina (Fig. 106D), a medioventral band of 4- to 5-pointed cristate microtrichia, and moderate leftward expansion; spermatheca elongate, reservoir 0.7× length of spermathecal duct, with a large basal lobe.

Paratypes. MAUl, Haleakala: Haleakala N.P., Kekuewa Hill, 0.7 km N Puu Ahulili, sift humus/moss, 1600 m, 16-V-1993, Liebherr & Medeiros (CUIC, 1); Kipahulu Valley, sifting litter, 1800 m, 08-V-1991, Jessel & Medeiros (CUIC, 1), Central Pali Tr., beating vegetation at night, 1200 m, 29-IV-1991, Liebherr & Medeiros (CUIC, 2), sifting leaf/moss litter, 1200 m, 29-IV-1991, Liebherr & Medeiros (CUIC, 1), beating vegetation at night, 910 m, 30-IV-1991, Liebherr & Medeiros (CUIC, 1), under boards/logs/tarps, 910 m, 30-IV-1991, Liebherr & Medeiros (CUIC, 1), Charlie Camp, mossy tree trunks at night, 1425 m, 25-II-1984, Gagné (BPBM, 1).

Etymology. We take pleasure in naming this species from Kipahulu after Arthur C. Medeiros of Haleakala National Park, to recognize the great assistance and many kindnesses offered during JKL's surveys of Haleakala carabid beetles.

Distribution. This species lives in Kipahulu Valley, and Kekuewa Hill near the southeast margin of windward forest on Haleakala, East Maui (Fig. 104).

Habits. Adults of B. medeirosi are active on mossy ohia lehua (Metrosideros) trunks at night, within sifted humus and moss from tree trunks and crotches. One collection was made from under camp debris at a fence crew’s abandoned tent camp, indicating occupation of terrestrial microhabitats as well.

Phylogenetic relationships. This species is the adelphotaxon of a clade of five big-headed species: B. anomalala to B. lenta (Fig. 9). It is allopatric with all of them, being geographically isolated in Kipahulu Valley, among the eastern reaches of Haleakala.

**Blackburnia (Blackburnia) anomalala (Blackburn), new combination**
(Figs. 102C, 104, 105B, 107)

*Disenochothus anomalus* Blackburn, 1878a: 121; Sharp, 1903: 201.

**DIAGNOSIS.** Differing from *B. agilis* and *B. medeirosi*, and similar to *B. brevipes* and *B. cephalotes* in presence of distinct transverse mesh microsculpture on pronotum and elytra. Differing from the latter two species in: 1, eyes more convex, ocular ratio 1.39-1.43; 2, discal elytral striae more punctate (Fig. 102C-E); 3, striae 6-8 evanescent, reduced to a series of fine punctures; and 4, smaller body size, standardized body length 8.3-9.0 mm.

**Pterothorax.** Metepisternum slightly elongate, lateral margin 0.50× length of anterior margin; flight wings vestigial, not extended beyond metanotum.

**Male genitalia.** Median aedeagal lobe stout, evenly curved medioventrally, ventral excavation extended onto elongate, parallel apex with bluntly rounded tip (Fig. 107A); median lobe basally broad, constricted apicolaterally, tapered to a finely rounded tip, apex therefore attenuate (Fig. 107B).

**Female reproductive tract.** Gonocoxa broad, gonocoxite 1 with apical fringe of 10 setae, 5-6 at medioapical angle, 4-5 small setae laterally (Fig. 107C); gonocoxite 2 broadly triangular with broadly rounded apex, 3 lateral ensiform setae and 2 dorsal ensiform setae, lateral setae 0.25× length of gonocoxite 2; apical nematiform setae very long, 1.0× length of gonocoxite 2; bursa copulatrix moderately elongate, about 1.4× length of common oviduct, with parallel-sided dorsal pouch near vagina (Fig. 107D), a medioventral band of
Fig. 107. *B. (Blackburnia) anomala*. A. Male aedeagal median lobe with internal sac everted, right lateral view. B. Male aedeagal median lobe, euventral view. Stippled portions of male drawings indicate damaged portions of dissection. C. Left female gonocoxa, ventral view. D. Female bursa copulatrix and spermatheca, ventral view, showing parallel-sided dorsal pouch, leftward expansion, and spermathecal reservoir with large basal lobe.
4- to 5-pointed cristate microtrichia, and leftward expansion; spermatheca elongate, reservoir 0.8× length of spermathecal duct, with a large basal lobe.

**Lectotype** ♂ labeled with 3 parallel lines, the top broadest, and a diagonal ink slash across lines at pinhole—Blackburn’s Maui code (Zimmerman 1957)—and “Dis. anomalus” handwritten on reverse of card (BMNH) hereby designated.

**Distribution.** Apparently restricted to elevations of about 1200 to 1500 m near Olinda, judging from collections made only by Blackburn and Perkins (Fig. 104).

**Habits.** Perkins’ only mention of this species is: “March 31st [1894] . . . outside the forest under a dead Koa limb a Disenochus different from former specimens (D. anomalus probably)” (Perkins 1894a). This collection was made between his 5000 ft. elevation camp near Ukulele Camp and Olinda.

**Phylogenetic relationships.** This species is adelphotaxon of the species pair *B. brevipes* of Molokai plus *B. cephalotes* of West Maui (Fig. 9). This is the third instance of a species triplet in Division 1 defining an area relationship wherein Molokai and West Maui are most closely related areas, with Haleakala the adelphotaxon to them (the other two instances are discussed under treatments of *B. frigida* and *B. sharpii*). Consistent with the hypothesis that populations occupying the highest elevation habitats among the three areas were the first to diverge to species level (Liebherr 1997), *B. anomala* is known from 1515 m elevation, whereas *B. brevipes* has been recorded as low as 1180 m, and *B. cephalotes* to 890 m.

**Blackburnia (Blackburnia) brevipes** (Sharp), new combination
(Figs. 102D, 105C, 108, 109)

*Disenochus brevipes* Sharp, 1903: 201.

*Disenochus flavitarsis* Sharp, 1903: 202 (new synonymy).

**DIAGNOSIS.** Of the 3 species with broad head, narrow prothorax, and transverse pronotal and elytral microsculpture, but without dorsal elytral setae (Fig. 105B-D), *B. brevipes* is largest, standardized body length 8.7-10.2 mm; elytral striae with rudimentary punctures (more punctate than those of *B. cephalotes*: Fig. 102D versus E); lateral elytral striae continuous from behind humerus to apex. As the name implies, the tarsomeres are short, robust, the length of metatarsomere 2 subequal to that of inner tibial spur.

**Pterothorax.** Metepistemum broad, lateral margin 1.3 to 1.4× length of anterior margin; flight wings vestigial, not extended beyond metanotum.

**Male genitalia.** Median aedeagal lobe stout, straight medioventrally, ventral excavation extended onto elongate, evenly downturned apex tapered to a finely rounded tip (Fig. 108A); median lobe basally broad, slightly constricted apicolaterally, tapered to a finely rounded tip, apex slightly attenuate (Fig. 108B).

**Female reproductive tract.** Gonocoxa broad, gonocoxite 1 with apical fringe of 10-11 setae, 4-5 at medioapical angle, 5-6 laterally (Fig. 108C); gonocoxite 2 broadly triangular with broadly rounded apex, 3 lateral ensiform setae and 2 dorsal ensiform setae, lateral setae 0.24× length of gonocoxite 2; apical nematiform setae elongate, 0.6× length of gonocoxite 2; bursa copulatrix elongate, about 1.6× length of common oviduct, with parallel-sided dorsal pouch near vagina, a medioventral band of 5-pointed cristate microtrichia, and leftward expansion; spermatheca ovoid, reservoir 0.9× length of short spermathecal duct, with a large basal lobe (Fig. 108D).

Distribution. Found in the mountains of Molokai, and historically as far west near the Meyer Sugar Plantation at Kalae (Fig. 109).

Localities. Within TNCH Kamakou Preserve, known from Hanalilolilo Trail, Puu Kolekole vicinity, and Kaunuohua, those localities encompassing an elevation range of
1180 to 1380 m. Most collections of this insect are in the highest, wettest forest near the rim of Pelekunu Valley.

**Habits.** Adults of *B. brevipes* have been found under rocks lying on the duff under large *Cibotium* tree ferns, in company with *B. puncticeps*. They have more commonly been encountered by sifting or fogging moss mats on trunks of larger ohia trees, or by beating vegetation at night. Commonly associated species in such situations include *B. longipes* and *B. constricta*. Nighttime beating records have come from ferns, *Melicope*, and *Metrosideros* (ohia lehua).

**Phylogenetic relationships.** This species is the adelphotaxon of the West Maui species *B. cephalotes* (Fig. 9).

**Blackburnia (Blackburnia) cephalotes** (Sharp), new combination

(Figs. 102E, 104, 105D, 110)

*Disenochus cephalotes* Sharp, 1903: 201.

**DIAGNOSIS.** Recognizable among the previous species by the almost smooth elytral striae (Fig. 102E), the remnants of punctures in striae 3-7 visible in quarter view, but sutural and second stria appearing smooth in all views; eyes slightly protruded (Fig. 105D), ocular ratio 1.32; elytral striae 6-7 continuous in apical half, more punctate toward base; elytral microsculpture transverse mesh to denser, more parallel transverse lines; tarsomeres short, robust, length of metatarsomere 2 subequal to that of inner tibial spur. Standardized body length 7.9-9.3 mm.

**Pterothorax.** Metepisternum broad, lateral margin 1.4× length of anterior margin; flight wings vestigial, not extended beyond metanotum.

**Male genitalia.** Median aedeagal lobe stout, medioventral margin slightly recurved, ventral excavation extended onto elongate, evenly downturned apex, tapered to a slightly more downturned, finely rounded tip (Fig. 110A); median lobe basally broad, tapered to a finely rounded tip, apex slightly asymmetrical (Fig. 110B).

**Female reproductive tract.** Gonocoxa broad, gonoxonite 1 with apical fringe of 7-8 setae, third seta from mesal margin subapical (Fig. 110D); gonoxonite 2 broadly triangular
Fig. 110. B. (Blackburnia) cephalotes. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view. D. Female bursa copulatrix, dorsal view, showing parallel-sided dorsal pouch near vagina, medial band of cristate microtrichia, leftward expansion, and spermatheca with large basal lobe.

with broadly rounded apex, 3 lateral ensiform setae and 2 dorsal ensiform setae, lateral setae 0.17× length of gonocoxite 2; apical nematiform setae elongate, 0.6× length of gonocoxite 2; bursa copulatrix elongate, about 1.5× length of common oviduct, with parallel-sided dorsal pouch near vagina, a medial band of 3- to 5-pointed cristate microtrichia, and leftward expansion (Fig. 110D); spermatheca elongate, reservoir 0.9× length of short spermathecal duct, with a large basal lobe.

Lectotype ♀ labeled “♀ Disenochus cephalotes Type D.S. West Maui Mts. 4000 ft. Perkins. IV.1894." (BMNH) hereby designated.

Distribution. This species has been found at elevations from 910 to 1275 m on the leeward side of the West Maui mountains, as well as during one of Perkins' visits to Kapilau (Perkins 1894a, 23 April) (Fig. 104).
Localities. Known from Hanaula Springs, Hanaula; Lihau summit, Lihau Natural Area Reserve, and Puu Kukui Trail just above Kualalewelewe Cabin.

Habits. Of the seven specimens, four are from arboreal situations; one beaten from Freycinetia near Kualalewelewe Cabin, and three sifted from mossy ohia lehua (Metrosideros) on Lihau summit. Like the other forest-dwelling big-headed species for which we have data—i.e., B. agilis, B. medeirosi, B. brevipes—individuals of this species spend a substantial portion of their adult life in arboreal microhabitats.
Fig. 113. Distributional records for B. (Blackburnia) terebrata (●), and B. (Blackburnia) lenta (○).

**Phylogenetic relationships.** This West Maui species is the adelphotaxon of the Molokai species *B. brevipes*.

*Blackburnia (Blackburnia) terebrata* (Blackburn), new combination
(Figs. 102G, 111A, 112, 113)
*Disenochus terebratus* Blackburn, 1881 (March): 227; Blackburn & Sharp, 1885: 214.
*Prodisenochus terebratus* Sharp, 1903: 211.

**Diagnosis.** Immediately recognizable among all species of the subgenus by presence of both the lateral and basal pairs of pronotal setae (Fig. 102G), and 4 large, flat-bottomed depressions in anterior half of eighth elytral stria; pronotum with lateral marginal bead reduced, lateral depression extremely narrow; basal marginal bead effaced medially; elytral basal groove obsolete laterad scutellum, lateral elytral depression ended on humerus; elytra parallel-sided, sides very steep; discal elytral striae punctate, punctures deep and pitlike; dorsal body surface shining, microsculpture obsolete (Fig. 111A). This species is also unique in the occasional unilateral presence of middle dorsal elytral seta; anterior and posterior setae absent. Standardized body length 6.1-6.7 mm.

**Pterothorax.** Metepisternum with several large punctures, short, nearly trapezoidal, lateral margin length 1.9 to 2.0× anterior; flight wings vestigial, not extended beyond metanotum.
Male genitalia. Median aedeagal lobe stout, straight to evenly curved medioventrally, elongate apex terminated in an acuminate tip (Fig. 112A); basal sagittal crest short and narrow; median lobe basally broad, evenly tapered to a rounded apex (Fig. 112B).

Female reproductive tract. Gonocoxite 1 with apical fringe of 5-6 widely spaced setae (Fig. 112C); gonocoxite 2 broadly triangular with broadly rounded apex, 3 lateral ensiform setae and 1-2 dorsal ensiform setae, lateral setae 0.17× length of gonocoxite 2; apical nematiform setae elongate, 0.6× length of gonocoxite 2; bursa copulatrix elongate, about 2.0× length of common oviduct, with horseshoe-shaped dorsal pouch near vagina, a dense medial band of 3- to 5-pointed cristate microtrichia, and leftward expansion (Fig. 112D); spermatheca ovoid, reservoir 0.6× length of spermathecal duct, with a large basal lobe.

Lectotypes. For *Disenochus terebratus*, lectotype ♀ on card with 3 parallel lines, the top line broadest, and an ink slash across lines at pin—Blackburn’s Maui code (Zimmerman 1957)—and “420” handwritten on back (BMNH) hereby designated. A second label reads “Sandwich Is.; 82/45 Disenochus terebratus Blkb.” For *Promecoderus fissulatus*, lectotype ♀ labeled “Type No.: 60821 // Olinda, Finsch fissulatus Karsch” (MNHU) hereby designated.

Distribution. This species was collected during the nineteenth century in the area near Olinda, on the northwest edge of the windward forest of Haleakala, East Maui (Fig. 113).

Localities. Restricted to Olinda, and Perkins’ Haleakala 4000 ft. (1210 m) and 5000 ft. (1515 m) localities—i.e., above Olinda and near Ukulele Camp.

Habits. Perkins collected one specimen under a log, 7-IV-1894 between his camp at Pogue’s mountain house and Olinda (Perkins 1894a). He mentions collecting the species again in May 1896 (Perkins 1896b), but does not elaborate regarding its habits. This lot of beetles (612) also contained *B. erro, B. frigida, B. rupicola*, and *B. sphodridiformis*, suggesting collecting across the forest edge ecotone. Perkins later recounts that this species “is found... beneath or in decaying logs and appears to be rare” (Perkins 1913, cxli).

Phylogenetic relationships. This species is the allopatric adelphotaxon of *B. lenta* (Fig. 9). The distribution of each species is (or was) limited to western Haleakala: *B. terebrata* along the western edge of the windward forest at about 1500 m elevation, *B. lenta* well above timberline at nearly 3000 m elevation, just west of the summit caldera (Fig. 113).

**Blackburnia (Blackburnia) lenta** (Sharp), new combination

(102F, 111B, 113, 114)

*Pseudobroscus lentus* Sharp, 1903: 196.


DIAGNOSIS. Among species with broad head and without dorsal elytral setae, *B. lenta* (Fig. 111B) is unique is having the pronotal lateral marginal bead nearly completely effaced, with only remnants of a groove in one specimen visible near obsolete front angles (Fig. 102F); humeri very reduced; basal groove of elytra difficult to trace laterad scutellum; deep elytral striae with deep pitlike punctures; dorsal microsculpture greatly reduced, body surface shiny. Standardized body length 9.7 mm.

Pterothorax. Metepisternum broad, lateral margin 1.6× length of anterior margin; flight wings vestigial, not extended beyond metanotum.
Fig. 114. *B. (Blackburnia) lenta*. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view. D. Female bursa copulatrix, dorsal view, showing rectangular dorsal pouch near vagina, limited field of cristate microtrichia on left side of bursa, leftward expansion, and spermatheca with large basal lobe.

**Male genitalia.** Median aedeagal lobe stout, medioventrally recurved, elongate apex downturned from median shaft, terminated in an acuminate tip, apex extended $4.33 \times$ its depth past opening of internal sac (Fig. 114A); basal sagittal crest elongate, broad; median lobe basally broad, slightly constricted apicolaterally, apex slightly attenuate, tip acuminate (Fig. 114B).

**Female reproductive tract.** Gonocoxite 1 with apical fringe of 6-7 widely spaced setae, several of the setae split apically (Fig. 114C); gonocoxite 2 broadly triangular with broadly
rounded apex, 3-7 lateral ensiform setae and 1-2 dorsal ensiform setae, lateral setae 0.25×
length of gonocoxite 2; apical nematiform setae elongate, and third seta present unilaterally,
longest seta 0.5× length of gonocoxite 2; bursa copulatrix elongate, about 2.0× length of
common oviduct, with rectangular dorsal pouch near vagina, a small field of sparsely
distributed 5-pointed cristate microtrichia on left side of bursa, and a large leftward
expansion narrowed toward entrance of spermathecal duct (Fig. 114D); spermatheca ovoid,
reservoir 0.5× length of spermathecal duct, with a large basal lobe.

**Lectotype** § labeled “♀ Pseudobroscus lentus Type D.S. Haleakala 10000 ft. 11.iv.1894.
Perkins. 346.” (BMNH) hereby designated. On this day Perkins hiked from Pogue’s
mountain house above Olinda to the top of Haleakala, by way of Ukulele Cave, in which
Blackburn had stayed. The series of *B. lenta* was taken at some point above the cave but not
within 200 ft. elevation of the summit, in company with *B. frigida* (Perkins 1894a).

**Distribution.** The two series totaling 5 specimens are from near the summit of Haleakala,
East Maui (Fig. 113), presumably along the road to the summit.

**Localities.** Found only near the summit of Haleakala at 2880 to 3030 m elevation.

**Habits.** Perkins collected two specimens on 9-IV-1894 when he walked up from Olinda
and collected from 9000 ft. to the summit (Perkins 1894a), additionally collecting *B.
rupicola* and *B. frigida*. He returned two days later and found three more specimens
between 9500 ft. and the summit. He collected only during the day, and found these beetles
under stones, though “everything has to be exactly right as to position of rock, dampness,
etc., for this insect” (Sharp 1903, 289). Later he notes “it was found under stones, a few
weeks after the disappearance of the snow-cap” (Perkins 1913, cxl). Beetles of this species
have not been collected since.

**Phylogenetic relationships.** This species is the adelphotaxon of *B. terebrata* (Fig. 9).

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**Blackburnia (Blackburnia) micantipennis** (Sharp), new combination
(Figs. 111C, 115, 116)

**Disenochus micantipennis** Sharp, 1903: 206.

**DIAGNOSIS.** This species looks superficially like *B. costata* because of the sinuate, pitted
pronotum and costate elytral intervals (Figs. 49B, 111C), but differs—along with *B.
waialeale*—in: 1, antennomere 3 covered with sparse pelage of setae; 2, dorsal elytral setae
absent; 3, microsculpture obsolete on vertex of head, elevated portions of pronotal disc, and
eytral intervals; 4, elytral striae completely punctate to apex; and 5, flight wings vestigial,
not extended beyond metanotum. Markedly elevated elytral costae are present throughout
the length of the sutural, fifth, and seventh intervals, and basally on the interval 3. This
species is distinguished from its adelphotaxon, *B. waialeale*, by broader humeri (Fig. 111C-
D), and presence of basal pronotal setae. *Blackburnia waialeale* has more distinct elytral
carinae, with interval 3 carinate throughout its length, and smaller carinae on intervals 6 and
8. Standardized body length 6.9-8.4 mm.

**Pterothorax.** Metepisternum punctate, quadrate, lateral margin 1.6 to 1.9× length of
anterior margin; flight wings vestigial, not extended beyond metanotum.

**Male genitalia.** Aedeagal median lobe gracile, recurved medioventrally, ventral
excavation extended onto moderately elongate apex tapered to a broadly rounded tip (Fig.
CARABIDAE PART I: PLATYNINI

Fig. 115. *B. (Blackburnia) micantipennis*. A. Male aedeagal median lobe, internal sac everted, right lateral view. B. Male aedeagal median lobe, evventral view. C. Left female gonocoxa, ventral view. D. Female bursa copulatrix, ventral view, showing horseshoe-shaped dorsal pouch (dp) near vagina, lateral bursal glands (bg), medial band of cristate microtrichia (cmt), leftward expansion (ex), and elongate spermatheca (sp).

115A); basal sagittal crest moderately elongate, broad; median lobe slightly constricted on left margin near apex, tapered to a finely rounded tip (Fig. 115B).

**Female reproductive tract.** Gonocoxa elongate, gonocoxite 1 with apical fringe of 6-7 setae in single series (Fig. 115C); gonocoxite 2 parallel-sided, narrow, apex rounded, with 3 peglike lateral ensiform setae, and 1-2 peglike dorsal ensiform setae, lateral setae 0.14× length of gonocoxite 2; apical nematiform setae elongate, 0.50× length of gonocoxite 2; bursa copulatrix elongate, 1.85× length of common oviduct, with a horseshoe-shaped dorsal
pouch at apex of vagina, paired lateral bursal glands, a median ring of spikelike, 2-, and 4-pointed cristate microtrichia, and a moderate leftward expansion (Fig. 115D); spermatheca elongate, reservoir subequal to length of spermathecal duct, without a basal lobe.

**Lectotype** ♂ labeled “♂ Disenochus micantipennis Type D.S. Mts. Waimea, Kauai. 4000 ft. V.1894. Perkins” (BMNH) hereby designated.

**Distribution.** This species is known only from the more mesic, leeward reaches of Waimea Canyon, Kauai (Fig. 116).

**Localities.** Recorded from above Waimea, Kaholuamano, Waialae Stream, the high plateau along Mohihi-Waialae Trail above Waialae Cabin, and Koaiie Stream. Known localities range in elevation from 605 to 1270 m.

**Habits.** Nothing is recorded about the way of life of this species in Perkins’ notes. This species’ aggregate collecting history includes a much reduced presence in twentieth-century samples: 1894 (78 specimens); 1895 (17 specimens); 1896 (7 specimens); 1911, 1914, 1919 (1 specimen each); 1935 (3 specimens). Based on the superficial similarity to *B. costata*, combined with records near streams, riparian tendencies are predicted for this species.
Phylogenetic relationships. This species is the adelphotaxon of *B. waialeale* (Fig. 9). The two species are allopatrically distributed, *B. micantipennis* along tributaries of the Wai'anae River, *B. waialeale* in the summit bog of Mt. Waialeale (Fig. 116). These two species are the adelphotaxon of the Kauai species *B. elegans* plus the Oahuan *B. kamehameha*. In turn, these four species comprise the adelphotaxon of five species distributed from Oahu to Maui Nui (*B. insignis* to *B. kipahulu* of Fig. 9). All nine species are strictly terrestrial, being found on the ground surface, on moss mats, or resting under objects on the ground. The phylogenetic affinity of these species is therefore a good predictor of their ecological preference.

*Blackburnia (Blackburnia) waialeale* Liebherr, new species
(Figs. 111D, 116, 117)

DIAGNOSIS. Like *B. micantipennis* in the setose third antennomere, pronotum with markedly sinuate basolateral margins (Fig. 111C-D), absence of dorsal elytral setae, costate elytral intervals 1, 5, and 7, and absence of microsculpture on vertex and pronotal disc outside of discal punctures, but, with: 1, pronotum narrower; 2, elytral humeri narrower, basal groove not markedly carinate on humerus; 3, third elytral interval costate throughout length, not just basally; 4, metafemur with increased setation, 4-5 anteroventral setae, and 13-17 dorsoapical setae, arranged in 4-5 transverse rows of 3-5 setae. *Blackburnia elegans* is also a Kauaian species with pitted pronotum, no pronotal setae, and costate elytral intervals, but it has pronotal lateral marginal depressions obsolete, and elytral costae much more rounded (Fig. 118A). Standardized body length 8.5-8.8 mm.

DESCRIPTION. Head broad, vertex elevated as a callus, bordered anteriorly by bilateral pairs of concentric wrinkles, frontoclypeal grooves obsolete anteriorly, present from frontoclypeal suture to anterior supraorbital setae as a diagonal wrinkle; eyes small, slightly convex, appearing laterally elevated by supraorbital groove extended to behind eye, ocular ratio 1.33; antennal scape with elongate dorsal seta and 1-2 shorter apical setae; antennal pedicel with longer outer seta and apical ring of up to 8 setae; third antennomere sparsely covered with fine setae; labrum shallowly and broadly emarginate; apical two maxillary palpomeres and apical labial palpomere sparsely covered with fine, elongate setae; mentum tooth rounded apically.

Prothorax. Pronotum with a moderately broad, irregularly punctate, lateral marginal depression, and without lateral setae; basolateral margin markedly sinuate, hind angles obtusely rounded; laterobasal depressions densely punctate, bordered laterally by smooth elevated margin, bordered behind by very fine, indistinct marginal bead; basal marginal bead traceable inside laterobasal depressions, effaced medially; median base irregularly covered with rounded pits, their inner surfaces covered with cuticular wax—the surface can be scratched with a minuten—and therefore appearing glaucous; median longitudinal impression obscured basally due to large pits, finely inscribed on disc, defining the middle of an elongate depressed area covered with irregular pits, some joined together to form irregular transverse wrinkles; anterior transverse impression traceable as a linear, depressed series of pits extended nearly to protruded, rounded front angles; anterior marginal bead complete, but depressed relative to cuticle just caudad; area adjacent to anterior marginal bead lined with very small punctures. Prosternal process medioventrally concave.
Elytra. Humeri narrow, elytra elongate-ovoid, subapical sinuation indicated by slightly concave lateral margin before angulate sutural apex associated with tight fusion of the two elytral halves at median suture; basal groove markedly recurved on humerus, but anterior margin of groove not markedly elevated; sutural interval greatly elevated, highest at fused suture; angulate costae on intervals 3, 5, and 7, lower rounded costae on intervals 6 and 8, intervals 2 and 4 flat, though irregularly wrinkled in association with strial punctures; elytral striae deeply punctate throughout their length, punctures separated by width of their diameters; scutellar seta present just laterad elevated scutellar striole, dorsal elytral setae absent; 13-15 lateral elytral setae.

Pterothorax. Metepisternum punctate, quadrate, lateral margin 1.3 to 1.8× length of anterior margin; flight wings vestigial, not extended beyond metanotum.

Legs. Profemur without anteroventral setae, with 3 posteroventral setae; mesocoxa with 1 ridge seta; mesofemur with 4 anteroventral setae; metacoxa trisetose, with 2 lateral setae and 1 mesal seta; metafemur with 4-5 anteroventral setae, and 13-17 dorsoapical setae, setae arranged starting with a single seta just beyond midlength, and 3-4 irregular, progressively apical transverse rows of 3-5 setae; tarsomeres parallel-sided, tarsomere 4 only slightly expanded due to apical lobes; metatarsomere 4 with subequal inner and outer lobes, outer lobe 0.9× median basal length of segment; tarsomeres 1-4 with densely packed, thick, ventrolateral setae, without a distinct median space; tarsomere 5 with ventrolateral rows of 6 setae, each subequal to depth of tarsomere at point of setal insertion.

Abdomen. Sternites II-IV with large punctures laterally; males with 1 apical seta each side sternite VII, female with 2 setae each side.

Coloration. Head and pronotal disc piceous, shining, elytra slightly paler, rufopiceous, these contrasted against testaceous palpi, basal 3 antennomeres, and legs; ventral surface of head and prothorax piceous, metathorax and abdominal base rufopiceous, abdominal sternites testaceous toward abdominal apex; coxae brunneous to rufous, elytral epipleura brunneous basally, testaceous toward apex.

Microsculpture. Vertex with indistinct transverse mesh microsculpture on callus, labrum with evident transversely stretched sculpticells in irregular transverse rows; pronotal disc with slight transverse lines on cuticle between pits; elytra with indistinct parallel lines around pits on disc, transverse sculpticells evident in pits lacking cuticular wax.

Male genitalia. Aedeagal median lobe gracile, straight to slightly curved medioventrally, ventral excavation continued onto elongate apex slightly downturned just before finely rounded tip (Fig. 117A); basal sagittal crest obsolete; median lobe gracile in ventral view as well, evenly tapered to a narrowly rounded tip (Fig. 117B).

Female reproductive tract. Gonocoxite I with apical fringe of 6 setae (Fig. 117C); gonocoxite 2 parallel-sided, apex broadly rounded, with 3 peglike lateral ensiform setae and 2 peglike dorsal ensiform setae, lateral setae 0.14× length of gonocoxite 2; apical nematiform setae very long, 0.82× length of gonocoxite 2; bursa copulatrix elongate, 1.65× length of common oviduct, with lateral bursal glands, broadly rounded dorsal pouch, medial band of 2- and 3-pointed cristate microtrichia, and slight leftward expansion; spermatheca elongate, reservoir 0.9× length of spermathecal duct, without a basal lobe (Fig. 117D).

Holotype ♀ labeled “HI: Kauai Waialeale summit 16-V-1995 lot 02 1515-1530 m mossy creekbank at night J.K. Liebherr” (CUIC).

Paratypes. KAUAI: Waialeale, 1515 m, 21-XII-1969, Rice (BPBM, 3), summit, under rocks on clay, 1530 m, 16-V-1995, Liebherr (CUIC, 4).
Fig. 117. *B. (Blackburnia) waialeale*, new species. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view. D. Female bursa copulatrix, ventral view, showing lateral bursal glands (bg), broadly rounded dorsal pouch near vagina (dp), medial band of cristate microtrichia (cmt), leftward expansion (ex), and elongate spermatheca without basal lobe.

**Etymology.** The species epithet is taken from the type locality, treated as a noun in apposition. Waialeale means rippling water in Hawaiian.

**Distribution.** This species is so far known only from the summit area of Mt. Waialeale (Fig. 116). Its apparent restriction to that area allows definition of a Waialeale Summit area of endemism on Kauai: that area predicted to exist based on the unique Metrosideros/Dubautia/Oreobolus bog association occurring at the summit (Asquith 1995).

**Habits.** This beetle was found under rocks on clayish volcanic soil on rock outcroppings in the summit area of Mt. Waialeale. One specimen was taken at night walking on a rocky creekbank in one of the gulches near the summit plateau. No specimens were found in numerous sift samples of arboreal mosses, suggesting that this species is strictly terricolous, at least during the limited period during which it was encountered in May 1995. If this species proves to be restricted to terrestrial microhabitats involving moist, open soil, its ecological preference would be analogous to that of *Blackburnia frigida* of Haleakala.
Blackburnia frigida has been found almost exclusively above timberline, suggesting that B. waialeale may possess a relictual tundra distribution that was much more extensive when Mt. Waialeale achieved its greatest stature—2600 m—at the end of its shield-building volcanic stage (Carson & Clague 1995). Similarly, the closest relatives of B. frigida—B. viridis of West Maui and B. munroi of Molokai—are restricted to creekbeds and open soil associated with land slips, again probably relictually distributed habitats that were much more extensive when Kamakou and Puu Kukui volcanoes attained their greatest elevation—3300 m and 3400 m, respectively—and were topped by abundant open habitats above timberline.

Phylogenetic relationships. This species is the adelphotaxon of B. micantipennis (Fig. 9).

Blackburnia (Blackburnia) elegans (Sharp), new combination
(Figs. 118A, 119, 120)
Anchotefflus elegans Sharp, 1903: 198.

DIAGNOSIS. This species is diagnosed by: 1, absence of lateral pronotal setae; 2, slightly sinuate pronotal basolateral margins, basal marginal bead continuous; 3, very narrow elytral humeri; 4, convex, nearly costate elytral intervals (Fig. 118A), and completely punctate elytral striae; and 5, absence of discernible microsculpture on frons, vertex, and elevated portions of pronotal disc and elytral intervals. Standardized body length 7.7-9.6 mm.

Pterothorax. Metepisternum punctate, narrow and elongate, lateral margin 1.8 to 2.2× anterior margin; flight wings vestigial, not extended beyond metanotum.

Male genitalia. Aedeagal median lobe gracile, straight medioventrally, deep ventral excavation extended onto short, thick apex tapered to a bluntly rounded tip (Fig. 119A); basal sagittal crest short, moderately broad; median lobe moderately broad basally, evenly narrowed to pointed tip (Fig. 119B).

Female reproductive tract. Gonocoxa elongate, gonocoxite 1 with apical fringe of 8-10 setae, setae in 2 or 3 series on medioapical angle (Fig. 119C); gonocoxite 2 narrow, apex pointed, with 3-4 peglike lateral ensiform setae and 2-3 dorsal ensiform setae, all ensiform setae 0.11× length of gonocoxite 2; apical nematiform setae elongate, 0.53× length of gonocoxite 2; bursa copulatrix elongate, about 1.5× length of common oviduct, with a small, membranous, parallel-sided dorsal pouch, no apparent bursal microtrichia, and a large leftward expansion of bursal wall just basal entrance of spermathecal duct (Fig. 119D); spermatheca ovoid, reservoir 0.6× length of spermathecal duct, without a basal lobe.

Variation. Specimens considered B. elegans from Mt. Waialeale summit are the largest seen for this species, ranging from 8.5 to 9.6 mm standardized body length. The Mt. Waialeale specimens also exhibit much less punctuation on the vertex and neck; some specimens have only narrow longitudinal bands of indistinct punctures just mesocaudad the posterior supraorbital setae. Conversely, the smallest specimens from the west side of the island—e.g., from Pihea Trail just east of Kalalau Pali—have much broader longitudinal bands of punctures mesocaudad the posterior supraorbital setae, those bands connected by a transverse band of punctures on the dorsally impressed neck. Specimens from Alakai Swamp Trail at Kawaikoi Stream, and from Kaholuamano (i.e., Waialae Cabin area) exhibit
Fig. 118. *Blackburnia* species habitus, dorsal view. A. *B. (Blackburnia) elegans*. B. *B. (Blackburnia) kamehameha*, new name. C. *B. (Blackburnia) insignis*. D. Elytron holotype of *B. insignis* var. *kaalensis*. 
intermediate levels of vertex punctation. This east-west transect also involves a change in elevation, with eastern sites near the summit of Waialeale being the highest. More specimens from more sites, at a variety of elevations, are required to test for environmental or geographic variables that might be associated with this morphological variation.

**Lectotype** σ labeled “♂ Anchotefflus elegans Type D.S. Kauai. VII.1896. Perkins. 631” (BMNH) hereby designated. Perkins’ lot 631 was collected on the “high plateau” (Anonymous n.d.), meaning Mohihi-Alakai Trail above Waialae Cabin, north of the headwaters of Waialae River.
**Distribution.** Found across the Alakai Swamp from Waialeale to Pihea, as well in more leeward reaches of Waimea Canyon, Kauai (Fig. 120).

**Localities.** Found across the highest portions of the Kauai caldera, including Kaholouamano, Waialae River and Cabin, high plateau along Mohihi-Waialae Trail, Waialeale summit, Alakai Swamp Trail near Kawaikoi Stream, and Pihea Trail. These sites span 1120 to 1545 m elevation.

**Habits.** This species lives strictly on the ground, and has been found under logs, rocks, and moss mats, often in very wet situations such as wet swales in boggy habitat. Beetles have also been found under rocks along a stream bed.

**Phylogenetic relationships.** This species is geographically isolated from its adelphotaxon, *B. kamehameha* of Oahu (Fig. 9).
**Blackburnia (Blackburnia) kamehameha** Liebherr & Zimmerman, new name  
(Figs. 118B, 121, 122)

*Anchotefflus gracilis* Sharp, 1903: 195 (junior homonym of *Atelothrus gracilis* Sharp, 1903).

**Diagnosis.** An exceedingly slender, completely piceous beetle with elongate legs (Fig. 118B), characterized by a smooth pronotal disc and punctate pronotal base and laterobasal depressions; absence of both lateral pronotal setae; extremely reduced humeri and elongate elytral apex; punctate elytral striae; absence of dorsal elytral setae; and a deep pit set into the shiny cuticle at the suture between sternites II and III. Standardized body length 8.4-9.0 mm. The sister species, *B. elegans* of Kauai, differs in the paler legs, punctate pronotal disc, more quadrate pronotal hind angles, broader humeri (Fig. 118A), and punctate sternite II.

**Pterothorax.** Mesepisternum slightly punctate, other sternites smooth; metepisternum smooth, variously elongate, lateral margin 1.7 to 2.3× length of anterior margin; flight wings vestigial, not extended beyond metanotum.

**Male genitalia.** Aedeagal median lobe gracile, straight medioventrally, apex elongate, extended 4.0× thickness of apex at opening of internal sac to a finely rounded tip (Fig. 121A); basal sagittal crest short, narrow; median lobe narrow laterally, evenly tapered to a finely rounded tip (Fig. 121B).

**Female reproductive tract.** Gonocoeca elongate, gonocoxite 1 with apical fringe of 8-9 setae, 6 setae at medioapical angle (Fig. 121C); gonocoxite 2 narrow, subparallel, apex finely rounded, with 3 peglike lateral ensiform setae and 2 dorsal ensiform setae, lateral ensiform setae 0.14× length of gonocoxite 2; apical nematiform setae elongate, 0.77× length of gonocoxite 2; bursa copulatrix elongate, about 1.67× length of common oviduct, with a small, membranous, triangular dorsal pouch, a medial band of 3- and asymmetrical 4-pointed cristate bursal microtrichia, and an elongate left-directed diverticulum (Fig. 121D); spermatheca elongate, reservoir 1.1× length of spermathecal duct, without a basal lobe.


**Etymology.** The replacement name for this species honors Kamehameha, who conquered Oahu and Maui from Hawaii, and achieved his last victory at Nuuanu Pali, where his army vanquished the Oahuan. *Blackburnia kamehameha* occupies the north Koolau’s, its ancestors having colonized Oahu from Kauai. As such, *B. kamehameha*’s ancestry stems from the only Hawaiian kingdom Kamehameha failed to subjugate.

**Distribution.** Known mostly from the northern Koolau Mountains of Oahu (Fig. 122).

**Localities.** Recorded from Kawailoa Gulch, Kaiapapa, Kaluanui, Castle Trail, Poamoho Trail, Punaluu, Kahana, Puu Kaumakua, Schofield-Waikane Trail, and Puu Keahiakawehi massif at Tripier Ridge. Known from localities ranging from 700 to 850 m elevation.

**Habits.** Like *B. elegans*, this species lives on the ground. Beetles have been recorded under rocks on the ground, walking on open trail at night, and perching on moss mats at night. Perkins records this species “on rocks in a mountain stream after a heavy spate, and [it] probably lives beneath stones on the margins of these streams” (Perkins 1913, cxl). The beetles’ thin body shape, irregular cuticle, and stationary stance on moss mats makes them cryptic in that situation, looking like the fruiting structures of the moss.

**Phylogenetic relationships.** *Blackburnia kamehameha* is the adelphotaxon of *B. elegans* of Kauai (Fig. 9).
Fig. 121. *B. (Blackburnia) kamehameha*, new name. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, evventral view. C. Left female gonocoxa, ventral view. D. Female bursa copulatrix, ventral view, showing medial band of cristate bursal microtrichia, large leftward expansion, and spermatheca.

*Blackburnia (Blackburnia) insignis* Sharp
(Figs. 118C-D, 122, 123)

*Blackburnia insignis* Sharp, 1878: 179; Blackburn & Sharp, 1885: 213; Sharp, 1903: 191.

*Blackburnia insignis* var. *kaalensis* Sharp, 1903: 191 (new synonymy).

DIAGNOSIS. Of species lacking dorsal elytral setae and exhibiting large pitlike punctures on the pronotum and in the elytral striae, *B. insignis* is diagnosed by: 1, vertex impunctate, broad depression mesad anterior supraorbital seta; 2, eyes slightly convex, ocular ratio 1.30; 3, pronotal basolateral margins sinuate, hind angles obtuse (Fig. 118C); 4, dorsal surfaces of tarsomeres sparsely covered with fine setae. Standardized body length 10.3-10.6 mm.
Pterothorax. Mesepisternum and metepisternum deeply punctate, metepisternum elongate, lateral margin 1.8 to 2.2× length of anterior margin; flight wings vestigial, not extended beyond metanotum.

Male genitalia. Aedeagal median lobe gracile, broadly expanded medioventrally, ventral excavation extended onto evenly downturned, elongate apex tapered to an acuminate tip, tip extended 3.33× thickness of apex at opening of internal sac (Fig. 123A); basal sagittal crest elongate, broad; median lobe moderately broad basally, tapered to a finely rounded tip (Fig. 123B).

Female reproductive tract. Gonocoxa elongate, gonocoxite 1 with apical fringe of 9-10 setae, inner 2 in double series (Fig. 123C); gonocoxite 2 elongate, parallel-sided, apex rounded, with 3-5 peglike lateral ensiform setae and 2 peglike dorsal ensiform setae, lateral setae 0.10× length of gonocoxite 2; apical nematiform setae moderately elongate, 0.42 to 0.43× length of gonocoxite 2; bursa copulatrix elongate, 1.6× length of common oviduct, with small, apically rounded dorsal pouch, medial band of 3- to 6-pointed cristate microtrichia, and a leftward expansion 2/3 distance from base to spermathecal duct entrance; spermatheca ovoid, reservoir 0.60× length of spermathecal duct, with a small basal lobe.
Fig. 123. B. (Blackburnia) insignis. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view.

Types. For Blackburnia insignis, holotype ♀ labeled “Blackburnia insignis D.S. Oahu Dec'. 1877 T. Blackburn” (BMNH). A “?” symbol is in pencil on card, the rest in ink. There is a matching ♂ specimen (MNHP) that corresponds to the specimen Sharp (1878) mentions in his description, but evidently did not have before him at description. Sharp (1903) states that Blackburn collected the pair in July, so the “Dec.” label date must be in error. As the paper describing this species was published in January 1878, perhaps this date corresponded to the time of preparation, labeling, and description. For Blackburnia insignis kalensis, holotype labeled “422, Kaala Mts. Oahu, 2000 ft. Perkins III 1893” (BMNH).

Nomenclatural note. Sharp (1903, 191) described the variety kalensis based on fused elytra found at 605 m elevation in Waianae Valley, leeward Mt. Kaala (Perkins 1892). This variety cannot be differentiated geographically from the nominate form, as both are found on the Mt. Kaala massif. Moreover, we find Sharp’s diagnostic characters for recognition of this variety unconvincing, as the elytral intervals are little different (Fig. 118D) from those of other Waianae Range specimens collected later by Perkins (Fig. 118C). As Sharp presented the name in the combination Blackburnia insignis var. kalensis before 1961, it is interpreted as a subspecific name synonymous with nominate B. insignis.

Distribution. This species has historically been found on the Mt. Kaala massif, and sparsely along the Koolau Mountain Range, Oahu (Fig. 122). Perkins wrote the following about collecting these elytra in March 1893, “On almost my last collecting day around Kaala I found in one gulch vast numbers of elytra of a fine looking Carabid, but none alive,
so that either it was out of season, or else had ceased to inhabit that particular gulch
[Blackburnia insignis var. kaalensis]" (Perkins 1892, 12). The presence of many elytra of
this otherwise rarely collected species suggests that Perkins found the remains of beetles
derived from generations that lived over a number of years.

Localities. In the Waianaes, known from 600 to 900 m on Mt. Kaala, with most records
from the leeward Waianaee Valley. In the Koolaus, recorded from Honolulu (Perkins), no
doubt meaning the mountains above Honolulu, and from Poamoho Trail (elytron only, VI­
1955, Ford, BPBM). This latter record is the only twentieth-century collection. That this
species never seems to have occupied the highest elevation habitats on Mt. Kaala probably
spelled its doom in the face of destruction by big-headed ant, Pheidole megacephala, and
other arthropod invaders.

Habits. As with the prior two species, all records are associated with ground-level
situations—i.e., under rocks. Thus we infer that this species inhabited strictly terrestrial
microhabitats. This restriction to the ground may have enhanced its susceptibility to
marauding ants.

Phylogenetic relationships. This species is the adelphotaxon of B. blaptoides (Fig. 9),
known from the southern Koolau Mountains (Fig. 122). Together, these two species are the
adelphotaxon of the Maui Nui species triplet, B. puncticeps (B. derodera + B. kipahulu).

Blackburnia (Blackburnia) blaptoides Blackburn
(Blackburnia blaptoides Blackburn, 1878b: 157; Blackburn & Sharp, 1885: 213.

DIAGNOSIS. This markedly distinctive species (Fig. 124A) has not been seen alive during
the past 100 years. The eyes are small and almost flat, ocular ratio 1.24; vertex, pronotum,
elytral striae, all thoracic, and abdominal sternites II-IV markedly punctate; pronotum
laterally sinuate, base medially expanded posteriorly, without bead; elytra inflated, humeri
very broad, disc extremely convex; scutellar seta and dorsal elytral setae absent; 9 lateral
elytral setae; profemur with 2 setae on anterior surface; mesofemur with 4-5 anteroventral
setae; body surface shiny between pits, microsculpture obsolete. Standardized body length
11.3 mm.

Pterothorax. The punctate metepisternum is quadrate, lateral margin 1.6× length of
anterior margin; flight wings vestigial, not extended beyond metanotum.

Male genitalia. The single known specimen is a female.

Female reproductive tract. Gonocoxa elongate, gonocoxite 1 with apical fringe of 8
setae (2 setae worn down in specimen, Fig. 125A); gonocoxite 2 elongate, parallel-sided,
apex rounded, 3 peglike lateral ensiform setae and 2 peglike dorsal ensiform setae, the
longest 0.12× length of gonocoxite 2; apical nematiform setae only slightly elongate, 0.34×
length of gonocoxite 2 (may be worn); bursa copulatrix elongate, about 1.6× length of
common oviduct, with a narrow quadrate dorsal pouch near vagina, a medial band of 3- and
4-pointed cristate microtrichia, a leftward expansion halfway between base and spermathecal duct entrance; spermatheca ovoid, reservoir 0.56× length of spermathecal
duct, with a small basal lobe.
Fig. 124. Blackburnia species habitus, dorsal view. A. (Blackburnia) blaptoides. B. B. (Blackburnia) puncticeps. C. B. (Blackburnia) derodera. D. B. (Blackburnia) kipahulu, new species.
Fig. 125A. *B. (Blackburnia) blaptoides* female gonocoxa, ventral view. Fig. 125B-C. *B. (Blackburnia) puncticeps*. B. Male aedeagal median lobe, right lateral view. C. Male aedeagal median lobe, euventral view.

**Holotype** ♀ originally mounted on card with 3 parallel lines, the topmost thickest, with a pencil “♀” symbol in lower right corner (BMNH). The specimen is now remounted on a cardboard point, with the disassociated abdominal sternites glued to card; female gonocoxae and reproductive tract are held in a glycerine vial. The specimen lost distal portions of antennae and legs when they were glued to the card, and the specimen subsequently handled. All body parts except right protarsomere I are accounted for either attached to specimen or to the card.

**Distribution.** Known only from the extant specimen collected on Konahuanui at 450 m by Blackburn (Fig. 122). Perkins collected a specimen on Lanihuli “under a detached stone . . . When I had turned out my captures of the day in the evening, I was called away to the telephone, leaving the insects on my table against the open window. On my return after a considerable delay, I found most of these had disappeared, and the great stream of the ant *Pheidole* was coming and going through the window and carrying off their booty. I could not recover my Carabid, which I have little doubt was *Deropristus blaptoides*, a single specimen of which was captured by Blackburn on a ridge across the valley from where I found the individual referred to” (Perkins 1892).

**Habits.** We know little except that this species was collected twice under stones (Perkins 1892, Sharp 1903, 289).
Phylogenetic relationships. This species is the adelphotaxon of *B. insignis* (Fig. 9), with which it was (or may still be) sympatric in the southern Koolau Mountains (Fig. 122).

**Blackburnia (Blackburnia) puncticeps** (Sharp), new combination

(Figs. 29H, 32D, 124B, 125B-C, 126, 127)

*Deropristus puncticeps* Sharp, 1903: 192.

**Diagnosis.** Similar to the two preceding species—*B. insignis* (Fig. 118C) and *B. blaptoides* (Fig. 124A)—in heavy punctuation of pronotum and elytral striae, but differing in: 1, broader pronotal lateral marginal depressions, and densely punctate, nearly obsolete laterobasal depressions; 2, obsolete basal elytral groove, the groove indicated by 3 large punctures cephalad of scutellar seta (Fig. 124B); 3, setose prosternal process. These 3 characteristics are shared with the following two species—*B. derodera* (Fig. 124C) and *B. kipahulu* (Fig. 124D)—but *B. puncticeps* is diagnosed by the broader pronotal lateral margins, presence of 3 short dorsal elytral setae in third elytral interval, and 3-4 anteroventral setae on mesofemur. The dorsal elytral setae are positioned near at 1/5, midlength, and 3/5 of elytral length on third interval. If they are rubbed, small pits associated with them are visible in clean specimens. Standardized body length 9.5-12.5 mm.

**Pterothorax.** Metepisternum with large punctures, quadrate, lateral margin 1.6 to 1.8× length of anterior margin; flight wings vestigial, not extended beyond metanotum.

**Male genitalia.** Aedeagal median lobe stout, markedly expanded medioventrally, euventral surface recurved, ventral excavation extended onto elongate apex angled relative to median shaft, tip extended 3.0× thickness of apex at opening of internal sac and tapered to an acuminate tip (Fig. 125B); median lobe moderately broad basally, tapered slightly to a broadly rounded apex (Fig. 125C).

**Female reproductive tract.** Gonocoxa elongate, gonocoxite 1 with apical fringe of 5-7 setae, 3-4 at medioapical angle, 2-3 laterally (Fig. 126A); gonocoxite 2 elongate, paralleled, apex rounded (Fig. 32D), with 3 peglike lateral ensiform setae and 1-2 dorsal ensiform setae, lateral setae 0.16× length of gonocoxite 2; apical nematiform setae elongate, 0.46 to 0.51× length of gonocoxite 2; bursa copulatrix very long, about 2.0× length of common oviduct, with a broadly quadrate dorsal pouch basally, a medial band of 3-pointed cristate microtrichia, and leftward expansion (Fig. 126B); spermatheca elongate, 0.8× length of spermathecal duct, with a small basal lobe.

**Lectotype ♀ labeled “♀ Deropristus puncticeps D.S. Molokai Perkins,” with “592” handwritten on reverse of card (BMNH) hereby designated. Perkins’ lot 592 is described as “Molokai Mts., boggy plateau about 4000 ft. below the densest forest, contains several good things (Carabidae), VI ‘96” (Anonymous n.d.).

**Distribution.** Found in the higher mountains of Molokai (Fig. 127).

**Localities.** Found in the higher forested areas of the Molokai mountains, most recently at localities within TNCH Kamakou Preserve, including above Waikolu Valley, Hanaliliolilo Trail, ridge above East Kawela Gulch, woods N and W of Pepeopae Bog, Puu Kolekole and vicinity, and Kauumohua. A collection from 1907 is labeled from 910 m elevation; all more recent records range from 1100 to 1380 m elevation.
Habits. Perkins first discovered this species by “turning over some fallen trees to get warm” (Perkins 1893) during a nasty, wet morning during his first visit to Molokai. All subsequent collections have been from the ground, with adults found under logs, by sifting litter at the base of Cibotium tree fern trunks, and on a mud stream bank. The most prevalent microhabitat they occur in, however, is the pincushion-shaped moss mats found on the forest floor. During an evening of heavy rain (16-V-1992, CUIC), 15 individuals were collected while they stood on wet moss mats; one pair was in copula. The following year (5-V-1993, CUIC), 13 individuals were collected on moss mats during dry nighttime conditions. Thus, this species appears to use moss mats as open arenas for nighttime activities, some of which lead to copulation. This “moss mat sitting” has been also observed in adults of the related Oahu species, *B. kamehameha* (see under Habits for that species).

Phylogenetic relationships. This species is the adelphotaxon for the Haleakala species pair *B. derodera + B. kipahulu* (Fig. 9). Based on patterns in other clades, the occurrence of a related species in West Maui is predicted.
**Blackburnia (Blackburnia) derodera** (Sharp), new combination  
(Figs. 124C, 128, 129)

*Deropristus deroderus* Sharp, 1903: 192.

**Diagnosis.** Like *B. blaptoides* and *B. puncticeps* in the densely punctate vertex, pronotum, and elytral striae, but pronotum quite narrow, median length slightly longer than maximum width, and lateral marginal depressions obsolete (Fig. 124C); basal elytral groove completely reduced, 4 large punctures between scutellum and start of lateral marginal bead on humerus. Differing from the adelphotaxon—*B. kipahulu* (Fig. 124D)—in presence of the basal pronotal seta, broader humeri, and shorter lobes on tarsomere 4; metatarsomere 4 with subequal inner and outer lobes 0.5× median basal length of segment. Standardized body length 9.1-10.8 mm.

**Pterothorax.** Punctate metepisternum moderately elongate, lateral margin 1.3 to 1.8× length of anterior margin; flight wings vestigial, not extended beyond metanotum.

**Male genitalia.** Aedeagal median lobe stout, broadly recurved medioventrally, elongate apex angulate with median shaft, extended 5.33× thickness of apex at opening of internal sac, tapered to an acuminate tip (Fig. 128A); basal sagittal crest short, moderately broad; median lobe moderately broad basally, tapered slightly to broadly rounded tip (Fig. 128B).

**Female reproductive tract.** Gonocoxa elongate, gonoxocite 1 with apical fringe of 10-11 setae, inner 7-8 setae in a double series (Fig. 128C); gonoxocite 2 subparallel, apex rounded, with 5 peglike lateral ensiform setae and 2-3 dorsal ensiform setae, lateral setae 0.12× length of gonoxocite 2; apical nematiform setae elongate, 0.61× length of gonoxocite 2 (3 setae unilaterally in dissected specimen); bursa copulatrix elongate, 1.6× length of common oviduct, with broadly rounded dorsal pouch basally, a medial band of 5-pointed cristate microtrichia, and leftward expansion; spermatheca ovoid (Fig. 128D), reservoir 0.6× length of spermathecal duct, with a small basal lobe.

**Lectotype** ♀ labeled “♂ Deropristus deroderus Type D.S. Maui. X96. 5000 ft.” (BMNH) hereby designated.
Fig. 128. *B. (Blackburnia) derodera*. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view. D. Female spermatheca, ventral view.

**Distribution.** Sparsely distributed across the windward forest of Haleakala, East Maui (Fig. 129), though not sympatrically with its adelphotaxon, *B. kipahulu*.

**Localities.** Known from Perkins’ collections at 5000 ft. on Haleakala, most likely west of Waikamoi Gulch, and from Upper Hana Forest at 2150 m elevation (Whittle, UHEM). The only possible forested localities of this elevation on the northeast rift are near the heads of Hanawi and Kuhiwa Streams.
Fig. 129. Distributional records for *B. (Blackburnia) derodera* (●) and *B. (Blackburnia) kipahulu*, new species (○).

**Habits.** As with *B. puncticeps*, known only from ground-level situations, the only recorded ecological information being "under logs, stems of the fern, burnt stumps etc. on the forest and above it, but where the forest once stood" (Perkins lot 382, Anonymous n.d.).

**Phylogenetic relationships.** This species is the adelphotaxon of *B. kipahulu* (Fig. 9), and the distributions of the two species allopatrically span much of the windward face of Haleakala (Fig. 129). The Hana Volcanics of Holocene and Pleistocene age—the youngest lava flows to erupt out of the northeast rift zone lying to the north of Kipahulu Valley (Langenheim & Clague 1987)—serve as the most likely vicariant mechanism to have isolated populations ancestral to the present-day species, *B. derodera* and *B. kipahulu*.

**Blackburnia (Blackburnia) kipahulu** Liebherr, new species
(Figs. 124D, 129)

**DIAGNOSIS.** Sharing the densely punctate pronotum with obsolete laterobasal depressions, obsolete elytral basal groove, and setose prosternal process with *B. puncticeps* and *B. derodera*, but diagnosed by: 1, pronotum lacking basal seta, basolateral margin more sinuate (Fig. 124D); 2, humeri narrow; 3, tarsi lobate, tarsomere 4 broad with lobes subequal to median basal length of segment. Standardized body length 10.2 mm.

**DESCRIPTION.** Head narrow, with very slight dorsal impression on neck, eyes slightly convex, ocular ratio 1.40; frontoclypeal grooves obscured by punctures covering frons and
vertex, punctures irregularly distributed, in some instances separated by less than their diameters; antennal pedicel with longer outer seta and 3 ventroapical setae; gena behind eye largely impunctate, but genal area bordering gula punctate; labrum broadly and shallowly emarginate; mentum tooth broadly truncate.

**Prothorax.** Pronotum with obsolete lateral marginal depressions, basolateral margin sinuate, hind angles glabrous, obtuse; entire surface covered with large round punctures, only several on disc joined to form elongate wrinkles; lateral margin beaded; laterobasal depressions difficult to define due to punctate surface; basal marginal bead indistinct directly inside hind angles, otherwise effaced; median longitudinal impression finely incised, evident even between adjacent punctures, obsolete before anterior transverse impression, which is evidenced by diagonal series of punctures leading toward slightly protruded, finely rounded front angles. Prosternum, proepisternum, and proepipleuron punctate, the latter slightly so; mesal portion of procoxal cavity bordered with large punctures extended onto prosternal process; prosternal process with one seta on medioposterior surface (more may be present in nature).

**Elytra.** Elytral humeri narrow, humeral groove only a short distance mesad humerus; elytra widest at midlength, subapical sinuation completely reduced, lateral margin convex apically; elytra fused, sutural intervals elevated on both halves of elytra, other elytral intervals convex; elytral striae punctate throughout their length, punctures in some instances separated by less than their diameters, for others farther apart; scutellar seta and dorsal elytral setae absent; 8-9 lateral elytral setae.

**Pterothorax.** Mesepistemum with several large punctures, mesosternum punctate around mesocoxal cavities, mesosternum broadly punctate; metepisternum with irregular row of punctures along mesal margin, trapezoidal, lateral margin 1.5× length of anterior margin; flight wings presumed vestigial (specimen not relaxed).

**Legs.** Profemur without anterior setae, with 2 posteroventral setae; mesocoxa with 1 ridge seta; mesofemur with 2 anteroventral setae; metacoxa irregularly punctate, bisetose, mesal seta absent; metafemur with 2 anteroventral setae, dorsoapically glabrous; tarsomeres parallel-sided, slightly broadened, metatarsomere 4 lobate, length of outer lobe 1.2× that of inner lobe, and subequal to median basal length of segment; tarsomeres 1-4 with dense ventral vestiture of elongate setae that shield the median glabrous area from ventral view; tarsomere 5 ventrolaterally with 6 setae each side subequal to depth of tarsomere at point of setal insertion.

The single male specimen is remarkable in having expanded protarsomeres that lack the ventral articuloseatae (Stork 1980) seen in males of all other species of Platynini known to us. Protarsomeres 1-4 bear 5-6 longitudinal rows of fine trichoid setae each side between the narrow mediolongitudinal glabrous area and each lateral row of stoutier, more widely spaced setae. The protarsi are broader than in *B. puncticeps*, with tarsomere 4 having apical lobes 1.3× as long as the median basal length of the tarsomere. The configuration in the lone male specimen is as if 6 rows of fine trichoid setae replace 2 rows of male articuloseatae. In this sense, the vestiture of the protarsomeres is identical to that of a female of *B. puncticeps*. This condition might be dismissed as an anomaly—possibly an anterior-posterior gynandromorph—except for its occurrence in *Notonomus peronii* Castelnau de LaPorte of Australia (Sloane 1902; K. W. Will, pers. comm.). Observing mating behavior in either of these two species would shed light on the functional significance of the male articuloseatae in other species of Carabidae.
Abdomen. Sternites II-V punctate laterally, sternite IV punctate across body; male with a single apical seta each side of sternite VII.

Coloration. The specimen is teneral; head capsule darkest, rufobrunneous, pronotum and elytra progressively paler, brunneous; legs and antennae testaceous. When mature specimens are found, they will most likely be colored as *B. derodera*—i.e., shiny rufopiceous body, with dark brunneous antennae and legs.

Microsculpture. Vertex smooth, shiny between punctures, with indistinct parallel wrinkles or isodiametric sculpticells associated with some punctures; pronotum shiny between punctures, indistinct wrinkles run on concentric circles around punctures; elytra shiny between punctures, indistinct isodiametric sculpticells visible in some punctures; ventral body surface shiny, lacking evident microsculpture.

Male genitalia. The single male specimen is teneral, and was not dissected. Nonetheless, the aedeagal median lobe and ventral paramere is visible through the unsclerotized integument of this teneral specimen. The median lobe is broad medially, tapered evenly to a broadly rounded tip, not unlike those of closely related species (Figs. 125C, 128B).

Female reproductive tract. The single known specimen is a male.

Holotype $\delta$ labeled “Kipahulu Valley Maui Camp 2, 1250 m, 18-20.VIII.67 // N. Wilson Collector BISHOP” (BPBM).

Etymology. The species epithet recognizes the type locality, Kipahulu Valley Scientific Reserve of Haleakala National Park, treating the locality name as a noun in apposition.

Distribution. This species is so far known only from the holotype collected at Camp 2 in Kipahulu Valley, Maui (Fig. 129).

Phylogenetic relationships. This species is the adelphotaxon of *B. derodera* (Fig. 9), distributed to the north of the northeast rift zone, Haleakala (Fig. 129).

Subgenus *Metromenus* Sharp, 1884

DIAGNOSIS. Relative to the large amount of morphological divergence that defines monophyly of the entire subgenus *Blackburnia*, species grouped in *Metromenus* are best characterized as vestigially winged *Colpocaccus*. The basal tarsomeres are dorsolaterally sulcate to a greater or lesser degree in all species; *B. kahili* from Kauai exhibits the least sulcate tarsi. This condition corresponds to the primitive condition for this radiation. Flight loss is the single unreversed synapomorphy supporting monophyly of this subgenus. Nonetheless, taxonomically this subgenus is extremely easy to diagnose by two criteria: 1, flight wings vestigial; 2, basal tarsomeres dorsolaterally sulcate.

Character evolution. Even though all species exhibit vestigial flight wings, the length of the remnants varies somewhat. Most species possess padlike wing vestiges extended slightly beyond the apex of the metanotum. *Blackburnia sphodriformis* has longer vestiges in the form of micropterous straps extended in length to about the fourth or fifth lateral elytral setae (Sharp 1903, plate VI). Within subgenus *Metromenus*, members of one clade of Kauaiian species—*B. optima*, *B. opaca*, and *B. alternans*—have wing rudiments so short as not to extend past the metanotal posterior margin.

The elytral configurations exhibited by species in this subgenus reflect the loss of functional constraints on an operational flight apparatus. All species exhibit humeri that are tightly rounded or angulate. The humeri in one clade are moderately to extremely narrow.
Conversely, in a second clade the humeri have evolved to a broader condition, herein called abacoid due to analogous similarity with the pterostichine genus *Abax* Bonelli, whereby angulate humeri are positioned much farther apart laterally, resulting in the parallel or subparallel lateral margins of the elytra. In addition, the lateral margins of the elytra are more explanate just behind the humeri, gradually narrowed toward the subapical sinuation. This configuration can be observed in *B. paludicola*, and all members of its adelphotaxon with the exception of the cave species *B. howarthi*, and its adelphotaxon, *B. debilis* and *B. kuiki*, which have reverted to the more primitive condition of narrow humeri.

Cladistic analysis presented above optimizes the basal node defining the redefined subgenus *Metromenus* as the prothoracic condition whereby the lateral pronotal setae are present and the basal setae absent. This diagnosis was used by Sharp (1903) to define his genus *Mesothriscus*. However, within this clade, all other possible pronotal setation patterns
have evolved—i.e., -/+, +/-, and -/- lateral/basal setation. Sharp treated these conditions as the genera Atelothrus Sharp, Platynus Bonelli, and Metromenus Sharp, respectively. As groups defined by the four pronotal configurations are all polyphyletic, such a system is rejected. Rather, the predominant pronotal configuration—that of the glabrous “Metromeni” of Sharp—is used as the subgeneric name. Sharp (1903, 186) wrote “Had I not adopted the condition of the wings and the thoracic setae as a basis for genera, our Hawaiian Carabidae would have appeared as members of only three or four genera.” The present recognition of 4 subgenera reflects the discounting of those character systems in favor of comprehensive
character and cladistic analysis. Nonetheless, pronotal setation is an extremely useful tool for field identification, and is used extensively in the keys. We present it below for species-level diagnosis.

**Tarsal structures.** Though many species in subgenus *Metromenus* may appear superficially similar, tarsal structure varies greatly in the group, and serves as a useful diagnostic tool. The tarsomeres on most Hawaiian Platynini are expanded apically, with tarsomere 4 in many species appearing triangular in outline. This configuration is observed in species of the subgenus *Colpocaccus* (Fig. 20B-D), and is considered part of the groundplan for the Hawaiian radiation. Within subgenus *Metromenus*, this apical expansion of tarsomeres 1-4 is widespread (Figs. 130A, C, G, 131A, C, E, G, 133A, C, G, E). Nonetheless, several species exhibit narrower, more tubular tarsomeres typical for taxa outside the Hawaiian radiation (Fig. 130E). In several species, the tarsomeres have evolved to be broader over their entire length, in some species in association with shortened tarsomeres (Fig. 131C), in some species with longer tarsomeres (Fig. 133C, E, G).

Ventral tarsal vestiture also varies among *Metromenus* species. Plesiomorphically, tarsomeres 1-4 bear ventrolateral setae in 2-3 rows, with a median glabrous area between them. This condition is perhaps best assessed on tarsomere 4 (Figs. 130B, D, F, H, 131B, D, H, 132B, D, 133B). The number of ventrolateral rows of setae may be as many as 4 or more, giving the ventral surface of the tarsomeres a thicker covering of setae while retaining the glabrous median area (Fig. 131F). The ventral vestiture may be denser, obscuring the median glabrous area, especially on tarsomere 4 (the segment that consistently comes in contact with the substrate, Fig. 133D, F, H).

Species of subgenus *Blackburnia* exhibit substantially less evolutionary change in tarsal structure, partly because all species but one lack dorsolateral sulci. These plesiomorphic structures are retained in subgenus *Metromenus*, and are variously modified. Most species exhibit moderate to distinct dorsolateral sulci, best observed on tarsomeres 1-3 (Figs. 130A, C, E, G, 131A, F-G, 132C, 133C, G). In several species, the sulci have become reduced,
Fig. 133. Scanning electron micrographs of metatarsomeres of *Blackburnia (Metromenus)* species: dorsal view of right metatarsomere, ventral view of left. A (62x), B (59x); *B. sphodriforinis*. C (60x), D (73x); *B. dyscolea*. E (96x), F (166x); *B. palmae*. G (76x), H (216x); *B. gracilis*.

with the inner or posterior sulcus being more prone to reduction than the outer or anterior groove (Fig. 133A). Conversely, the dorsolateral sulci are deep in nine other species in the subgenus, resulting in medially carinate tarsomeres (Fig. 132A).

The configuration of the apical lobes of tarsomere 4 is also functionally related to how many setae can be in contact with the substrate during walking and running. An apical emargination of tarsomere 4 resulting in lobes 0.75 to 1.0× the median basal length of the tarsomere appears to be the groundplan condition for this structure based on its presence in the subgenera *Protococcus* and *Colpococcus* (Fig. 20). From this condition, lineages of subgenus *Metromenus* have been modified in two directions, so that: 1, the apical emargination of tarsomere 4 is reduced, with apical lobes less than half the basal median tarsomere length (e.g., Figs. 130E, 131A, 132A, C); and 2, the apical emargination is
elongate, with the apical lobes as long or longer than the median basal tarsomere length (Figs. 130A, 131C, E, 133C, G, E). Species such as *B. epicurus* and *B. sphodriformis* (Figs. 131G, 133A) retain the plesiomorphic lobe length. It is of interest that in all different tarsal lobe configurations observed in the Hawaiian radiation, in all taxa the outer apical lobe of metatarsomere 4 is no more than 1.5× the length of the inner lobe, and in most taxa the two lobes are of more similar length, often subequal. This differs from many other radiations of tropical Platynini—e.g., Mexico (Whitehead 1973), Madagascar (Basilewsky 1985), and New Guinea (Darlington 1952)—within which taxa exhibit fourth tarsomeres with the outer lobe 2 to 3× as long as the inner lobe.

The ventral setae of tarsomere 4 are complemented by a pair of apical setae located at the hind angles of the tarsomere, plesiomorphically very close to the apex of the lobe (Figs. 20D, 130A, C, E, 131A, 132C). These setae in many taxa are removed from the distal margin of the tarsomere in species with lobate tarsomere 4 (Figs. 131C, E, 133C, E, G). In non-lobate species, the apical setae are more likely to be removed from the apex by being situated on the dorsal margin of the less emarginate apex (Figs. 130G, 131G, 133A).

Most Hawaiian species possess fifth tarsomeres with evident ventrolateral rows of setae. Having these setae subequal to the depth of the tarsomere at the point of setal insertion is one of the characters defining monophyly of subgenus *Blackburnia* (e.g., Fig. 29D). Possession of visible ventrolateral setae (25× magnification), but shorter than the depth of the tarsomere is the groundplan for the Hawaiian radiation (e.g., Fig. 20A), and this condition is retained throughout most of subgenus *Metromenus*. Nonetheless, two species on Kauai—*B. kahili* and *B. alternans*—have ventrolateral metatarsomere 5 setae as minute pegs, visible only at magnifications of 125× or more (Fig. 130F).

Focusing on the most dramatic tarsal modification in subgenus *Metromenus*—i.e., development of bilobate tarsomere 4 (Figs. 131C, E, 133C, E, G)—tarsal evolution within the subgenus has resulted in two independent origins of elongate inner and outer lobes of tarsomere 4. Within the Oahu fauna, *B. caliginosa* and *B. mutabilis* are sister species that both exhibit outer lobes of length 1.5 to 1.7× the median basal length of the tarsomere (Fig. 131C, E). Ventrally, *B. caliginosa* exhibits plesiomorphic tarsal vestiture—i.e., 2-3 rows each side of ventrolateral setae (Fig. 131D). *Blackburnia mutabilis* has an increased number of rows of setae on tarsomere 4 (Fig. 131F). In both species, a glabrous median space is evident (Fig. 131D, F). The second origin of a bilobate tarsomere 4 implicates 4 species: *B. dyscolea* (Fig. 133C); *B. gracilis* (Fig. 133G); and *B. platynoides* from Maui Nui; and *B. palmae* (Fig. 133E) from Oahu. In this instance, development of increased ventral setation goes beyond that seen in *B. mutabilis*, with tarsomeres of *B. palmae* being most setose (Fig. 133F). In these taxa, each ventrolateral band is made up of 8 rows of setae, and the 2 lateral bands of setae approach each other more closely, restricting the median glabrous space.

Whereas the first group—*B. caliginosa* and *B. mutabilis*—can be collected by beating a variety of vegetation in Oahu, *B. palmae* is not only a vegetation climber on Oahu, but is known as the species most likely to be found between the tightly wrapped leaf axils of ieie plants (*Freycinetia arborea* Gaudichaud-Beaupré). The ieie habit is also observed in the 3 Maui Nui species related to *B. palmae*, supporting a connection between habitat preference and tarsal structure.
Evolution of the female reproductive tract. Whereas species of subgenus *Blackburnia* exhibit extensive modification of the female ovipositor and reproductive tract, the female tract and ovipositors vary much less dramatically within subgenus *Metromenus*. Much as in subgenus *Colpocaccus* (Fig. 30C, D), the *Metromenus* gonocoxa is characterized by a triangular gonocoxite 2, relatively short apical nematiform setae, 2-4 lateral ensiform setae (Fig. 134A), and a single dorsal ensiform seta (Fig. 134B). Gonocoxite 1 bears a more or less continuous row of apical setae (Fig. 134A).

One set of features examined in a preliminary way using scanning electron microscopy was found to vary, but because of the expense and lack of time, was not surveyed sufficiently to permit anything beyond healthy speculation. The apical sensory depression of gonocoxite 2 is so named because it houses not only 2 elongate nematiform setae, no doubt trichoid sensilla used for the female to assess ovipositor position relative to the substrate, but also a varied number of shorter furrow pegs (Ball & Hilchie 1983). Within
subgenus *Metromenus*, the number of furrow pegs ranges from 4 (Fig. 134C; also *B. vagans*), to 6 (Fig. 135B; also *B. pavida, B. foveolata, B. constricta, B. gracilis, B. asquithi*), to 8 (*B. epicurus*). Only 2 furrow pegs occur in *B. (Colpocaccus) posticata* and *B. (Colpocaccus) hawaiensis*. Likewise, *B. sulcipennis* and *B. frigida* of subgenus *Blackburnia* exhibit 2 furrow pegs, whereas several other species exhibit 4: *B. costata, B. corrusca, B. puncticeps*. Because it was not possible to examine all or even most species for these structures using SEM, nor assess the possibility of infraspecific variation in furrow peg number, this feature was not used for phylogenetic analysis. Nonetheless, our preliminary survey suggests that furrow peg number may have evolved to higher number in subgenus *Metromenus*, with the plesiomorphic condition being 2 pegs in the Hawaiian platynine radiation. Furrow peg function is unknown. The peg apex is slightly irregular, and may have small openings to permit hygroreception or some other chemoreception.
The gonocoxa is also sparsely covered with sensilla that appear to be recessed sensilla basiconica (i.e., pegs in pits). There appears to be some regularity to distribution of these sensilla (Figs. 134A, 135A, C-D, 136), though some sensillar positions are absent from some specimens, and other specimens have 2 sensilla in an area where others have only 1. Again, without assessment of infraspecific variation, coupled with adequate sampling across all taxa, use of this trait must be left for future investigators.

Gonocoxal characters useful for differentiating species of subgenus *Metromenus* are few. The breadth of the lateral ensiform setae varies, from shorter and narrower (Figs. 135C-D, 136A) to a derived condition of longer, broader setae (Fig. 136B-D). The number of lateral ensiform setae varies from 2 to 4, but this variation is observed within species, so is of little value for determining relationships.

The dorsal pouch of the bursa copulatrix varies somewhat within subgenus *Metromenus*. The pouch is entirely membranous, or it is defined by a sclerotized border, as in *B. perpolita* (Fig. 248D). In a number of taxa, the dorsal pouch articulates with laterally expanded sclerotic bands, giving the pouch a "winged" appearance (Fig. 225D).
The cristate bursal microtrichia that support monophyly of subgenus *Blackburnia* (Fig. 30A) are observed in a single cladistically basal species of this subgenus: *B. kahili* from the island of Kauai. In this species, most of the microtrichia are simple spikes (Fig. 30B), as in the rest of the subgenus, but a few 3-pointed cristate microtrichia are mixed in.

**Distribution.** The 73 species of subgenus *Metromenus* are distributed across all of the high Hawaiian Islands. Kauai supports 11 species of this clade, Oahu 22, Molokai 13, Lanai 3, West Maui 10, Haleakala or East Maui 15, and Hawaii Island only 1. Only one species occurs on more than one island: *B. sphodriformis* of Molokai, and West and East Maui.

**Phylogenetic relationships.** The subgenus *Metromenus* is the adelphotaxon of subgenus *Blackburnia* (Fig. 9). Most of the ambiguity in character support for various phylogenetic hypotheses of the Hawaiian *Blackburnia* radiation is localized within sg. *Metromenus* (Liebherr & Zimmerman 1998). Whereas hypothesized adelphataxons can be presented with some confidence for most taxa in subgenus *Blackburnia*, such hypotheses are much more speculative for this set of 73 species. Nonetheless, we feel it important to explicitly present our best supported hypotheses of species relationships, so that they can be evaluated as more phylogenetic data are incorporated into the analysis. Geographical and ecological information is also brought to bear. Though such information was not used to develop the hypotheses of relationship, it can be used to test such hypotheses.

Species living on Kauai make up the basal four divergent clades of this subgenus (Fig. 9). One of the next clades definable by the cladogram includes a large group of species found on Oahu, many placed by Sharp in his concept of the genus *Metromenus*: *B. huhula* to *B. oceanica* (Fig. 9). This Oahuan fauna is a paraphyletic group from which a clade of Maui Nui species arose by colonization of that island complex: the clade subtended by the species pair *B. lihau* and *B. calathoides* (Fig. 9). These species are characterized by broadly developed elytral humeri, often with a carinate interval 7: a group informally called the abacoid clade.

The adelphataxon to the above includes a basal clade of 4 species restricted to streamside habitats of Maui Nui and Hawaii Island: *B. kilauea* to *B. auana* (Fig. 9). Their adelphataxon includes two major clades of 14 and 17 species: the former—subtended by *B. epicurus*—predominately including species from Kauai and Oahu, the latter—subtended by *B. hakeakapa*—largely restricted to Maui Nui and Hawaii Island.

*Blackburnia (Metromenus) kahili* Liebherr, new species
(Figs. 137A, 138, 139)

**Diagnosis.** This species is extremely similar to the following *B. asquithi*, sharing a narrow habitus, asymmetrical lobes of metatarsomere 4, and pallid coloration (Fig. 137A-B). This species is diagnosed by: 1, shinier integument, vertex with only traces of isodiametric sculpticells, pronotal disc without extensive transverse wrinkles and with only indistinct transverse sculpticells, and elytral intervals with flat, shiny, transverse sculpticells arranged in irregular transverse rows; 2, pronotal lateral marginal depression flat, bordered with a distinct lateral bead; 3, elytra only narrowly paler, disc rufous to brunneous; 4, tarsomeres broadened apically, tarsomeres 2-3 flattened dorsally, metatarsomere 4 with elongate lobes, outer lobe 1.1 to 1.4× median basal tarsomere length. Standardized body length 6.8-7.4 mm.
DESCRIPTION. **Head** elongate, eyes small but convex, ocular ratio 1.56; frontoclypeal grooves broad, shallow, deepest just behind frontoclypeal suture, slightly wrinkled before anterior supraorbital setae; distinct dorsal impression behind posterior supraorbital setae, genae elongate and constricted behind the small eyes; antennal pedicel with longer outer seta and 2-3 short, apical setae; antennae elongate, extended to midlength of elytra; labrum straight apicommedially; mentum tooth triangular with finely rounded apex.

**Prothorax.** Lateral pronotal setae present, basal setae absent; lateral marginal depressions moderately broad, marginal bead present from just behind rounded, protruded front angles continuously to median base; basolateral margins slightly sinuate before obtuse-rounded hind angles; laterobasal depressions smooth, with slight tubercle along posterolateral margin of raised disc, margined laterally by upraised margin slightly broader than posterior marginal bead; median base smooth, basal marginal bead flat but continuous; longitudinal median impression extended from near hind margin to before anterior transverse impression; finely incised; pronotal disc convex, smooth, with only indistinct transverse wrinkles; anterior transverse impression distinct, extended to inside front angles; anterior margin upraised inside front angles, indistinct marginal bead traceable medially. Prosternal process narrow, convex medioventrally, margined along anterior portion of coxal cavity to ventralmost point of coxa.

**Elytra.** Humeri narrow, angulate, lateral margins of elytra convex behind humeri (Fig. 137A); basal grooves evenly curved to angulate humeri laterad scutellum; subapical sinuation rather deeply concave before rounded-angulate sutural apex; elytra flat medioventrally,

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Fig. 138. B. *(Metromenus) kahili,* new species. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view.
Fig. 139. Distributional records for *B. (Metromenus) kahili*, new species (■), *B. (Metromenus) asquithi*, new species (●).

Striae smooth, broad, slightly wavering; scutellar seta and 3 dorsal elytral setae present; 15–16 lateral elytral setae.

**Pterothorax.** Metepistemum short, narrow behind, 1.0 to 1.2× length of anterior margin.

**Legs.** Profemur without anteroventral setae, with 2 posteroverntral setae; mesocoxa with 1 ridge seta; mesofemur with 2 anteroventral setae; metacoxa bisetose, mesal seta absent; metafemur with 2 anteroventral setae; tarsomerses slightly expanded apically, basal 3 metatarsomerses with fine, shallow outer dorsolateral sulci and obsolete inner sulci; tarsomerses 2-3 on meso- and metalegs broad, flattened mediodorsally; tarsomere 4 asymmetrically lobate, outer apical lobe of fourth metatarsomere 1.20× length of inner lobe, and 1.1 to 1.4× median basal tarsomere length; tarsomerses 1-3 with 3 sparsely distributed ventrolateral rows of elongate setae, glabrous medially; tarsomere 5 without visible ventrolateral setae (125×).

**Abdomen.** Males with 1 apical seta each side of sternite VII, females with 3 each side.

**Coloration.** Head capsule brunnneous; pronotal and elytral discs concolorous, paler than head, rufous to rufobrunneous, their margins narrowly paler, flavous; pronotal and elytral epipleura, and legs uniformly pale testaceous, contrasted with brunnneous thoracic ventrites;
abdominal sternites darker medially, brunneous to piceous, with motiled flavous areas laterally and in apical half of sternite VII.

**Microsculpture.** Vertex of head shiny, with indistinct isodiametric sculpticells, neck impression with slightly more distinct microsculpture; pronotal disc with effaced transverse mesh, sculpticells more distinct in depressed areas around laterobasal depressions; pronotal median base, anterior transverse impression, and lateral marginal depressions with evident isodiametric sculpticells; elytra with distinct microsculpture of flat, slightly transverse sculpticells, arranged in slightly irregular transverse rows.

**Male genitalia.** Aedeagal median lobe gracile, shaft elongate, straight medioventrally, ventral excavation extended to elongate, downturned apex extended 2.0× thickness of apex at opening of internal sac, ended in a finely rounded tip (Fig. 138A); basal sagittal crest short and shallow to obsolete; median lobe narrow throughout, slightly constricted on right surface, tapered to a finely rounded tip (Fig. 138B).

**Female reproductive tract.** Gonocoxa basally broad, triangular gonocoxite 2 with acuminate apex (Fig. 138C); gonocoxite 1 with apical fringe of 12-13 setae, mesal 8 setae near medioapical angle in double and triple series; gonocoxite 2 with 3-4 lateral ensiform setae and 1 dorsal ensiform seta, lateral ensiform setae broad, elongate, 0.25× length of gonocoxite 2; apical nematiform setae short, 0.28× length of gonocoxite 2; bursa copulatrix symmetrical, subequal to length of common oviduct, with a broad, indistinct dorsal pouch; lateral band of bursal microtrichia mostly spikelike, but some microtrichia near edge of setal field cristate, with 2-3 points; spermatheca ovoid, reservoir 0.7× length of spermathecal duct, without basal lobe. This is the only species within subgenus *Metromenus* exhibiting any cristate bursal microtrichia.


**Paratypes.** KAUA: Mt. Kahili, beating ohia at night, 895 m, 21-V-1995, Liebherr (CUIC, 2), Polhemus (BPBM, 1).

**Etymology.** The species epithet is the name of the type locality, Mt. Kahili, used in apposition. *Blackburnia atra* (Figs. 60B, 62), represents the other carabid species known only from this mountain.

**Distribution.** This species is restricted to the knifelike ridge called Mt. Kahili, a southern spur of Kauai’s Waialeale massif (Fig. 139).

**Habits.** The limited information on *B. kahili* suggests it is primarily an arboreal species, resting among epiphytic growth during day and foraging on plant surfaces at night. The only known substrate plant is ohia lehua (*Metrosideros polymorpha*).

**Phylogenetic relationships.** This species is the adelphotaxon to the remaining 72 species of subgenus *Metromenus* (Fig. 9). Its basal cladistic position points to both the great age and isolation of Mt. Kahili. The next most basally divergent species of the subgenus is *B. asquithi*, distributed from Mt. Waialeale northwest across the high Alakai plateau (Fig. 139). Moving upward on the cladogram are: 1, two pectinate clades including species that began diversification on the Waialeale massif and its other spurs, such as Makaweli; then 2, species inhabiting the other younger islands. These area relationships are congruent with: 1, the initial isolation of Mt. Kahili from the Waialeale massif; 2, diversification of the subgenus across Waialeale and its other spurs; and 3, colonization of Oahu and Maui Nui from Kauai by ancestors of species presently occurring on those islands.
Blackburnia (Metromenus) asquithi Liebherr, new species
(Figs. 130A-B, 137B, 139, 140)

DIAGNOSIS. This and B. kahili are characterized by narrow body, with humeri reduced and angulate, and elytra ovoid and elongate (Fig. 137A-B). The pronotal and elytral margins are pale, and the legs are testaceous. These species, as well as similar looking species on Kauai—B. kauaiensis, B. optima, B. alternans, and B. opaca—also exhibit lateral pronotal setae, while lacking hind setae. However, B. asquithi and B. kahili have the apical lobes of metatarsomere 4 unequal in length, the outer lobe being longer. These two species also do not display the carinate elytral intervals characteristic of many species in the Kauaian carabid fauna. From B. kahili, this species can be recognized by: 1, shorter apical lobes of metatarsomere 4, outer lobe subequal to median basal length of segment (Fig. 130A); 2, pronotal and elytral margins more broadly flavous (Fig. 137B); 3, humeri
and anterior portions of elytra narrower; and 4, microsculpture more evident, vertex covered with isodiametric mesh, and isodiametric sculpticells on elytra with raised margins, giving granulate appearance. In addition, the tarsomeres are cylindrical in this species, as is usual for the subgenus Metromenus species, whereas tarsomeres 2-3 are broader and flatter in B. kahili. Standardized body length 6.1-7.6 mm.

DESCRIPTION. Head elongate, eyes small in diameter but convex, ocular ratio 1.59; frontoclypeal grooves composed of 2 depressed areas, an anterior depression with wrinkles radiating onto clypeus, and a posterior quadrate depression with wrinkles radiating laterally; dorsal impression of neck distinct, genae elongate and distinctly constricted behind the small eyes; antennal pedicel with longer outer seta and 2 shorter dorsoapical setae; antennae elongate, extended to midlength of elytra; labrum straight to slightly expanded medially; mentum tooth triangular with a rounded apex.

Prothorax. Lateral pronotal setae present, basal setae absent; lateral marginal depressions moderately broad, outer margin upraised but not beaded; basolateral margins barely sinuate, in many specimens straight before rounded hind angles; laterobasal depressions smooth, margined laterally by gently upraised margin, margin better defined posteriorly by a marginal bead effaced on median base; median base smooth, longitudinal median impression extended from near hind margin to before anterior transverse impression; pronotal disc depressed in vicinity of median impression, with numerous transverse wrinkles; anterior transverse impression distinct, extended to rounded, barely protruded front angles, impression broader in its lateral reaches; anterior margin slightly upraised inside front angles, flat medially, the margin’s surface irregular medially due to longitudinal wrinkles. Prosternal process narrow, flat medially, margined along anterior portion of coxal cavity to ventralmost point of coxa.

Elytra. Humeri and anterior portion of elytra narrow (Fig. 137B); basal groove slightly curved around pimplelike, upraised scutellar seta, then curved cephalad to angulate humeri; lateral margins divergent in basal half of elytra, then curved inward to subapical situation, which is positioned close to rounded sutural apex; elytral intervals convex, striae smooth, broad, slightly wavering; 3 dorsal elytral setae present, anterior seta in some specimens set in depression that spans third interval, in some specimens in a smaller depression, and in about 25% of specimens, absent altogether; 15-16 lateral elytral setae.

Pterothorax. Metepistemum short to very short, narrow to broad, lateral margin ranging from 1.2 to 1.7× length of anterior margin.

Legs. Profemur without anteroventral setae, with 2 posteroventral setae; mesocoxa with 1 ridge seta; mesofemur with 2 anteroventral setae; metacoxa bisetose, mesal seta absent; metafemur with 2 anteroventral setae; tarsomeres gracile, tarsomeres 1-3 with broad, shallow dorsolateral sulci, outer sulcus somewhat deeper, tarsomeres slightly convex medially; tarsomere 4 asymmetrically lobate, outer apical lobe of fourth metastarsomere 1.10 to 1.25× length of inner lobe, and 1.0 to 1.1× median basal tarsomere length; tarsomeres 1-3 with 3 sparsely distributed ventrolateral rows of elongate setae, glabrous medially; tarsomere 5 with 2 rows of 6 ventrolateral setae, each ½ to 1/5 tarsomere depth at point of setal insertion.

Abdomen. Males with 1 apical seta each side of sternite VII, females with 3 setae each side, in few specimens unilaterally 2 setae on one side for a total of 5.

Coloration. Head capsule brunneous, pronotum flavous with infuscated disc, elytra with broadly flavous margins and infuscated, piceous disc; pronotal and elytral epipleura,
antennae, and legs entirely pale testaceous, markedly contrasted with infuscated, brunneous to rufopiceous thoracic ventrites; abdominal sternites medially piceous, broadly paler laterally and on apical half of sternite VII.

**Microsculpture.** Vertex of head with evident isodiametric sculpticells; pronotal disc with distinct transverse microsculpture, producing alutaceous lustre; elytral intervals with distinct isodiametric sculpticells with raised margins, appearing granulate under oblique lighting.

**Male genitalia.** Aedeagal median lobe gracile, slightly recurved medioventrally, ventral excavation extended to elongate, downturned apex extended 1.67× thickness of apex at opening of internal sac, ended in a finely rounded tip (Fig. 140A); basal sagittal crest short and shallow to obsolete; median lobe narrow throughout, constricted on right surface, tapered to a finely rounded tip (Fig. 140B).

**Female reproductive tract.** Gonocoxa basally broad, triangular gonocoxite 2 with acuminate apex (Fig. 140C); gonocoxite 1 with apical fringe of 9 setae, mesal 4-5 setae near medioapical angle in double series; gonocoxite 2 with 4 lateral ensiform setae and 1 dorsal ensiform seta, lateral ensiform setae broad, elongate, 0.26× length of gonocoxite 2; apical nematiform setae short, 0.25× length of gonocoxite 2; bursa copulatrix symmetrical, constricted basally giving a veselike appearance, subequal to length of common oviduct, with a broad, indistinct dorsal pouch and a medial band of spikelike microtrichia (Fig. 140D); spermatheca ovoid, reservoir 0.7× length of spermathecal duct, without basal lobe.


**Paratypes.** KAUAI: Alakai Swamp Tr., moss mats/trail at night, 1150 m, 12-V-1991, Liebherr (CUIC, 1), ohia, scraping bark, 1150 m, 11-V-1991, Liebherr (CUIC, 18), trail at night, 1150-1180 m, 14-V-1991, Liebherr (CUIC, 2), Kawaikoi Str., ohia, scraping moss, 1120-1150 m, 16-V-1991, Liebherr (CUIC, 1), Kilohana mi. 3.0-3.5, ohia, scraping moss, 1210 m, 14-V-1991, Liebherr (CUIC, 4), Pihea Tr. junction, beating vegetation, 1180 m, 12-V-1991, Liebherr (CUIC, 22), beating vegetation at night, 1180 m, 12-V-1991, Liebherr (CUIC, 9), fern (low), beat at night, 1180 m, 15-V-1991, Liebherr (CUIC, 2), under logs, 1180 m, 17-III-1991, Liebherr (CUIC, 3); Kohola S.P., Puu o Kila, wet middle forest, 1250 m, 02-03-XII-1976, Sleeper (CASC, 1); Mohihi-Alakai Tr., moss mats on ohia trunks, 1320 m, 19-V-1995, Liebherr (CUIC, 2), Pihea Tr., under logs/moss mats, 1200 m, 10-III-1991, Liebherr (CUIC, 1), Waialae Falls, nr., 1210 m, 14-IV-1920, Kusche (BPBM, 1); Waialae Cabin, beating fern at night, 1180 m, 18-V-1995, Liebherr (CUIC, 25), 0.2-0.6 km SSW, beating fern at night, 1120 m, 19-V-1995, Liebherr (CUIC, 1), 0.3 km N, beating fern at night, 1180 m, 20-V-1995, Liebherr (CUIC, 6), Waiakele summit, beating mossy ohia, 1515-1530 m, 16-V-1995, Liebherr (CUIC, 8), 17-V-1995, Liebherr (CUIC, 13), beating mossy ohia at night, 1515-1530 m, 16-V-1995, Liebherr (CUIC, 8), 17-V-1995, Liebherr (CUIC, 17), beating vegetation, 1515-1530 m, 16-V-1995, Polhemus (BPBM, 2), 17-V-1995, Polhemus (BPBM, 2), beating vegetation at night, 1515-1530 m, 16-V-1995, Asquith (CUIC, 5), 17-V-1995, Liebherr (CUIC, 8), Asquith (CUIC, 18), mossy creekbank at night, 1515-1530 m, 16-V-1995, Liebherr (CUIC, 1), yellow pan trap 1515-1530 m, 17-V-1995, Polhemus (BPBM, 1).

**Etymology.** This species is named in honor of Dr. Adam Asquith, who is a current rival to famed Hawaiian entomologists such as Otto Swezey for comprehensive knowledge of Hawaiian insects, their habits, and environments.
Distribution. This species is distributed from Mt. Waialeale summit northwest across the Alakai Swamp and upper reaches of Waimea Canyon, Kauai (Fig. 139).

Habits. During the breeding season (May), most adults of this species are associated with arboreal plant situations, either walking on plant surfaces at night or resting in mosses during day. Substrate plant genera include Clermontia and Metrosideros, as well as low stature ferns. On several occasions, May collections included adults walking on moss mats or mossy stream banks at night. Limited late winter collections in March have been from under logs, indicating that overwintering may take place out of the trees.

Phylogenetic relationships. This species’ penultimately basal cladistic position within the subgenus Metromenus (Fig. 9) supports its early origin during radiation of this clade in Kauai. By virtue of its distribution spanning the area from Mt. Waialeale to Kalalau Valley, B. asquithi is sympatric with most other species of Kauaian Blackburnia.

**Blackburnia (Metromenus) pauma Liebherr, new species**
(Figs. 137C, 141, 142)

**DIAGNOSIS.** Unique in the following combination: 1, pronotal basolateral margin convex before rounded, glabrous hind angles (Fig. 137C), pronotal basal margin continuous medially, lateral pronotal setae present; 2, anterior dorsal elytral setae set in foveate depressions; 3, elytral intervals broadly convex, elytral striae smooth and deep, impunctate; and 4, labrum with median pair of setae reduced so that only 1 median seta is usually present, or both median setae absent altogether; females with 2 apical setae each side of sternite VII. Standardized body length 6.1-8.1 mm.

**DESCRIPTION.** Head. Eyes slightly convex, ocular ratio 1.45; frontoclypeal grooves broad and shallow on frons, diffusely wrinkled posteriorly near anterior supraorbital setae; antennal pedicel with longer outer seta and 2-4 apical setae (see Variation section below); labrum straight apically, median pair of setae reduced, either 2 very small setae, a single seta, or absent altogether; mentum tooth truncate to markedly bifid apically.

Prothorax. Pronotal lateral margins convex near lateral pronotal setae, straight or slightly convex cephalad rounded hind angles (Fig. 137C); lateral marginal depressions narrowest at lateral setae, broader at rounded front angles; laterobasal depressions evenly bordered by raised basolateral margins, their surface sparsely punctate adjacent to convex disc; median base smooth, basal marginal bead complete; median longitudinal impression deep just before median base, fine on disc; anterior transverse impression deep, median apex depressed; anterior marginal bead complete. Prosternal process flat ventrally, unmarginated.

Elytra convex, disc elevated relative to scutellum and depressed apex; lateral margins broadly convex, subapical sinuation distinct, sutural apex tightly rounded to angulate; basal groove recurved laterad scutellum to tightly rounded humeri; elytral intervals broadly convex, intervening striae deep, smooth, impunctate; scutellar seta present; anterior dorsal elytral setae set in foveate depressions that cross third interval, posterior 2 dorsal setae set in such foveate depressions or not; 14-15 lateral elytral setae.

Pterothorax. Metepisternum short, broad, trapezoidal, lateral margin 1.3 to 1.5× length of anterior margin.
**Legs.** Profemur without anteroventral setae, with 2 posteroventral setae; mesocoxa with 1 ridge seta; mesofemur with 2 anteroventral setae; metacoxa bisetose, mesal seta absent; metafemur with 2 anteroventral setae; tarsomeres gracile, tarsomeres 1-3 with fine dorsolateral sulci, broadly convex medially; metatarsomere 4 emarginate, outer apical lobe 0.33× median basal tarsomere length; basal tarsomeres with 3 rows of sparse, elongate
ventrolateral setae, medial glabrous area twice as wide as distance between lateral rows; tarsomere 5 with two ventrolateral rows of 6 setae, each much shorter than depth of tarsomere at point of setal insertion.

**Abdomen.** Males with 1 apical seta each side of sternite VII, females with 2 each side.

**Coloration.** Head capsule and elytral disc shiny rufopiceous, pronotal disc, elytral suture, and lateral margins contrasting paler, rufous; antennal scape rufotestaceous, segments 2-4 darkest, with smoky infuscation, outer segments brunneous; trochanters and femora testaceous, the latter with smoky infuscation at middle of length, tibiae and tarsi rufous; pronotal and elytral epipleura rufous, paler than rufopiceous thoracic sternites; abdominal sternites medially rufopiceous, slightly paler laterally.

**Microsculpture.** Dorsal body surface shiny; frons with reduced isodiametric microsculpture, sculpticells more distinct in frontoclypeal grooves and in dorsal impression of neck; pronotal disc with reduced transverse mesh microsculpture, median base and laterobasal depressions a mix of isodiametric and transverse sculpticells; elytral intervals with transverse mesh microsculpture, with sculpticells forming regular transverse rows.

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Fig. 142. Distributional records for *B. (Metromenus) pauma*, new species (●), and *B. (Metromenus) ambiens* (■).
Male genitalia. Aedeagal median lobe gracile, broadly expanded medioventrally, shaft straight; ventral excavation extended to short, slightly downturned apex ended in a broadly rounded tip extended in length subequal to thickness of apex at opening of internal sac (Fig. 141A); basal sagittal crest broad, elongate; median lobe slightly constricted laterally near midlength, tapered to a rounded tip (Fig. 141B).

Female reproductive tract. Gonocoxa basally broad, triangular gonocoxite 2 with acuminate apex (Fig. 141C); gonocoxite 1 with apical fringe of 8-9 setae, mesal 2-3 setae near medioapical angle in double series; gonocoxite 2 with 2-3 lateral ensiform setae and 1 dorsal ensiform seta; apical nematiform setae short, 0.23× length of gonocoxite 2; bursa copulatrix symmetrical, subequal to length of common oviduct, with medial band of spikelike bursal microtrichia (Fig. 141D); dorsal bursal pouch evident as a V-shaped notch in band of bursal microtrichia; spermatheca ovoid, reservoir 0.4× length of spermathecal duct, without basal lobe.

Variation. Specimens from Mt. Waialeale summit exhibit more and longer apical setae on the antennal pedicel: 3-4 easily visible setae about as long as diameter of segment, accompanying the single longer outer seta. Conversely, Alakai and Pihea Trail specimens have 2-3 very short setae on the apical portion of the pedicel. Waialeale specimens are also larger than Alakai-Pihea Trail specimens: standardized body length from 6.8-8.1 mm versus 6.1-6.8 mm. As both of these traits vary continuously, even among the small number of specimens from a limited number of sites (Fig. 142), we recognize only one species.

The variation in body size, wherein Mt. Waialeale specimens are larger than Alakai-Pihea specimens, is also observed in B. elegans. Perhaps environmental factors, such as differences in temperature or moisture associated with elevation and topography, are responsible for these parallel patterns of geographic variation.


Etymology. The species epithet pauma means bent or curved in Hawaiian, referring to the evenly curved pronotal basolateral margins with rounded hind angles (Fig. 137C).

Distribution. This species is distributed across Alakai Swamp from Mt. Waialeale to Kilohana, Kauai (Fig. 142).

Habits. This species both climbs vegetation and is active on the ground. Adults have been collected by pitfall trapping, and by looking under logs and on trails, and along mossy stream banks at night. They have also been found by beating moss-covered ohia lehua (Metrosideros polymorpha) and other vegetation at night.

Phylogenetic relationships. This species is the adelphotaxon of the Kauai species, B. ambiens plus the East Maui species, B. ulaula (Fig. 9).
**Blackburnia (Metromenus) ambiens** (Sharp), new combination

*(Figs. 137D, 142, 143)*

*Platynus ambiens* Sharp, 1903: 228.

**DIAGNOSIS.** One of only 3 species of *Blackburnia* with both the lateral and posterior pronotal setae (Fig. 137D); the others are the related East Maui species, *B. (Metromenus) howarthi* (Fig. 192A) and *B. (Metromenus) calathiformis* (Fig. 187B). *Blackburnia ambiens* is characterized by: 1, rounded pronotal hind angles; 2, tightly rounded, not angulate elytral humeral groove; 3, elytral intervals with isodiametric sculpticells in transverse rows; 4, stout tarsi, basal metatarsomere less than 2× length of inner tibial spur. Standardized body length 7.3 mm.

**Pterothorax.** Metepisternum short, broad, lateral margin 1.3× length of anterior margin.

**Male genitalia.** Aedeagal median lobe stout, medioventral margin expanded, ventral excavation extended to short apex ended in a downturned, bluntly rounded tip, tip extended in length subequal to thickness of apex at opening of internal sac (Fig. 143A); basal sagittal crest very nearly obsolete; median lobe basally broad, laterally constricted near tightly rounded tip (Fig. 143B).

**Female reproductive tract.** This species is currently known only from male specimens. **Holotype** ♂ labeled “Platynus ambiens Type D.S. Kauai Perkins” (BMNH). The card-mounted specimen has been dissected.

**Distribution.** The known locality is in the northwestern Alakai Swamp, Kauai (Fig. 142).
Localities. The only known extant specimen beside the holotype is one collected by C.N. Forbes on Alakai Swamp Trail, VII-1917 (BPBM), even though Perkins (1920, 276) reported existence of 3 specimens in his possession “... preserved many years ago in alcohol for purposes of dissection ...”

Habits. As Forbes was a botanist, and he did not mention any plant association, we assume he collected his specimen from a ground-level situation, though that assumption must be tested by recollecting this species.

Phylogenetic relationships. This species is geographically isolated from its adelphotaxon, *B. ulaula* of Haleakala, East Maui (Fig. 9).

*Blackburnia (Metromenus) ulaula* Liebherr, new species
(Figs. 144A, 145, 146)

**Diagnosis.** A small species, standardized body length 5.6-6.6 mm, with: 1, body flavous to rufous, legs and epipleura not markedly contrasted with color of venter, though femora slightly paler in some specimens; 2, pronotum with lateral setae present, basal margin straight mesad evident but rounded hind angles, basolateral margins straight cephalad of hind angles (Fig. 144A); 3, humeri somewhat narrow, but basal groove tightly rounded, not angulate, on humerus; 4, tarsomeres short, basal metatarsomere less than 2× length of inner tibial spur, dorsolateral sulci broad, shallow, metatarsomeres 1-3 broadly convex mediad; 5, females with 2 apical setae each side of sternite VII.

**Description.** Head capsule broad, eyes small in diameter but convex, ocular ratio 1.45; labrum elongate, median length 0.5× width, front margin broadly emarginate, median pair of setae present or absent; frontoclypeal grooves broad, shallow, indistinct; antenna I pedicel with longer outer seta and 3-4 apical setae; mentum tooth broadly rounded to slightly bifid.

Prothorax. Pronotal lateral margins nearly evenly convex from basal to front angles, margin straight for short distance before evident but rounded hind angles; lateral marginal depression narrow near lateral setae, slightly broader near rounded and slightly protruded front angles, bordered laterally by a fine marginal bead; laterobasal depressions broad, flat, with a tubercle, bordered laterally by slightly raised margin, posteriorly by a distinct basal marginal bead that is continuous, though finer, mediad; median base smooth, not distinct from disc; median longitudinal impression extended from median base to cephalad of shallow anterior transverse impression; anterior marginal bead fine but continuous mediad. Prosternal process convex ventrally, unmargined posteriorly.

Elytra. Humeri moderately narrow, elytra broadest just cephalad the distinct subapical sinuations; lateral marginal depression narrow throughout length; basal groove evenly recurved laterad scutellum, tightly rounded on humerus; elytral intervals moderately convex, striae finely incised, impunctate; scutellar seta present; 3 dorsal elytral setae in depressions not extended more than 0.5× width of third interval; 12-13 lateral elytral setae.

Pterothorax. Metepisternum moderately elongate, broad, trapezoidal, lateral margin 1.3 to 1.5× length of anterior margin.

Legs. Profemur without anteroventral setae, with 2 posteroverental setae; mesocoxa with 1 ridge seta; mesofemur with 2 anteroventral setae; metacoxa bisetose, mesal seta absent; metafemur with 2 anteroventral setae; tarsomeres short, tarsomeres 1-3 with fine dorsolateral sulci, broadly convex mediad; metatarsomere 4 nearly straight apically, outer
apical lobe 0.3× median basal tarsomere length; basal tarsomeres with 3 rows of sparse, elongate ventrolateral setae, medial glabrous area twice as wide as distance between lateral rows; tarsomere 5 with two ventrolateral rows of 6 setae, each much shorter than depth of tarsomere at point of setal insertion.

**Abdomen.** Males with 1 apical seta each side of sternite VII, females with 2 setae.

**Coloration.** Nearly uniformly colored, from flavous to brunneous, though head capsule usually darkest; basal 3 antennomeres, palpi, and femora palest, testaceous, outer antennomeres, tibiae, tarsi, thoracic and abdominal sternites darker, brunneous.

**Microsculpture.** Head capsule with evident though reduced isodiametric microsculpture; pronotal disc with reduced transverse mesh microsculpture, median base and laterobasal depressions with distinct isodiametric sculpticells; elytra with transversely stretched sculpticells arranged in transverse rows, sculpticells slightly effaced, and therefore producing a slight alutaceous lustre.

**Male genitalia.** Aedeagal median lobe gracile, broadly expanded medioventrally, shaft nearly straight; ventral excavation extended to short, downturned apex ended in a broadly rounded tip extended in length subequal to thickness of apex at opening of internal sac (Fig. 145A); basal sagittal crest shallow, short; median lobe slightly constricted laterally near midlength, tapered to a finely rounded tip (Fig. 145B).
Fig. 145. B. (Metromenus) ulaula, new species. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view.

Female reproductive tract. Gonocoxa basally broad, triangular gonocoxite 2 with acuminate apex (Fig. 145C); gonocoxite 1 with apical fringe of 8-10 setae, mesal 4-5 setae near medioapical angle in double series; gonocoxite 2 with 2 lateral ensiform setae and 1 dorsal ensiform seta; apical nematiform setae moderately elongate, 0.29× length of gonocoxite 2; bursa copulatrix symmetrical, subequal to length of common oviduct, with medial band of spikelike bursal microtrichia and broad dorsal bursal pouch; spermatheca elongate, reservoir 1.3× length of spermathecal duct, without basal lobe.


Paratypes. MAUl, Haleakala: Haleakala N.P., Kipahulu Valley, Central Pali Tr., beating vegetation at night, 910 m, 30-IV-1991, Liebherr & Medeiros (CUIC, 1), 1200 m, 29-IV-1991, Liebherr & Medeiros (CUIC, 5), sifting leaf/moss litter, 910 m, 30-IV-1991, Liebherr & Medeiros (CUIC, 1), 1200 m, 29-IV-1991, Liebherr & Medeiros (CUIC, 6), Kipahulu west rim ESE Kuiki, ohia, sifting humus, 1850 m, 15-V-1993, Liebherr & Medeiros (CUIC, 1), Northeast Rift, Midecamp Bog Cabin, ohia, sifting humus, 1665 m, 18-V-1993, Liebherr & Medeiros (CUIC, 1); Hana For. Res., Heleleikeoha Str. fence camp, pyr. fog ohia w/ moss, 1615 m, 11-V-1998, Liebherr (CUIC, 2), Polhemus (NMNH, 11), pyr. fog Cibotium, 12-V-1998, Liebherr (CUIC, 1), pyr. fog ohia w/ moss (CUIC, 10), Polhemus (NMNH, 2), ridge S fence camp, pyr. fog ohia w/ moss, 1785 m, 12-V-1998, Polhemus (NMNH, 6), Heleleikeoha Str., ridge W, under logs, 1740 m, 11-V-1998, Ewing (CUIC, 1), 12-V-1998, Liebherr (CUIC, 1); Hanawi N.A.R., Kopiliula Str., uluhe fern under tent, 1120 m, 03-V-1998, Liebherr (CUIC, 1), Kuhiwa Vy., Poouli Cabin, pyr. fog ohia w/ moss, 1590
Fig. 146. Distributional records for *B. (Metromenus) ulaula*, new species.

m, 05-V-1998, Liebherr (CUIC, 2), Polhemus (NMNH, 10), pyr. fog ohia roots/trunk, 06-V-1998 (NMNH, 2), pyr. fog ohia w/ moss, 1590 m, 06-V-1998, Liebherr (CUIC, 3); Koolau For. Res., Koolau Gap, Halehaku, pyr. fog ohia w/ moss, 1325 m, 13-V-1998, Liebherr (CUIC, 4), Kula Pipeline Rd., pyr. fog koa, 1160 m, 15-V-1998, Liebherr (CUIC, 1), pyr. fog moss ohia/logs (CUIC, 3), pyr. fog ohia w/ moss, Polhemus (NMNH, 4), Kula Pipeline Rd. W Waikamoi Gulch, pyr. fog ohia w/ moss, 960 m, 15-V-1998, Polhemus (NMNH, 4), pyr. fog ohia + *Cibotium*, 970 m, Liebherr (CUIC, 6); Waikamoi Flume, under boards, 1300 m, 26-V-1997, Liebherr (CUIC, 7), Waikamoi Gulch to Haipuaena Gulch, under boards/wet ohia for., 1300 m, 11-IV-1991, Liebherr (CUIC, 45), Waikamoi Gulch, moss, beating/sifting, 1300 m, 09-V-1991, Liebherr (CUIC, 6), under boards/wet ohia for., 1300 m, 09-V-1991, Liebherr (CUIC, 5).

**Etymology.** The species epithet *ulaula* is the Hawaiian word for the color red, indicative of the reddish body color of individuals of this species.

**Distribution.** This species is widely distributed across the windward forests of Haleakala, East Maui (Fig. 146).

**Habits.** Adults of *B. ulaula* have been found predominantly on the ground, either under boards and logs, or in sifted humus. This species must also climb vegetation to some degree, as about 10% of collected individuals have been beaten from vegetation at night.

**Phylogenetic relationships.** This species is the lone representative of its clade on Haleakala, West Maui, and is geographically isolated from its adelphotaxon, *B. ambiens* of Kauai (Fig. 9). This area relationship, taken in isolation, supports colonization directly from Kauai to Maui Nui. When viewed in the context of patterns across the platynine radiation,
it suggests progressive colonization from Kauai to Oahu and then Maui Nui, with subsequent extinction of related species on the more highly eroded island of Oahu, as discussed in Liebherr (1997).

Blackburnia (Metromenus) kauaiensis (Sharp), new combination
(Figs. 144B, 147, 148)

Mesothriscus kauaiensis Sharp, 1903: 226.

DIAGNOSIS. This (Fig. 144B) and the next 4 species—B. transiens, B. optima, B. alternans, and B. opaca (Fig. 149)—are the sole species within subgenus Metromenus to possess costate elytral intervals. In its least developed condition, as in B. kauaiensis, elytral intervals 1, 5, and 7 are more elevated and medially angulate than the other intervals. This condition, based both on cladistic relationships in Liebherr & Zimmerman (1998) and on those in the cladistic analysis above, has arisen 5 times independently across the radiation, in all lineages in an ancestor residing on Kauai. In addition to the distinctive carinae, this species is diagnosed by: 1, anterior and posterior dorsal elytral setae centered in foveate depressions completely interrupting the convex third elytral interval; 2, elytra with flat, transversely stretched sculpticells arranged in transverse rows, the surface dark brunneous, shiny, not glaucous or granulate; and 3, tarsomeres stout, basal metatarsomeres slightly less than 2.0× length of inner tibial spur. Some B. alternans have the anterior dorsal elytral seta in a foveate depression, and the elytral microsculpture is not much rougher than that of B. kauaiensis. The two species are distinguished from each other by the very small and flat eyes in B. alternans, ocular ratio 1.35-1.40, versus the more protuberant eyes of B. kauaiensis, ocular ratio 1.45-1.50. Moreover, B. kauaiensis tends to be larger: standardized body length 6.0-7.2 mm.

Pterothorax. Metepisternum short, broad, trapezoidal, lateral margin 1.1 to 1.5× length of anterior margin.

Male genitalia. Aedeagal median lobe gracile, broadly expanded medioventrally, ventral excavation extended to elongate, downturned apex extended 1.67× thickness of apex at opening of internal sac, ended in an acuminate tip (Fig. 147A); basal sagittal crest obsolete; median lobe narrow throughout, constricted on right surface, tapered to a finely rounded tip (Fig. 147B).

Female reproductive tract. Gonocoxa basally broad, triangular gonocoxite 2 with acuminate apex (Fig. 147C); gonocoxite 1 with apical fringe of 11-13 setae, mesal 5-6 setae near medioapical angle in double series; gonocoxite 2 with 3 lateral ensiform setae and 1 dorsal ensiform seta; apical nematiform setae short, 0.23× length of gonocoxite 2; bursa copulatrix symmetrical, 1.4× length of common oviduct, with medial band of spikelike bursal microtrichia interrupted by a V-shaped notch of glabrous membrane on dorsal bursal surface, broadest end apical; spermatheca elongate, reservoir 1.0× length of spermathecal duct, without basal lobe.

Lectotype ♀ labeled “♀ Mesothriscus kauaiensis Type D.S. 527. Koholualamo, Kauai, 4000 ft. Perkins iv.1895.” (BMNH) hereby designated. Perkins' lot 527 is from the area now known as Kaholualamo, on the southeastern rim of Waimea Canyon.

Distribution. This species is broadly distributed over montane Kauai (Fig. 148).
Localities. Known from Pihea Trail, Alakai Swamp Trail at Kawaiolino Stream and at Pihea Trail junction, as well as Waialeale summit, Kaholuamano, and Mt. Kahili. Localities range in elevation from 895 to 1530 m.

Habits. This species is active on the ground as well as plant surfaces. It has been beaten from Metrosideros (ohia lehua) and low ferns at night. It can also be seen running on open trails or moss mats and mossy stream banks at night. Late winter records are from under logs and moss mats, suggesting overwintering in association with ground level situations. Nonetheless, adults have been captured in pitfall traps in May and July, indicating movement on the ground during the breeding season as well as when new adults are emerging.

Phylogenetic relationships. This species is the adelphotaxon of four other carinate Kauai species: B. optima to B. alternans (Fig. 9). It is sympatric over parts of its range with the geographically restricted species B. optima and B. opaca (Figs. 148, 152), and though records for B. kauaiensis are sparser, its distribution overlaps almost entirely the distribution of B. alternans (Fig. 156).
Blackburnia (Metromenus) optima (Sharp), new combination
(Figs. 149A, 150, 151, 152)

*Mesothriscus optimus* Sharp, 1903: 227.

**DIAGNOSIS.** Pronotal setation as in *B. kauaiensis*, *B. alternans*, and *B. opaca*, but diagnosed by: 1, angulate carinae on elytral intervals 1, 3, 5, 7, and a less raised angulate interval 6, all carinae continuous except for that on interval 3, which is interrupted by the dorsal elytral setae; 2, eyes small but convex, ocular ratio 1.55 (Fig. 149A); 3, pronotal lateral margins moderately broad, basal marginal bead complete; and 4, females with 3 apical setae each side of sternite VII (as in *B. kauaiensis*, but opposing *B. alternans* and *B. opaca*, which have 2 setae each side). Standardized body length 6.6-6.7 mm.

**Pterothorax.** Metepisternum short, broad, almost rectangular, lateral margin 1.3× length of anterior margin.

**Male genitalia.** Aedeagal median lobe gracile, straight medioventrally, ventral excavation extended to downturned apex extended 1.33× thickness of apex at opening of
Fig. 149. Blackburnia species habitus, dorsal view. A. B. (Metromenus) optima. B. B. (Metromenus) transiens. C. B. (Metromenus) opaca. D. B. (Metromenus) alternans.
Fig. 150. B. (Metromenus) optima. A. Male aedeagal median lobe, internal sac everted, right lateral view. B. Male aedeagal median lobe, euventral view.

internal sac, ended in a rounded tip (Fig. 150A); basal sagittal crest elongate and narrow; median lobe moderately narrow basally, tapered evenly to a finely rounded tip (Fig. 150B).

**Female reproductive tract.** Gonocoxa basally broad, triangular gonocoxite 2 with acuminate apex (Fig. 151A); gonocoxite 1 with apical fringe of 13-14 setae, mesal 8 setae nearest medioapical angle in double series; gonocoxite 2 with 2 lateral ensiform setae and 1 dorsal ensiform seta; apical nematiform setae short, 0.26× length of gonocoxite 2; bursa copulatrix symmetrical, subequal to length of common oviduct, with a broad rounded dorsal pouch (Fig. 151B) and medial band of spikelike bursal microtrichia; spermatheca ovoid, reservoir 0.7× length of spermathecal duct, without basal lobe.

**Lectotype** σ labeled “σ Mesothriscus optimus Type D.S. 258. Mts. Waimea, Kauai, 4000 ft. Perkins. V 1894” (BMNH) hereby designated. Perkins’ lot 258 is described as “Mts. above Waimea, Kauai, about 4000 ft. V ‘94” (Anonymous n.d.). During this time he stayed in the mountain house of George C. Munro, and collected with him (Perkins 1894b). He also mentions visiting with the Gay family, suggesting he was in the vicinity of Kaholauamano. A specimen collected in VIII-1896, lot 631, is labeled “high plateau,” most likely the plateau of the Alakai along Mohihi-Waialae Trail above Waialae Cabin. This was the site of Perkins’ “1st Camp 4000 ft.” (Perkins 1895a, b, Liebherr and Polhemus 1997a). This area is designated as type locality.

**Distribution.** This species is known from Perkins’ collections in the eastern reaches of Waimea Canyon and Kalalau, Kauai (Fig. 152).

**Localities.** Besides the Perkins localities, collected at Kalalau Ridge in Kokee State Park.

**Habits.** This rare species is known from three specimens, two from Perkins and one collected by E.C. Van Dyke (CASC). Nothing is known of its way of life.

**Phylogenetic relationships.** This species is placed within the five-species clade of carinate Kauai species in subgenus *Metromenus* (Fig. 9). *Blackburnia optima* shares the leeward forest habitats occupied by the related *B. opaca* and *B. alternans* (Figs. 152, 156).
Fig. 151. *B. (Metromenus) optima*. A. Left female gonocoxa, ventral view. B. Female bursa copulatrix, dorsal view, showing vaselike base, broad folded margin of dorsal pouch, and spermatheca.
**Blackburnia (Metromenus) transiens** (Sharp), new combination  
(Figs. 148, 149B, 153)

*Atelothrus transiens* Sharp, 1903: 221.

**Atelothrus transiens** Sharp, 1903: 221.

DIAGNOSIS. Within this clade of species united by synapomorphies of elytral carination and granulate microsculpture, this species stands out by presence of basal pronotal setae and absence of lateral setae, illustrating the evolutionary plasticity of these setae. *Blackburnia transiens* may also be diagnosed by: 1, presence of sharp-edged carinae on elytral intervals 1, 3, 5, and 7, with the other intervals evenly angulate (Fig. 149B); and 2, head, pronotal lateral marginal depressions, and elytra with distinct microsculpture, which on the elytra comprises rough-sided isodiametric sculpticells not arranged in transverse rows. Standardized body length 5.3-6.9 mm.

**Pterothorax.** Metepisternum short, broad, trapezoidal, lateral margin 1.5 to 1.6× length of anterior margin.

**Male genitalia.** Aedeagal median lobe gracile, elongate, slightly recurved medioventrally, ventral excavation extended to elongate, downturned apex extended 1.33× thickness of apex at opening of internal sac, ended in a rounded tip (Fig. 153A); basal
Fig. 153. B. (Metromenus) transiens. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view.

sagittal crest elongate and narrow; median lobe narrow throughout, straight on right surface, tapered on left to a finely rounded tip (Fig. 153B).

**Female reproductive tract.** Gonocoxa basally broad, triangular gonocoxite 2 with acuminate apex (Fig. 153C); gonocoxite 1 with apical fringe of 8-10 setae, mesal 4 setae near medioapical angle in double series; gonocoxite 2 with 3 lateral ensiform setae and 1 dorsal ensiform seta; apical nematiform setae short, 0.25× length of gonocoxite 2; bursa copulatrix symmetrical, subequal to length of common oviduct, with a broad rounded dorsal pouch and medial band of spikelike bursal microtrichia; spermatheca ovoid, reservoir 0.7× length of spermathecal duct, without basal lobe.

**Lectotype** ♂ labeled “Atelothrus transiens Kauai, 2500 ft., II 1897” and “668” on reverse of card (BMNH) hereby designated. Perkins’ lot 668 came from a camp at 760 m in Makaweli Valley (Anonymous n.d.), on the south flank of Waialeale massif.

**Distribution.** This species is known only from the Makaweli region of Kauai (Fig. 148).

**Localities.** Perkins collected the 54 known specimens of this species from what he called “Makaweli, 2500 ft.” during February 1897. During this trip “in the mountains of the Makaweli district,” Perkins did not collect above 3000 ft. (910 m) (Perkins 1897), though he mentions collecting on the ridge between Hanapepe and Makaweli—i.e., in the vicinity of Peapoa Peak (Armstrong 1983) south of the Olokele River Canyon.

**Habits.** Perkins (1913, cxli) believed this species was restricted to arboreal microhabitats.
**Phylogenetic relationships.** This species is geographically isolated among the carinate *Metromenus* clade (Fig. 9) by its occupation of the ridge bordered by the Olokele and Hanapepe Rivers (Fig. 148).

*Blackburnia (Metromenus) opaca* (Sharp), new combination

(Figs. 149C, 152, 154)

*Mesothriscus opacus* Sharp, 1903: 227.

**DIAGNOSIS.** Unique among carinate Kauaiian species by the irregularly papillose elytral carinae (Fig. 149C), which are elevated and angulate on intervals 1, 3, 5, and 7, whereas the intervening intervals are irregularly elevated medially, the medially elevated portions isolated into a series of irregular papillae; eyes small but convex, ocular ratio 1.55-1.60; laterally setose pronotum with moderately broad lateral margins flavous, contrasted with brunneous disc; elytra with granulate isodiametric microsculpture giving surface a leathery appearance. As in *B. alternans*, females have only 2 apical setae each side of sternite VII. Standardized body length 5.4-6.6 mm.

**Pterothorax.** Metepisternum short, broad, trapezoidal, lateral margin 1.2 to 1.3× length of anterior margin.

**Male genitalia.** Aedeagal median lobe gracile, slightly recurved medioventrally, ventral excavation extended to slightly downturned apex extended in length 1.3× thickness of apex at opening of internal sac, ended in a rounded tip (Fig. 154A); basal sagittal crest short and broad to obsolete; median lobe moderately broader basally, slightly constricted laterally along right side, tapered to a finely rounded tip (Fig. 154B).

**Female reproductive tract.** Gonocoxa basally broad, triangular gonocoxite 2 with acuminate apex (Fig. 154C); gonocoxite 1 with apical fringe of 9 setae, mesal 4 setae near medioapical angle in double series; gonocoxite 2 with 2-3 shorter lateral ensiform setae and 1 dorsal ensiform setae, lateral ensiform setae 0.14× length of gonocoxite 2; apical nematiform setae short, 0.28× length of gonocoxite 2; bursa copulatrix symmetrical, subequal to length of common oviduct, with a broad, indistinct dorsal pouch and a medial band of spikelike bursal micrornichia; spermatheca ovoid, reservoir 0.7× length of spermathecal duct, without basal lobe.

**Lectotype** ‡ labeled "♀ Mesothriscus opacus Type D.S. 529. Koholuamano, Kauai, 4000 ft. Perkins. iv.1895. (BMNH) hereby designated. The type was collected on 13.IV.1895 (Anonymous n.d.), a day that Perkins hiked far back into the Alakai above Kaholuamano (Perkins 1895a). He did not record collecting this peculiar looking species.

**Distribution.** This species is found in the mountains across the higher reaches of Waimea Canyon, Kauai (Fig. 152).

**Localities.** Recorded from Kokee State Park area at Ka Uno o Hua Ridge, Kumuwela Ridge, and Halemanu. It is also recorded from south of Mohihi Ridge. Perkins collected this species at Kaholuamano. Elevations of these localities span 910 to 1280 m.

**Habits.** The only information about way of life of this species comes from a collection under logs and rocks made along Ka Uno o Hua Ridge, 21-VII-1937 (Zimmerman, BPBM), suggesting that this species inhabits forest-floor microhabitats.

**Phylogenetic relationships.** This species is sympatric (Figs. 152, 156) with its adelphotaxon, *B. alternans* (Fig. 9).
Blackburnia (Metromenus) alternans (Sharp), new combination
(Figs. 130E-F, 149D, 155, 156)

Mesothriscus alternans Sharp, 1903: 228.

DIAGNOSIS. This species has the eyes much reduced (Fig. 149D), and the neck elongate; pronotum narrow, laterally setose, with narrow lateral marginal depressions; elytral carinae on intervals 1, 3, 5, and 7 angulate with tightly rounded apices; tarsomeres short, basal metatarsomere less than 2.0× length of inner tibial spur; females with 2 apical setae each side of sternite VII. In dorsal microsculpture, *B. alternans* approaches *B. kauaiensis*, but the very flat eyes in this species (Figs. 144B, 149D) associated with an elongate neck, giving the head a pedunculate appearance, are easy means of identification. Standardized body length 5.0-6.6 mm.

**Pterothorax.** Metepisternum short, broad, rectangular, lateral margin 1.2 to 1.4× length of anterior margin.

**Male genitalia.** Aedeagal median lobe gracile, straight medioventrally, ventral excavation extended to evenly curved apex extended in length subequal to thickness of apex at opening of internal sac, ended in a finely rounded tip (Fig. 155A); basal sagittal crest elongate and narrow to obsolete; median lobe moderately broader basally, constricted laterally along length, tapered asymmetrically to a finely rounded tip (Fig. 155B).
Fig. 155. *B. (Metromenus) alternans*. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view.

**Female reproductive tract.** Gonocoxa basally broad, triangular gonocoxite 2 with finely rounded apex (Fig. 155C); gonocoxite 1 with apical fringe of 8 setae, mesal 3 setae near medioapical angle in double series; gonocoxite 2 with 2 lateral ensiform setae and 1 dorsal ensiform seta; apical nematiform setae short, 0.28× length of gonocoxite 2; bursa copulatrix symmetrical, subequal to length of common oviduct, with a medial band of spikelike bursal microtrichia, a V-shaped notch of glabrous membrane on dorsal surface, the broadest end apical; spermatheca elongate, reservoir 1.0× length of spermathecal duct.

**Lectotype** ♀ labeled “♂ Mesothriscus alternans Ind. typ. D.S. Waimea 4000 ft. V.1894. Perkins 262” (BMNH) hereby designated. Perkins’ lot 262 is described as “Mts. above Waimea, Kauai, 100 Carabids, about 4.000 ft. V ‘94” (Anonymous n.d.). As for *B. optima*, this period of Perkins’ collecting included the southeast rim of Waimea Canyon and the high plateau above Waialae Cabin.

**Distribution.** This species exhibits one of the more widespread distributions in the mountains of Kauai, being found from Mt. Kahili to Nualolo (Fig. 156).
**Localities.** Found in Kokee State Park at Ka Uno o Hua Ridge, Honopu Trail, Mililii Ridge, Kumuwela Ridge, and Halemanu, as well as along Nualolo Trail. Eastward into Alakai Swamp recorded from Pihea and Alakai Swamp Trails and their junction, Lehua Makanoe bog, Mohihi Ridge, Kawaiki Stream, Koaie Stream, Kaholuamano, Waiiaa Falls, Makaweli, and Wahiawa Stream. These sites range from 605 to 1395 m elevation.

**Habits.** This species follows the typical Kauai life cycle in which winter records (December to March) involve adult beetles being found under logs, or within moss and leaf litter on the ground. During May this species is commonly encountered on the ground, where it can be seen walking on open mud or on moss mats at night. Ground activity within the closed-canopy forest is supported by the capture of many adults via pitfall traps in May and July (Asquith, BPBM/CUIC). Adults also climb vegetation, with substrate plants including *Clermontia, Metrosideros* (ohia lehua), and low ferns.

**Phylogenetic relationships.** This species is the adelphotaxon of *B. opaca* (Fig. 9).
**Blackburnia** (Metromenus) huhula Liebherr, new species
(Figs. 157A, 158, 159)

**DIAGNOSIS.** This peculiar species is characterized by small, flat eyes, palpomeres covered with a sparse pelage of fine setae, a 4-setose anterior labral margin (or median pair of setae very small), a cordate and laterally setose pronotum, and medially flat elytra with sutural interval and lateral and apical margins paler than disc (Fig. 157A). Standardized body length 5.4-6.1 mm. This species shares with the following two species—*B. muscicola* and *B. paludicola*—pronotum with complete basal marginal bead, antennal pedicle with 4 apical setae in addition to longer outer seta, apically truncate mentum tooth, and visible isodiametric microsculpture on vertex of head. *Blackburnia muscicola* and *B. paludicola* are considerably larger and darker (Fig. 157B-C), and lack the first listed characters above.

**DESCRIPTION.** **Head.** Eyes very flat, though only moderately reduced in diameter, ocular ratio 1.33; frontoclypeal grooves deepest just caudad frontoclypeal suture, linearly extended posteriorly to mesad anterior supraorbital setae; neck only slightly constricted, dorsal impression very shallow; antennal pedicel with 4 apical setae in addition to longer outer seta; labrum straight apically, median pair of setae reduced, very small, or absent, apical margin therefore appearing 4-setose; mandibles slightly elongate, extended beyond labrum 0.83x distance from dorsal condyle to anterior labral margin; apical two segments of maxillary palpomeres and apical labial palpomere covered with a sparse pelage of fine setae; mentum tooth apical truncate or broadly rounded.

**Prothorax.** Pronotum markedly cordate, front angles protruded, lateral marginal depressions broadly explanate without marginal bead; lateral pronotal setae present, basal setae absent; basolateral margins sinuate before obtuse-angulate hind angles; laterobasal depressions broad, with a low, diagonally raised tubercle, laterally bordered by explanate margin, bordered posteriorly by an indistinctly raised margin laterad tubercle, by a marginal bead mesad tubercle; median base smooth, margined posteriorly by complete marginal bead; median longitudinal impression present on disc, finely inscribed, extended to before the very shallow, indistinct anterior transverse impression; median apex bordered with anterior marginal bead. Prosternal process convex, unmargined posteriorly.

**Elytra** with disc flat; basal groove recurved onto anteriorly protruded, tightly rounded to slightly angulate humeri; lateral margins outside ninth stria explanate; subapical sinuation distinct, sutural apex tightly rounded; elytral intervals slightly convex, striae impunctate, slightly wavering; scutellar seta and 3 dorsal elytral setae present; 13-15 lateral elytral setae.

**Pterothorax.** Metepisternum short, broad, trapezoidal, lateral margin 1.2 to 1.3x length of anterior margin.

**Legs.** Profemur without anteroventral setae, with 2 posteroventral setae; mesocoxa with 1 ridge seta; mesofemur with 2-3 anteroventral setae; metacoxa bisetose, mesal seta absent; metafemur with 2 anteroventral setae; tarsomeres gracile, basal tarsomere cylindrical, tarsomeres 2-3 slightly expanded apically; basal 3 tarsomeres with distinct dorsolateral sulci, metatarsomeres 2-3 medially subcarinate; metatarsomere 4 apically emarginate, outer apical lobe 0.3x median basal tarsomere length; basal tarsomeres with 3 rows of elongate ventrolateral setae, median glabrous space about as broad as distance between lateral rows; tarsomere 5 with two ventrolateral rows of 6 setae equal to or greater than depth of tarsomere at point of setal insertion.
Abdomen. Males with 1 apical seta each side of sternite VII, females with 3 each side, occasional specimens with 2 unilaterally for a total of 5 setae.

Coloration. Head capsule darkest, brunneous; pronotum and elytra with pale brunneous disc and broadly flavous margins; palpi, antennae, pronotal and elytral epipleura, and legs testaceous except for slightly darker femoral-tibial joints, contrasted with brunneous thoracic ventrites; abdominal sternites brunneous medially, broadly paler laterally, lateral reaches concolorous with elytral epipleura.

Microsculpture. Vertex of head with visible isodiametric microsculpture, sculpticells flat and shiny, microsculpture on dorsal neck constriction more raised and transverse; elytral disc covered with distinct transverse mesh microsculpture; elytra covered with distinct isodiametric mesh, sculpticells flat on median 7 intervals, more granulate on outer 2 intervals and at apex; thoracic and abdominal venter covered with a swirled mesh of transverse sculpticells.

Male genitalia. Aedeagal median lobe gracile, straight medioventrally, shallow ventral excavation extended to slightly angulate, blunt apex ended in a rounded tip (Fig. 158A); basal sagittal crest obsolete; median lobe very slender throughout length, needlelike, evenly tapered to a finely rounded tip (Fig. 158B).

Female reproductive tract. Gonocoxa basally broad, triangular gonocoxite 2 with acuminate apex (Fig. 158C); gonocoxite 1 with apical fringe of 7 setae in single series; gonocoxite 2 with 2 lateral ensiform setae and 1 dorsal ensiform seta; apical nematiform
setae short, 0.24× length of gonocoxite 2; bursa copulatrix symmetrical, 0.7× length of common oviduct, with rounded dorsal pouch and medial band of spikelike microtrichia; spermatheca elongate, reservoir 0.8× length of spermathecal duct, without basal lobe.

**Holotype** ♂ labeled “HI: Oahu Mt. Ka‘ala 18-V-1991 el. 1210 m J.K. Liebherr beating ohia & tree ferns” (CUIC).

**Paratypes.** OAHU, Waianae Range: Mt. Kaala, 01-III-1980, Linney (UHEM, 1), 1200 m, X-1959, Beardsley (BPBM, 1), 1210 m, VII-1954, Ford (BPBM, 1), 1220 m, 31-VIII-1966, Gillogly & Gillogly (NMNH, 2), ground, 1220 m, 28-IV-1938, Hoyt (BPBM, 1), summit, 03-I-1925, Swezey (BPBM, 1), ohia/fern/moss, beat/sift, 1210 m, 22-IV-1991, Liebherr (CUIC, 1), sifting litter, tree fern, 1210 m, 18-V-1991, Liebherr (CUIC, 1), ohia/tree ferns, beating, 1210 m, 18-V-1991, Liebherr (CUIC, 1), under rocks, road debris, 1210 m, 18-V-1991, Liebherr (CUIC, 2), Berlese leaf & log litter, 1175 m, 08-VI-1991 Newton & Thayer (FMNH, 3).

**Etymology.** The species epithet **huhula** is Hawaiian for body hair, denoting setose pelage covering the palpi.

**Distribution.** This species is known only from the summit bog area of Mt. Kaala Natural Area Reserve, Oahu (Fig. 159).
**Habits.** Recorded predominantly from terrestrial microhabitats, including sift samples of leaf, log, and fern litter, as well as under wet roadside debris. Thus we infer that this species occupies terrestrial microhabitats.

**Phylogenetic relationships.** This species is the adelphotaxon of a large clade successively subtended by the two Oahu species, *B. muscicola* and *B. paludicola* (Fig. 9). All three species are sympatrically distributed on Mt. Kaala, in the Waianae Mountains (Figs. 159, 162), suggesting substantial secondary dispersal after origin of these species.

*Blackburnia (Metromenus) muscicola* (Blackburn), new combination
(Figs. 130C-D, 157B, 159, 160)

Anchomenus muscicola Blackburn, 1877: 144.
Metromenus muscicola: Blackburn & Sharp, 1885: 211.
Mesothriscus prognathus Sharp, 1903: 223 (new synonymy).

**Diagnosis.** Among species with laterally setose, cordate pronota (Figs. 157A-C, 209), *B. muscicola* and the following species, *B. paludicola*, stand apart due to the distinct isodiametric microsculpture on the vertex, and the distinctly angulate pronotal hind angles (Fig. 157B-C). Metatarsomere 4 of *B. muscicola* is emarginate, with the outer apical lobe 0.6× median basal tarsomere length; apical setae of metatarsomere 4 located at the apex of the lobe on both inner and outer sides (Fig. 130C), not positioned toward dorsum and therefore away from apex (contra Fig. 130G). As mentioned under *B. huhula*, the antennal pedicel of that species, *B. muscicola*, and *B. paludicola* all exhibit 4 apical setae in addition to the longer outer seta. Standardized body length 5.9-8.2 mm.

**Pterothorax.** Metepisternum moderately shortened, broad, lateral margin 1.3 to 1.4× length of anterior margin.

**Male genitalia.** Aedeagal median lobe gracile, slightly expanded medioventrally, ventral excavation extended to slightly downturned apex ended in a rounded tip, tip extended 1.67× thickness of apex at opening of internal sac (Fig. 160A); basal sagittal crest shallow to obsolete; median lobe moderately slender basally, slight constriction on right side, tapered to rounded tip (Fig. 160B).

**Female reproductive tract.** Gonocoxa basally broad, triangular gonocoxite 2 with acuminate apex (Fig. 160C); gonocoxite 1 with apical fringe of 10 setae, mesal 4 near medioapical angle in double series; gonocoxite 2 with 3 lateral ensiform setae and 1 dorsal ensiform seta; apical nematiform setae short, 0.26× length of gonocoxite 2; bursa copulatrix symmetrical, subequal to length of common oviduct, constricted basally into a vaselike configuration, with a rounded dorsal pouch and a medial band of spikelike bursal microtrichia (Fig. 160D); spermatheca elongate, reservoir 0.8× length of spermathecal duct, without basal lobe.

**Types.** For *Anchomenus muscicola*, lectotype ♂ on 2-lined card, with top line thickest—Blackburn’s Oahu code (Zimmerman 1957)—and “muscicola” handwritten on reverse of card. For *Mesothriscus prognathus*, holotype ♀ labeled “♀ Mesothriscus prognathus Type D.S. Oahu Koebele” (BMNH).

**Distribution.** This species is found on Mt. Kaala, and along the entire Koolau Range, Oahu (Fig. 159).
Fig. 160. *B. (Metromenus) muscicola*. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view. D. Female bursa copulatrix, ventral view, showing vaselike base, medial band of spikelike microtrichia, and spermatheca.

**Localities.** In the Waianae Mountains, recorded from Mt. Kaala summit and Dupont Trail, plus Puu Kalena. Distributed along the length of the Koolau Range, including Kawaiola Gulch, Kaluanui and Castle Trail, Helemano, Poamoho Trail, Punalu'u, Kahana, Wahiawa, Puu Kaaumakua, Schofield-Waikane Trail, north peak of Eleao massif, Puu Keahiakahoe massif at Tripler Ridge, Puu Lanihuli, Nuuana Pali, Konahuanui, Pauoa Flats, Tantalus, Maunawili, and Waialae Iki.

**Habits.** This species is active both on the ground and climbing in vegetation. It has been collected from *Cibotium, Gunnera, Metrosideros*, and bananas. Beetles have been observed...
in terrestrial situations including creekbeds and open trails at night. Specimens have been found under rocks, logs, or boards during day. This species has the distinction of being collected by Perkins “above Jim Dole’s house,” indicating support of Perkins’ collecting activities by the socioeconomically most powerful people of Hawaii.

**Phylogenetic relationships.** This species is the putative adelphotaxon of 26 other species in the *B. paludicola-B. haleakala* clade (Fig. 9). *Blackburnia muscicola* is broadly sympatric with most other Oahu species, including the other eight in its adelphotaxon plus others in less closely related lineages.

*Blackburnia (Metromenus) paludicola* Liebherr, new species
(Figs. 157C, 161, 162)

**DIAGNOSIS.** As *B. muscicola* with cordate, laterally setose pronotum with obtusely angulate hind angles and posteriorly expanded laterobasal margins (Fig. 157B-C), antennal pedicel with longer outer seta and 4 shorter apical setae, and distinct isodiametric microsculpture on vertex of head, but, substantially broader, the prothoracic margins broadly elevated and elytral humeri laterally expanded. The sister-taxon relationship between the two species is obvious, with this species exhibiting allometric increase in the lateral dimensions of pronotum and elytra. Standardized body length 6.3-7.8 mm.

**DESCRIPTION.** Head elongate, eyes moderately convex, ocular ratio 1.53; frontoclypeal grooves deeply impressed, broad, narrowing in an outwardly directed triangle directed at anterior supraorbital setae; frons with indistinct, longitudinal median impression between anterior supraorbital setae; neck indicated by distinct dorsal impression; labrum straight apically, with 6 setae, mesal pair about ½ length of outer pair; mentum tooth apically truncate to bifid.

**Prothorax.** Pronotum with broadly explanate lateral margins, lateral depressions upturned to margin without a marginal bead; laterobasal depressions deepest just lateral raised median base, then evenly upraised on broadly elevated, sinuate basolateral margin; hind angles obtusely angulate, laterobasal margin posteriorly expanded laterad median base; basal marginal bead present behind laterobasal depressions and across most of median base, slightly effaced at middle; median base with extensive longitudinal wrinkles; median longitudinal impression extended to basal margin, finely incised on disc, and extended cephalad of markedly impressed anterior transverse impression, which extends toward tightly rounded, protuberant front angles; anterior marginal bead continuous across front of pronotum. Prosternal process flat to slightly convex medioventrally.

**Elytra.** Basal groove recurved to rounded, laterally expanded humeri; a broad, flat area cephalad the base of sixth and seventh intervals, inside rounded humeral angle; lateral margins somewhat explanate, a flattened lateral depression visible outside lateral setae in anterior half of elytra; subapical sinuation present, sutural apex obtusely angulate, with slight rounded tubercle; elytral intervals broadly convex, striae smooth and deep; scutellar seta and 3 dorsal elytral setae present; 14-16 lateral elytral setae.

**Pterothorax.** Metepisternum short, broad, trapezoidal, lateral margin 1.4 to 1.6× length of anterior margin.
Fig. 161. B. (Metromenus) paludicola, new species. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view.

**Legs.** Profemur without anteroventral setae, with 2 posteroventral setae; mesofemur with 1 ridge seta; metasemur with 2 anteroventral setae; metacoxa bisetose, mesal seta absent; metatamur with 2 anteroventral setae; tarsomeres gracile, tarsomere 1 slightly expanded apically, tarsomeres 2-3 slightly more expanded; tarsomeres 1-3 with distinct dorsolateral sulci, medially carinate; metastasome 4 apically emarginate, outer apical lobe 0.4 to 0.5× median basal tarsomere length; basal tarsomeres with 3 rows of elongate ventrolateral setae, medially glabrous; tarsomere 5 with two ventrolateral rows of 6 setae much shorter than depth of tarsomere at point of setal insertion.

**Abdomen.** Males with 1 apical seta each side of sternite VII, females with 3 each side.

**Coloration.** Head and elytral disc piceous; clypeus, labrum, mandibles, pronotal disc, and elytral margins brunneous; pronotal margins paler yet, flavobrunneous; legs, palpi, antennal scape, and apex of sternite VII flavous, pronotal and elytral epipleura slightly darker, flavobrunneous; thoracic and abdominal venter, except abdominal apex, brunneous.

**Microsculpture.** Vertex of head with distinct isodiametric microsculpture, sculpticells flat and shiny; dorsal impression of neck with more raised, slightly transverse sculpticells; pronotal disc with distinct transverse mesh microsculpture, lateral marginal depressions, laterobasal depressions, and median base covered with swirled isodiametric mesh; elytral intervals with isodiametric sculpticells, their surfaces flat and shiny; outer two elytral intervals with marked granulate isodiametric microsculpture, sculpticells raised medially; thoracic and abdominal venter covered with distinct transverse mesh.
Male genitalia. Aedeagal median lobe gracile, broadly expanded medioventrally, ventral excavation extended to slightly downturned, elongate apex ended in a finely rounded tip, tip extended 2.67× thickness of apex at opening of internal sac (Fig. 161A); basal sagittal crest shallow to obsolete; median lobe moderately slender basally, tapered to a finely rounded tip (Fig. 161B).

Female reproductive tract. Gonocoxa basally broad, triangular gonocoxite 2 with acuminate apex (Fig. 161C); gonocoxite 1 with apical fringe of 10 setae, mesal 6 near medioapical angle in double series; gonocoxite 2 with 2-3 lateral ensiform setae and 1 dorsal ensiform seta; apical nematiform setae short, 0.22× length of gonocoxite 2; bursa copulatrix symmetrical, subequal to length of common oviduct, constricted basally into a vaselike configuration, with a rounded dorsal pouch and a medial band of spikelike bursal microtrichia; spermatheca elongate, reservoir 0.9× length of spermathecal duct, without basal lobe.

Holotype ♂ labeled “HI: Oahu Mt. Ka’ala 22-IV-1991 el. 1210 m J.K. Liebherr under bog boardwalk” (CUIC).

Doubtful locality: Tantalus, 21-V-1965, Tsuda (BPBM, 1); probably a labeling error.

Etymology. The species epithet paludicola indicates the bog-loving nature of this species.

Distribution. This species is found from Mt. Kaala to Puu Kanehoa, Waianae Range, Oahu (Fig. 162).

Habits. Like its adelphotaxon, B. muscicola, this species is recorded from both arboreal and terrestrial microhabitats. It has been collected in association with Cheirodendron (olapa), Cibotium (tree fern), Metrosideros (ohia lehua), and low ferns. On the ground adults have been found in flotsam along Makaha Stream, by treading the grass and algal margins of small pools, by sifting litter from tree ferns and ohia leaves, under roadside debris, and under boards of the Mt. Kaala summit bog boardwalk. The predilection for hiding under boardwalks during day leads to mortality of these species as entomologists and others walk on these devices. Thus, even though this species is restricted geographically, it exhibits generalized habits by living among terrestrial litter and arboreal moss mats and other epiphytes.

Phylogenetic relationships. This species is the putative adelphotaxon of a clade comprising 7 Oahu species plus 18 others living on Maui Nui. Of the seven Oahu species, six are restricted to the Koolau Mountain Range: B. foisiipennis (Fig. 162), B. fugitiva (Fig. 166), B. proterva (Fig. 168), B. paloloensis (Fig. 171), B. barda, and B. oceanica (Fig. 174).
Fig. 163. *B. (Metromenus) fossipennis*. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view.

**Blackburnia (Metromenus) fossipennis** (Blackburn), new combination
(Figs. 157D, 162, 163)

*Anchomenus fossipennis* Blackburn, 1877: 146.

*Metromenus fossipennis*: Blackburn & Sharp, 1885: 212; Sharp, 1903: 239.

**DIAGNOSIS.** Sharing with *B. paloloensis*, the foveate dorsal elytral setae (Figs. 157D, 169D), and with the following 2 species—*B. fugitiva* and *B. proterva*—the granulate transverse mesh microsculpture on pronotal disc, sinuate basolateral pronotal margins (Figs. 157D, 164), and medially effaced pronotal basal marginal bead. In addition, antennal pedicel with 6 apical setae accompanying longer outer seta; elytral intervals convex, striae deep, finely incised, impunctate; females with 3 apical setae each side of sternite VII. Standardized body length 4.9-6.7 mm. Most individuals of this species exhibit a glabrous pronotum, though a few sport either lateral or basal setae, or both (see Variation below).

**Pterothorax.** Metepisternum short, broad, trapezoidal, lateral margin 1.1 to 1.4× length of anterior margin.

**Male genitalia.** Very similar to *B. paloloensis*; median lobe narrow near basal bulb, expanded on eudorsal surface near midpoint of shaft, medioventral margin straight (Fig. 163A); ventral excavation extended to slightly downturned apex ended in a finely rounded tip extended in length 1.67× thickness of apex at opening of internal sac; basal sagittal crest shallow; median lobe broad near middle of shaft, tapered near slightly acuminate apex, then narrowed toward a finely rounded tip (Fig. 163B).

**Female reproductive tract.** Gonocoxa basally broad, triangular gonocoxite 2 with acuminate apex (Fig. 163C); gonocoxite 1 with apical fringe of 6-7 setae in single series;
Table 10. Configurations of pronotal setae among specimens of *B. fossipennis*: -/-, pronotum glabrous; +/-, lateral setae present and basal setae absent; +/+, lateral and basal setae present.

<table>
<thead>
<tr>
<th>Configuration</th>
<th>-/-</th>
<th>+/-</th>
<th>+/+</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. specimens</td>
<td>154</td>
<td>2</td>
<td>5</td>
</tr>
</tbody>
</table>

gonocoxite 2 with 2-3 lateral ensiform setae and 1 dorsal ensiform seta; apical nematiform setae short, 0.23× length of gonocoxite 2; bursa copulatrix symmetrical, subequal to length of common oviduct, with medial band of spikelike microtrichia and collarlike dorsal bursal pouch; spermatheca ovoid, reservoir 0.70× length of spermathecal duct, without basal lobe.

**Variation.** Nearly all individuals have glabrous pronota: however a few have been observed with lateral setae, or both lateral and basal setae (Table 10). Both species constituting the adelphotaxon of *B. fossipennis*-i.e., *B. fugitiva* and *B. proterva*-exhibit monomorphic absence of both setae, and so the rare expressions of setae in *B. fossipennis* must be considered derived reversals to the plesiomorphic condition.

**Lectotype.** * on card with 2 parallel lines, the top line thickest—Blackburn’s Oahu code (Zimmerman 1957)—and “fossip” handwritten on reverse (BMNH) hereby designated.

**Distribution.** This species is distributed along the entire Koolau Mountain Range of Oahu (Fig. 162).

**Locality.** Recorded from the length of the Koolaus, including Kawailoa Ridge, Poamoho Trail, Puu Kaaumakua, north peak of Eleao massif, Waialani Stream, Puu Keahiakahoe massif at Tripler Ridge, Puu Lanihuli, Nuuanu-Manoa Ridge, Konahuanui (both north and south summits), Manoa Valley, Tantalus, Mt. Olympus, Waialae Nui, and Niu Valley. These collecting sites span 605 to 960 m elevation.

**Habits.** Adults have been beaten from vegetation during day and night, including substrate plants of the genera *Astelia*, *Cibotium* (tree fern), *Freycinetia* (ieie), *Machaerina*, *Metrosideros* (ohia lehua), and also collected from under uluhe fern. Beetles are also commonly encountered at night as they walk along open muddy trails. In this species it appears that a widespread distribution co-occurs with generalized preference for a variety of plant and terrestrial substrates.

**Phylogenetic relationships.** This species is the sympatric adelphotaxon of the sympatric species pair, *B. fugitiva* and *B. proterva* (Figs. 9, 162, 166, 168). Extensive sympatry of closely related species is a characteristic of the Koolau Mountains’ *Blackburnia* fauna. The present-day configuration of this range represents about one-half of the original expanse of the Koolau volcano. The northeastern half precipitously collapsed into the Pacific Ocean due to volcanic activity along the northwest-southeast tending rift zones extended from the caldera that was centered on the present-day city of Kailua (Langenheim & Clague 1987, Moore et al. 1989). Species now found along the length of the range are descended from the remnants of a much more expansive biota that lived on the mature Koolau volcano. Mature Koolau achieved a maximum elevation of 1900 m, double that of the present-day range (Carson & Clague 1995). What are now windward pali, or cliffs, along the range—e.g., Nuuanu Pali—were situated more toward the leeward edge of the volcano.
when it was whole. The precipitous cliffs of Nuuanu Pali were formed only after the collapse of Koolau, through a combination of headward erosion by windward streams, and marine erosion during higher stands of the Pacific Ocean (Stearns 1946). When Koolau was a mature shield volcano, areas along the extent of the present-day crest would have been much drier, with the biota predominantly dependent on fog moisture, much as at present-day Kaupohole and Auwahi, Haleakala, Maui. For many Blackburnia species of that primordial Oahu, this type of habitat would have been highly unfavorable, as extensive epiphytic growth and moist leaf litter would not have existed along this leeward crest. It is likely that the species now found along the length of the Koolaus colonized the middle reaches of the newly windward crest as forest developed there after the Koolau collapse. Source areas for this colonization would have been at the southern and northern ends of the range—i.e., the previous northwestern and southeastern edges of the windward forest. The intervening bulk of the windward forest would have been cast adrift on tsunamis associated with the foundering of the northeastern volcanic flank (Moore et al. 1989).

**Blackburnia (Metromenus) fugitiva** (Blackburn), new combination
(Figs. 164A, 165, 166)

*Anchomenus fugitivus* Blackburn, 1877: 147.

*Metromenus fugitivus*: Blackburn & Sharp, 1885: 212; Sharp, 1903: 240.

**DIAGNOSIS.** This and the next species, *B. proterva*, have frons with marked isodiametric microsculpture, pronotum with granulate isodiametric microsculpture across base, and elytra broad and convex with apex flavous and disc piceous. *Blackburnia fugitiva* differs in: 1, the broader pronotum with barely sinuate basolateral margins and obtuse-rounded hind angles (Fig. 164A); 2, more broadly flavous elytral apex—i.e., more than 1/3 distance from apex to posterior dorsal elytral setae pale; and 3, larger body size, standardized body length 6.0-8.2 mm. Additionally, antennal pedicel with longer outer seta accompanied by 4 shorter apical setae; females with 2 apical setae each side of sternite VII.

**Pterothorax.** Metepisternum short, broad, trapezoidal, lateral margin 1.1 to 1.2× length of anterior margin.

**Male genitalia.** Aedeagal median lobe gracile, slightly expanded medioventrally, shaft nearly straight near middle of length; ventral excavation extended to evenly curved apex ended in a finely rounded tip extended in length 1.33× thickness of apex at opening of internal sac (Fig. 165A); basal sagittal crest broad; median lobe slightly constricted near midlength, tapered to a finely rounded tip (Fig. 165B).

**Female reproductive tract.** Gonocoxa basally broad, triangular gonocoxite 2 with acuminate apex (Fig. 165C); gonocoxite 1 with apical fringe of 11 setae, mesal 4-6 near medioapical angle in double series; gonocoxite 2 with 2 lateral ensiform setae and 1 dorsal ensiform seta; apical nematiform setae short, 0.23× length of gonocoxite 2; bursa copulatrix symmetrical, subequal to length of common oviduct, with medial band of spikelike bursal microtrichia and broad dorsal bursal pouch; spermatheca elongate, reservoir 0.90× length of spermathecal duct, without basal lobe.

**Lectotype** ♀ on card with 2 parallel lines, the top line thickest—Blackburn’s Oahu code (Zimmerman 1957)—and “fugitivus” handwritten on reverse (BMNH) hereby designated.
**Distribution.** This species is known from Kaluanui south to Konahuanui, in the Koolau Mountain Range, Oahu (Fig. 166).


**Habits.** Found both on vegetation and the ground. Adults have been beaten from *Cibotium, Machaerina, Metrosideros*, and found under bark of rotten *Acacia koa* (Perkins?, 30-1-1910, BPBM). At night, beetles are active on trails and open areas. They have been found during the day in leaf litter and under stones. Much as in the related *B. fossipennis*, then, this species exhibits a generalized ecological preference for terrestrial and arboreal microhabitats in the Koolaus.

**Phylogenetic relationships.** This species is the adelphotaxon of the sympatric *B. proterva* (Fig. 9); see discussion above under *B. fossipennis*.
CARABIDAE PART I: PLATYNINI

Fig. 165. B. (Metromenus) fugitiva. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euvентрal view. C. Left female gonocoxa, ventral view.

**Blackburnia (Metromenus) proterva (Blackburn), new combination**
(Figs. 164B, 167, 168)

*Anchomenus protervus* Blackburn, 1877: 145.
*Metromenus protervus*: Blackburn & Sharp, 1885: 212; Sharp, 1903: 240.
*Metromenus angustifrons* Sharp, 1903: 234 (new synonymy).

**DIAGNOSIS.** Like *B. fugitiva* in the marked isodiametric microsculpture across frons and pronotal base, convex elytral disc, and flavous elytral apex contrasted with piceous disc, but smaller, standardized body length 5.5-6.9 mm; pronotum narrower with more sinuate basolateral margins and more distinctly obtuse-angulate hind angles (Fig. 164B). The apical flavous elytral band is quite narrow in some specimens, with only area beyond fused ends of striae 3 and 4 pale. This species exhibits variation in the configuration of the eyes, ranging from only slightly to markedly convex, ocular ratio ranging from 1.43 to 1.60. This variation is associated with width of the individual, best evidenced by basal pronotal width.

**Pterothorax.** Metepisternum moderately short, broad, lateral margin 1.3 to 1.4× length of anterior margin.

**Male genitalia.** Aedeagal median lobe gracile, slightly expanded medioventrally, shaft nearly straight near middle of length; ventral excavation extended to evenly curved apex ended in a finely rounded tip extended in length 2.0× thickness of apex at opening of
Fig. 166. Distributional records for *B. (Metromenus) fugitiva*.

internal sac (Fig. 167A); basal sagittal crest short, broad; median lobe slightly constricted near midlength, tapered to a finely rounded tip (Fig. 167B).

**Female reproductive tract.** Gonocoxa basally broad, triangular gonocoxite 2 with acuminate apex (Fig. 167C); gonocoxite 1 with apical fringe of 8-9 setae in single series; gonocoxite 2 with 2 lateral ensiform setae and 1 dorsal ensiform seta; apical nematiform setae short, 0.20 × length of gonocoxite 2; bursa copulatrix symmetrical, 0.8 × length of common oviduct, with medial band of spikelike bursal microtrichia and rounded dorsal bursal pouch; spermatheca ovoid, reservoir 0.75 × length of spermathecal duct, without basal lobe.

**Types.** For *Metromenus protervus*, lectotype ♂ on card with 3 parallel lines, the top line thickest—Blackburn's Oahu code (Zimmerman 1957)—and “H proterv” handwritten on reverse (BMNH) hereby designated. For *Metromenus angustifrons*, holotype ♂ labeled “Metromenus angustifrons Type D.S. Honolulu Perkins 667” (BMNH). Perkins' lot 667 is described as “Mts. nr. Honolulu, 2-3.000 ft. Chalcis (variegated) + Coccinellid introduced by A. Koebele” (Anonymous n.d.).

**Distribution.** This species is distributed throughout much of the Koolau Mountain Range, Oahu (Fig. 168).
Localities. Broadly distributed but not as commonly encountered as the previous two species. Recorded localities include Castle Trail, Poamoho Trail, Puu Kaumakua, Schofield-Waikane Trail, Waipio Ridge, Puu Lanihuli, Konahuanui, Pauoa Ridge, Tantalus, Palolo Valley, Waialae Nui, and Waialae Iki. Collecting site elevations span 395 to 940 m.

Habits. Like *B. fossipennis* and *B. fugitiva*, found on vegetation and on the ground. Adults have been recorded from *Acacia* (koa), *Cibotium*, and rotten wood on *Pleomele (= Dracaena)*. Beetles have also been found by sifting litter and while active on open trails at night. Therefore, like the previous two closely related species, this is an ecological generalist exhibiting a broad Koolau distribution.

Phylogenetic relationships. This is the adelphotaxon of the sympatric Koolau Mountain species, *B. fugitiva* (Fig. 9).

*Blackburnia (Metromenus) audax* (Perkins), new combination
(Figs. 169A, 170, 171)


DIAGNOSIS. Pronotum trapezoidal, width at subangulate front angles 0.75× distance between distinct, nearly right hind angles (Fig. 169A), pronotal lateral margins subparallel in basal half of length, laterobasal depressions with large central tubercle; elytral humeri broad, angulate, lateral marginal depression wide caudad humerus to first lateral elytral seta; elytral intervals shiny, microsculpture of reduced isodiametric sculpticells; females with 2 apical setae each side of sternite VII. Standardized body length 5.5-6.6 mm.
**Pterothorax.** Metepisternum short, broad, trapezoidal, lateral margin 1.2 to 1.4× length of anterior margin.

**Male genitalia.** Aedeagal median lobe gracile, broadly expanded medioventrally; deep ventral excavation extended to evenly curved apex ended in a bulbous tip extended in length 2.5× thickness of apex at opening of internal sac (Fig. 170A); basal sagittal crest shallow, short; median lobe parallel-sided near midlength, tapered near apex to a finely rounded tip (Fig. 170B).

**Female reproductive tract.** Gonocoxa basally broad, triangular gonocoxite 2 with acuminated apex (Fig. 170C); gonocoxite 1 with apical fringe of 6-7 setae in single series; gonocoxite 2 with 2-3 lateral ensiform setae and 1 dorsal ensiform seta; apical nematiform setae short, 0.24× length of gonocoxite 2; bursa copulatrix symmetrical, subequal to length of common oviduct, with medial band of spikelike bursal microtrichia and collarlike dorsal bursal pouch (Fig. 170D); spermatheca ovoid, reservoir 0.75× length of spermathecal duct, without basal lobe.

**Lectotype** ♀ on card with “♀” handwritten on top, “Mt. Kaala about 3000 ft. ii02 RCLP” written on back // “Metromenus audax Type. RCLP.” // yellow card with “1311” (BPBM) hereby designated.

**Distribution.** This species is known only from between 910 and 1210 m elevation on Mt. Kaala in the Waianae Range, Oahu (Fig. 171).
Localities. Known only from the Mt. Kaala Natural Area Reserve, Oahu.

Habits. Adults have been encountered mostly in association with ground-level microhabitats: under boards, rocks, and roadside debris in the summit bog, and in tree fern litter and rotten logs. Nonetheless, adults have also been beaten from the “big three” of arboreal situations: *Cheirodendron* (olapa), *Cibotium* (tree fern), and *Metrosideros* (ohia lehua). Therefore this species is inferred to occupy primarily terrestrial microhabitats on the forest floor or bog surface.

Phylogenetic relationships. This species is the allopatric adelphotaxon of three sympatric Koolau Mountain species: *B. paloloensis*, *B. barda*, and *B. oceanica* (Figs. 9, 171, 174). Of these four species, only *B. audax* exhibits a quadrate pronotum (Fig. 169). This condition is shared among all of the more basally divergent species of the Maui Nui
clade subtended by the species pair *B. lihau* and *B. calathoides* (Figs. 9, 176, 180, 187, 192D, 199C-D, 206B). Therefore it appears that some ancestral relatives of present-day *B. audax*, either from the Waianae Mountains or perhaps the collapsed windward Koolaus (Moore et al. 1989), colonized Maui Nui early in its history.

**Blackburnia (Metromenus) paloloensis** Liebherr, new species  
(Figs. 169D, 171, 172)

**DIAGNOSIS.** Combining attributes of *B. barda* and *B. fossipennis*—i.e., 1, glabrous pronotum with convex basolateral margins before obtuse-rounded hind angles (Figs. 157D, 169B, D); and 2, convex, ovoid elytra with foveate depressions around dorsal elytral setae. In addition, metatarsomeres 1-3 with very fine and shallow dorsolateral sulci, median area broadly convex; metatarsomere 4 apically emarginate, outer lobe 0.67 × length of median tarsomere base; females with 2 apical setae each side of sternite VII. Standardized body length 6.0-6.8 mm.  
**DESCRIPTION.** **Head.** Eyes slightly convex, ocular ratio 1.50; frontoclypeal grooves broad, shallow, barely visible near anterior supraorbital seta; antennal pedicel with longer
outer seta plus 4 shorter apical setae; labrum quadrate, apical margin straight; mentum tooth apically truncate.

Prothorax. Pronotum orbicular, basolateral margins convex cephalad of rounded-angulate hind angles; lateral marginal depressions moderately broad, without marginal bead, lined with granulate isodiametric microsculpture; laterobasal depressions broad, bordered laterally and posteriorly by upraised margins, with broad, rounded tubercle in anterior portion; median base with fine longitudinal wrinkles, basal marginal bead present, though fine, medially; median longitudinal impression distinct on disc, extended cephalad.
of anterior transverse impression, which delineates depressed median apex of pronotum; anterior marginal bead continuous medially, extended to rounded, slightly protruded front angles. Prosternal process flat ventrally, unmargined posteriorly.

Elytra. Disc convexly raised relative to depressed scutellum, apex, and sides; basal elytral groove recurved laterad scutellum to angulate humeri; lateral marginal depression slightly broader cephalad of first lateral elytral seta, narrower caudad to broad, slightly concave subapical situation; sutural apex subangulate, with small mucronate thickening of margin at suture; elytral intervals broadly convex, striae deep, smooth, impunctate; scutellar seta present; dorsal elytral setae surrounded by foveate depressions, anterior and posterior setae in depressions that span third interval; 14-16 lateral elytral setae.

Pterothorax. Metepisternum moderately short, broad, lateral margin 1.3 to 1.4× length of anterior margin.

Legs. Profemur without anteroventral setae, with 2 posteroventral setae; mesocoxa with 1 ridge seta; mesofemur with 2 anteroventral setae; metacoxa bisetose, mesal seta absent; metafemur with 2 anteroventral setae; tarsomeres gradicule, tarsomeres 1-3 with very fine and shallow dorsolateral sulci, median area broadly convex; metatarsomere 4 apically emarginate, outer apical lobe 0.67× median basal tarsomere length; basal tarsomeres with 3 rows of sparse, elongate ventrolateral setae, medial glabrous area twice as wide as distance between lateral rows; tarsomere 5 with two ventrolateral rows of 6 setae, each much shorter than depth of tarsomere at point of setal insertion.

Abdomen. Males with 1 apical seta each side of sternite VII, females with 2 setae.

Coloration. Dorsal body surface uniformly brunneous, head, pronotal disc, and elytral intervals shiny, pronotal laterobasal depressions contrastingly granulate due to microsculpture; trochanters and femora testaceous with smoky infuscated cast, tibiae and tarsi brunneous; pronotal and elytral epipleura flavobrunneous, slightly paler than brunneous thoracic and abdominal venter.

Microsculpture. Head with evident isodiametric microsculpture, sculpticellae slightly effaced on middle of frons; pronotal disc with transverse microsculpture, sculpticellae more developed near median base, surface with indistinct alutaceous lustre; pronotal median apex, median base, and laterobasal depressions covered with isodiametric sculpticellae, most granulate in depressions; elytral intervals with isodiametric sculpticellae in irregular transverse rows.

Male genitalia. Aedeagal median lobe narrow near basal bulb, expanded on eudorsal surface near midpoint of shaft, medioventral margin straight (Fig. 172A); ventral excavation extended to slightly downturned apex ended in finely rounded tip, tip extended in length 1.67× thickness of apex at opening of internal sac; basal sagittal crest broad; median lobe broad near middle of shaft, tapered near slightly acuminate apex, then narrowed toward finely rounded tip (Fig. 172B).

Female reproductive tract. Gonocoxa basally broad, triangular gonocoxite 2 with acuminate apex (Fig. 172C); gonocoxite 1 with apical fringe of 11-13 setae, mesal 6-7 setae near medioapical angle in double series; gonocoxite 2 with 3 lateral ensiform setae and 1 dorsal ensiform seta; apical nematiform setae short, 0.20× length of gonocoxite 2; bursa copulatrix slightly asymmetrical, pleat folds on right side near entrance of common oviduct into bursa (Fig. 172D); bursa subequal to length of common oviduct, with medial band of spikelike bursal microtrichia and collarlike dorsal bursal pouch; spermatheca ovoid, reservoir 0.70× length of spermathecal duct, without basal lobe.
Holotype ♀ card mounted with separate label “Palolo Hts. Oahu. 3.IX.06” // card with “3” // “RCLPerkins Collection” // square red label (BPBM). A large label states “sp. n. sec Britton. Named bardus sp. men from description only compared sp. men with bardus type.”

Paratypes. OAHU, Koolau Range: Honolulu Mts., 545 m, Perkins (BPBM, 1), 605 m, Perkins (BPBM, 2); Palolo Heights, 03-IX-1906, Perkins (BPBM, 1).

Etymology. Palolo Heights in Honolulu is the only specifically recorded locality for this species, which is therefore named as from Palolo.

Distribution. This species is known only from mountains very near to present-day Honolulu (Fig. 171). The collecting locality is likely in the head of Palolo Valley. Around 1910, the only trails in upper Palolo Valley were the low and high trails to Kaau Crater: the low road following Waiomao Stream to just below the crater, the easier upper trail following the ridge southwest of the crater, then around the west side of the crater to the summit ridge (C.P. Ewing, pers. comm.). The high trail is the more likely interpretation of “Palolo Heights.”

Habits. The relatively low elevations recorded for this species do not bode well for its survival to the present day. One should look for it in situations common to related, sympatric species such as B. fossipennis and B. barda—i.e., by beating small mossy ohias common to the southern Koolaus, as well as by looking on open trail areas at night where it should be active on the ground.

Phylogenetic relationships. This species is the sympatric adelphotaxon for the sympatric species pair B. barda and B. oceanica (Figs. 9, 171, 174). Two of the three species in this triplet are restricted to the southern Koolaus.

**Blackburnia (Metromenus) barda** (Blackburn), new combination
(Figs. 169B, 173, 174)

*Anchomenus bardus* Blackburn, 1877: 146.

*Metromenus bardus*: Blackburn & Sharp, 1885: 212; Sharp, 1903: 240.

**DIAGNOSIS.** A large, uniformly reddish brown beetle with pale yellowish legs and antennae, standardized body length 8.5-8.9 mm; eyes little protruded, ocular ratio 1.30-1.35 (Fig. 169B); labrum with 4 apical setae, median pair absent; pronotum broad with barely sinuate basolateral margins before obtuse-rounded hind angles (thereby agreeing with *B. fugitiva*), both pronotal disc and laterobasal depressions with distinct microsculpture, therefore with alutaceous lustre; elytra broad, disc convex, intervals broadly convex, striae deep and broad, impunctate, lined with granulate sculpticells.

**Pterothorax.** Metepisternum moderately elongate, narrowed posteriorly, lateral margin 1.1 to 1.2× length of anterior margin.

**Male genitalia.** Aedeagal median lobe gracile, medioventral margin straight (Fig. 173A); ventral excavation extended to nearly straight apex with slightly downturned, bluntly rounded tip extended in length 1.33× thickness of apex at opening of internal sac; basal sagittal crest broad; median lobe slightly constricted on right side near midlength, tapered to a finely rounded tip (Fig. 173B).
Female reproductive tract. Gonocoxa basally broad, triangular gonocoxite 2 with narrowly acuminate apex (Fig. 173C); gonocoxite 1 with apical fringe of 13-15 setae, mesal 6-8 near medioapical angle in double series; gonocoxite 2 with 3 lateral ensiform setae and 1 dorsal ensiform seta; apical nematiform setae very short, 0.15× length of gonocoxite 2; bursa copulatrix symmetrical, subequal to length of common oviduct, with medial band of
spikelike bursal microtrichia and collarlike dorsal bursal pouch (Fig. 173D); spermatheca elongate, reservoir subequal to length of spermathecal duct, without basal lobe.

Lectotype ♀ on card with 3 parallel lines, the top line thickest—Blackburn’s Oahu code (Zimmerman 1957)—and “bardus” handwritten on reverse (BMNH) hereby designated.

Distribution. This species is patchily distributed along the Koolau Mountain Range, Oahu (Fig. 174).


Habits. The only ecological information associated with this species includes its activity on trails at night, and its collection through sifting mossy leaf litter.

Phylogenetic relationships. This species is the adelphotaxon of *B. oceanica* (Fig. 9), with both species distributed sympatrically in the Koolau Mountain Range (Fig. 174).
Fig. 175. *B. (Metromenus) oceanica*. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view. D. Female bursa copulatrix, ventral view, showing collarlike dorsal bursal pouch, medial band of spikelike microtrichia, and spermatheca (spermathecal gland deleted).

*Blackburnia (Metromenus) oceanica* (Blackburn), new combination
(Figs. 169C, 174, 175)

Anchomenus oceanicus Blackburn, 1877: 146.
Metromenus oceanicus: Blackburn & Sharp, 1885: 212; Sharp, 1903: 240.

DIAGNOSIS. Sharp (1903, 240) diagnosed this "remarkable insect" by its "extremely narrow, long head [Fig. 169C]," which approaches the cave species *B. howarthi* in reduction of the eyes. The ocular ratio of 1.35-1.40 is as large as it is due to the very narrow frons. This species is otherwise unmistakable due to: 1, pronotum narrow with sinuate basolateral margins and moderately broad lateral marginal depressions; and 2, elytra broad
and convex, with angulate humeri, moderately convex intervals, and deep, smooth striae. As in *B. barda*, the labrum has only 4 apical setae, the median pair being absent. Standardized body length 7.5-8.1 mm.

**Pterothorax.** Metepisternum moderately short, narrowed posteriorly, lateral margin 1.2× length of anterior margin.

**Male genitalia.** Aedeagal median lobe basally gracile, medioventral margin straight (Fig. 175A); deep ventral excavation extended to nearly straight, very short apex with slightly downturned, bluntly rounded tip extended in length subequal to thickness of apex at opening of internal sac; basal sagittal crest short, broad; median lobe evenly tapered to a finely rounded tip (Fig. 175B).

**Female reproductive tract.** Gonocoxa basally broad, triangular gonocoxite 2 with acuminated apex (Fig. 175C); gonocoxite 1 with apical fringe of 8 setae in single series; gonocoxite 2 with 2 lateral ensiform setae and 1 dorsal ensiform seta; apical nematiform setae short, 0.22× length of gonocoxite 2; bursa copulatrix symmetrical, subequal to length of common oviduct, with medial band of spikelike microtrichia and broad dorsal bursal pouch; spermatheca ovoid, reservoir 0.75× spermathecal duct length, without basal lobe (Fig. 175D).

**Lectotype** σ on card with 2 parallel lines, the top line thickest—Blackburn’s Oahu code (Zimmerman 1957)—and “*oceanicus*” handwritten on reverse (BMNH) hereby designated.

**Distribution.** The only known localities for this rarely collected insect are in the mid- to southern Koolau Mountains of Oahu (Fig. 174).

**Localities.** This species is known from only four specimens, with specific localities including Waimano Trail and Honolulu (17-I-1941, Maehler, BPBM).

**Habits.** The only biological information associated with this species is one collection from under a rock. Its cave insect habitus suggests that it spends its life hidden in moss, litter, and subterranean cavities.

**Phylogenetic relationships.** This species is the adelphotaxon of the sympatric *B. barda* (Fig. 9).

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**Blackburnia (Metromenus) lihau** Liebherr, new species

(Figs. 176A, 177, 178)

**DIAGNOSIS.** Similar to *B. oceanica* (Fig. 169C) in the reduced eyes, ocular ratio 1.35; but, with: 1, broader pronotum (Fig. 176A), the nearly right hind angles extended caudad median base, laterobasal depression with broad central tubercle; 2, a single supraorbital seta each side, anterior seta absent; and 3, elytral basal carina slightly elevated cephalad the tightly rounded hemeral angle. Standardized body length 6.7-7.0 mm.

**DESCRIPTION.** Head narrow, neck elongate, neck with distinct dorsal impression; frontoclypeal grooves deep just caudad frontoclypeal suture, with laterally radiating wrinkles, not extended toward eyes; anterior supraorbital seta absent, posterior setae present; antennal pedicel with longer outer setae plus 4 shorter apical setae; labrum slightly emarginate apically, median pair of setae either absent or represented by a single short seta, therefore labrum 4- or 5-setose; mentum tooth bifid.
Prothorax. Pronotal hind angles nearly right, basolateral margins sinuate before angles; lateral marginal depressions narrowest about 2/3 length from base, widened toward tightly rounded, protruded front angles; lateral pronotal seta present or absent (see Variation below), posterior seta absent; laterobasal depressions with broad central tubercle, irregularly wrinkled close to convex median base; median base with fine longitudinal wrinkles; basal marginal bead continuous, broader caudad laterobasal depressions; basal margin concave, posterior portions expanded caudad the tubercles of laterobasal depressions; median longitudinal impression extended nearly to basal margin, deepest near posterior of convex pronotal disc, finely incised on disc, extended cephalad of broad, shallow anterior transverse impression; anterior marginal bead obsolete medially, traceable in lateral reaches near front angles. Prosternal process convex ventrally, unmargined posteriorly.

Elytra basally broad, lateral marginal depressions broad caudad rounded humeri, gradually narrowing in posterior half of elytra toward distinct subapical sinuation; basal groove shallow laterad scutellum, deeper cephalad of fifth and sixth intervals; elytral intervals evenly convex, striae deep, smooth, impunctate; scutellar setae and 3 dorsal elytral setae present; 13 lateral elytral setae.

Pterothorax. Metepisternum short, broad, trapezoidal, lateral margin 1.1 to 1.2× length of anterior margin.
Legs. Profemur without anteroventral setae, with 2 posteroventral setae; mesocoxa with 1 ridge seta; mesofemur with 2 anteroventral setae; metacoxa bisetose, mesal seta absent; metafemur with 2 anteroventral setae; tarsomeres gracile, basal metatarsomere about 2× length of inner tibial spur; tarsomeres 1-3 with shallow dorsolateral sulci, median area broadly convex; metatarsomere 4 slightly emarginate apically, outer apical lobe 0.32× median basal tarsomere length; basal tarsomeres with 3 rows of sparse, elongate ventrolateral setae, medial glabrous area twice as wide as distance between lateral rows; tarsomere 5 with two ventrolateral rows of 6 setae, each much shorter than depth of tarsomere at point of setal insertion.
Fig. 178. Distributional records for B. (Metromenus) lihau, new species (■), B. (Metromenus) calathoides (●), and B. (Metromenus) ipu, new species (○).

Abdomen. Males with 1 apical seta each side of sternite VII, females with 3 each side.

Coloration. Head dark brunneous, contrasted with rufous pronotum and elytra; palpi, antennae, legs, and epipleura flavous with a smoky infuscated cast; thoracic and abdominal venter brunneous, apical abdominal sternite flavous.

Microsculpture. Vertex with isodiametric microsculpture, sculpticells flattest on middle of frons; pronotal disc with transverse mesh microsculpture, sculpticells flattest near median longitudinal impression, median apex and median base with isodiametric microsculpture, laterobasal depressions with isodiametric sculpticells raised into granulate surface; elytral intervals covered with a mixture of isodiametric and slightly transverse sculpticells in irregular transverse rows.

Male genitalia. Aedeagal median lobe gracile, medioventrally expanded, ventral excavation extended to nearly straight, very short apex tapered to a finely rounded tip extended in length 1.33× thickness of apex at opening of internal sac (Fig. 177A); basal sagittal crest short, narrow; median lobe slightly constricted on right side near midlength, evenly tapered to a finely rounded tip (Fig. 177B).

Female reproductive tract. Gonocoxa basally broad, triangular gonocoxite 2 with acuminate apex (Fig. 177C); gonocoxite 1 with apical fringe of 8 setae in single series; gonocoxite 2 with 2 lateral ensiform setae and 1 dorsal ensiform seta; apical nematiform setae somewhat elongate, 0.31× length of gonocoxite 2; bursa copulatrix nearly symmetrical, slightly expanded on right side, subequal to length of common oviduct, with medial band of spikelike bursal microtrichia and broad dorsal bursal pouch lined with
granulate microsculpture (Fig. 177D); spermatheca elongate, reservoir subequal to length of spermathecal duct, without basal lobe.

**Variation.** The 2 known specimens of *B. lihau* differ in pronotal setation. The male lacks pronotal setae, whereas the female has a single lateral seta on the left side, and 2 lateral setae on the right (a longer, thicker seta just cephalad a thinner one of about half the length). In this species, then, polymorphic presence of the lateral setae is compounded by instability of bilateral expression in even the single setose individual.

**Holotype** ♂ labeled “HI: West Maui Lihau N.A.R. Lihau summit forest moss on ohias 9-V-1993 lot 03 el. 1270 m // J.K. Liebheir collector” (CUIC).

**Allotype** ♀ collected on the same tree as the holotype.

**Etymology.** The species epithet *lihau* is the name of the type locality, used as a noun in apposition. The Hawaiian word *lihau* defines the gentle, cool rain considered lucky for fishermen.

**Distribution.** *B. lihau* is known only from the summit of Lihau, West Maui (Fig. 178).

**Habits.** The single pair of this species was collected together on a moss-covered trunk of an ohia lehua (*Metrosideros polymorpha*) in the summit copse. *Blackburnia lihau* likely uses arboreal moss mats for breeding habitat, given the single collection from that microhabitat during May. It should also be sought in leaf litter.

**Phylogenetic relationships.** This species is the adelphotaxon of the allopatrically distributed *B. calathoides* of East Maui (Figs. 9, 178).

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**Blackburnia (Metromenus) calathoides** (Sharp), new combination

(Figs. 176B, 178, 179)


**DIAGNOSIS.** Pronotum the most pronouncedly trapezoidal of all *Blackburnia* (Fig. 176B), the distance between pronotal hind angles 1.65 to 1.70× distance between front angles; eyes little protruded, ocular ratio 1.35-1.40; pronotal lateral marginal depressions broad throughout length; pronotal basolateral margins convex cephalad hind angles; elytral lateral marginal depressions broad from tightly rounded humeri to reduced subapical sinuation; metatarsomeres 1-3 with deep dorsolateral sulci, medially carinate. Standardized body length 6.4-7.7 mm.

**Pterothorax.** Metepisternum short, broad, trapezoidal, lateral margin 1.2 to 1.4× length of anterior margin.

**Male genitalia.** Aedeagal median lobe gracile, slightly expanded medioventrally, ventral excavation extended to short apex tapered to a finely rounded tip extended in length 1.33× thickness of apex at opening of internal sac (Fig. 179A); basal sagittal crest very broad, short; median lobe slightly constricted on right side near midlength, tapered to a finely rounded tip (Fig. 179B).

**Female reproductive tract.** Gonocoxa basally broad, triangular gonocoxtite 2 with acuminate apex (Fig. 179C); gonocoxtite 1 with apical fringe of 8-9 setae in single series; gonocoxtite 2 with 2 lateral ensiform setae and 1 dorsal ensiform seta; apical nematiform setae 0.24× length of gonocoxtite 2; bursa copulatrix nearly symmetrical, slightly expanded on left side, subequal to length of common oviduct, with medial band of spikelike bursal
Fig. 179. *B. (Metromenus) calathoides*. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view. D. Female bursa copulatrix, ventral view, showing liplike dorsal bursal pouch, medial band of spikelike microtrichia, and spermatheca.
microtrichia and liplike dorsal bursal pouch (Fig. 179D); spermatheca elongate, reservoir subequal to length of spermathecal duct, without basal lobe.

**Variation.** All specimens of *B. calathoides* from Waikamoi Gulch and adjacent forests exhibit a glabrous pronotum and a single pair of supraorbital setae: the posterior setae. To the east in Hana rain forest, specimens are polymorphic for both setational characters. Three specimens are known from near Kuhiwa Stream: 1, lacking anterior supraorbital setae but with left lateral pronotal seta; 2, with left anterior supraorbital and left lateral pronotal setae; and 3, with both lateral pronotal and right anterior supraorbital setae. A fourth specimen from Heleleikeoha Stream fence camp lacks lateral pronotal and anterior supraorbital setae as observed in Waikamoi.

**Holotype** $\sigma$ labeled “Metromenus calathoides Type D.S. Hal. 4000 ft Perkins V.95” (BMNH). Sharp inexplicably considered this label to designate Halemanu in Kauai, but subsequent collection of this species on East Maui affirms the more obvious interpretation that the type locality is Haleakala 4000 ft. (1210 m), a very typical Perkins collecting locality. This specimen would have been collected during the same month, perhaps syntopically, with the type of *Atelothrus stenopus*, junior synonym of *B. insociabilis*.

**Distribution.** This species is distributed from the western edge of Haleakala’s windward forest, east to the Hana rain forest, East Maui (Fig. 178).

**Localities.** Recorded from Waikamoi Flume between Waikamoi and Haipuaena Gulches (el. 1300 m), Honomanu Gulch in TNCH Waikamoi Preserve (el. 1700 m), Hanawi Natural Area Reserve, and Hana Forest Reserve at Heleleikeoha Stream fence camp at about 1600 m elevation.

**Habits.** Adults have been found under boards in wet ohia lehua forest along Waikamoi Flume, in moss mats covering trunks of large ohias, and in a gravel bar in Kuhiwa Stream.

**Phylogenetic relationships.** This species is the adelphotaxon of *B. lihau* of West Maui (Figs. 9, 178).

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**Blackburnia (Metromenus) cheloniceps** (Perkins), new combination

(Figs. 180A, 181, 182)

*Atelothrus cheloniceps* Perkins, 1917: 246.

DIAGNOSIS. Of all species with trapezoidal pronota, broadly elevated pronotal basolateral margins, and broad “abacoid” humeri, *B. cheloniceps* (Fig. 180A) is the only one with setose pronotal hind angles, the basal setae positioned $0.13 \times$ pronotal length cephalad of nearly right hind angles. Like *B. lihau* and *B. calathoides*, this species is characterized by: 1, mentum tooth bifid; and 2, females with 3 apical setae each side of sternite VII. Additionally, pronotal median basal margin concave, posterior margin expanded laterally behind laterobasal depressions; elytral lateral marginal depression broad caudad tightly rounded humeri, lateral margin markedly elevated laterad humerus. Standardized body length 7.4-8.4 mm.

**Pterothorax.** Metepisternum very short, broad, lateral margin 1.1 to 1.3 $\times$ length of anterior margin.

**Male genitalia.** Aedeagal median lobe gracile, very slender apically, evenly curved medioventrally, apex tapered to a finely rounded tip extended in length 1.5 $\times$ thickness of
Fig. 181. *B. (Metromenus) cheloniceps*. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view. D. Female bursa copulatrix, ventral view, showing broad dorsal bursal pouch lined with granulate microsculpture, medial band of spikelike microtrichia, and spermatheca.
Fig. 182. Distributional records for *B. (Metromenus) cheloniceps* (●), and *B. (Metromenus) platyophthalmica*, new species (■).

apex at opening of internal sac (Fig. 181A); basal sagittal crest very narrow; median lobe narrow basally, very slender apically in evventral view, tapered to a narrowly pointed tip (Fig. 181B).

**Female reproductive tract.** Gonocoxa basally broad, triangular gonocoxite 2 with acuminate apex (Fig. 181C); gonocoxite 1 with apical fringe of 7-8 setae in single series; gonocoxite 2 with 2 lateral ensiform setae and 1 dorsal ensiform seta; apical nematiform setae 0.24× length of gonocoxite 2; bursa copulatrix symmetrical, 0.8× length of common oviduct, with medial band of spikelike bursal microtrichia and broad dorsal bursal pouch lined with granulate microsculpture (Fig. 181D); spermatheca elongate, reservoir subequal to length of spermathecal duct, without basal lobe.

**Lectotype ♀ labeled “Molokai 4000 ft. RCLP 1902 // Atelothrus cheloniceps Type. R.C.L.P.” // yellow card with “1317” on it (BPBM) hereby designated.**

**Distribution.** This species is known only from the Pelekunu Valley rim south to the leeward edge of the forest, Molokai (Fig. 182).

**Localities.** Known from TNCH Kamakou Preserve, at Pepeopae Bog, and Puu Kolekole vicinity upward to Kaunuohua. The elevational range of these localities is 1180 to 1380 m.

**Habits.** Like *B. sphodriformis*, this species is most commonly encountered as it runs on fronds of *Cibotium* tree ferns at night. Lesser numbers of individuals have been encountered by beating *Metrosideros* (ohia lehua) and low ferns at night and during day. One individual has been found under logs on the ground. This pattern of collections is most consistent with resting in terrestrial microhabitats during daytime, and nighttime activities under cover of litter on the forest floor, accompanied by forays up into the foliage in search of food or mates.

**Phylogenetic relationships.** This species is the adelphotaxon of the species pair *B. platyophthalmica* and *B. ipu* (Fig. 9). *Blackburnia cheloniceps* is sympatric with the former (Fig. 182), though they exhibit different microhabitat preferences: *B. cheloniceps* lives in forests not necessarily near streams, and *B. platyophthalmica* has only been collected from moss covering a seep face along the headwaters of a stream. If these species diverged in allopatry, secondary dispersal has removed evidence of it. Alternatively it is possible, though difficult to test, that the two species diverged in parapatry, with *B. cheloniceps*
maintaining a predominantly epigean way of life, and *B. platyophthalmica* evolving as a cave species. Consistent with this second hypothesis would be discovery of *B. platyophthalmica* in larger caves or sinkholes on Molokai.

*Blackburnia (Metromenus) platyophthalmica* Liebherr, new species
(Figs. 180B, 182, 183)

**DIAGNOSIS.** Extremely similar to *B. cheloniceps* of Molokai (Fig. 180A), and *B. ipu* of Haleakala, Maui (Fig. 180C), due to broad basolateral extensions of pronotum, and broad abacoid elytral humeri with broad elytral lateral depressions (Fig. 180B). However, this species is diagnosed by: 1, eyes less convex, ocular ratio 1.39-1.43 (versus 1.46 in *B. cheloniceps*); 2, pronotum glabrous (versus basally setose in *B. cheloniceps* and laterally setose in *B. ipu*); 3, body pale, unicolorous flavous (versus mediodorsally piceous in *B. ipu*); and 4, metatarsomere 4 with apical lobes shorter, 0.23× median basal length of segment, not nearly 1/3 basal length of segment as seen in the other two species. Standardized body length 6.8-7.4 mm.

**DESCRIPTION.** Head narrow, elongate, eyes not projected beyond curvature of gena; neck with distinct dorsal impression; anterior supraorbital seta present or absent (absent in female holotype, present unilaterally left in male allotype), posterior supraorbital seta present; antennal pedicel with longer outer seta and 2 shorter apical setae; labral margin straight, median pair of setae very short, outer 2 pairs of normal length; frontoclypeal grooves deep just caudad frontoclypeal suture, then broadening toward mediodorsal margin of eye; mentum tooth rounded to slightly bifid apically.

**Prothorax.** Pronotal hind angles tightly rounded, slightly obtuse; basolateral margin broadly raised outside laterobasal depression, slightly sinuate before hind angle; lateral marginal depressions broad to rounded front angles, with only a slightly upturned edge; pronotum glabrous; laterobasal depressions deepest at medial 1/3 of width, broadly explanate laterally, with a broad median tubercle; median base smooth with indistinct longitudinal wrinkles, basal margin trisinuate, expanded caudad laterobasal depressions; basal marginal bead obsolete medially, indistinct caudad laterobasal depressions, obsolete at hind angles; median longitudinal impression deepest just before median base, finely incised on disc, broadened at broad, shallow anterior transverse impressions; anterior marginal bead nearly obsolete, slightly evident only inside lateral depressions. Prosternal process convex medially, unmargined posteriorly.

**Elytra** basally broad, lateral marginal depressions broad caudad slightly angulate humeri, narrowed in apical half of elytra; basal groove depressed, slightly angulate near base of third stria; elytral intervals broadly convex, striae deep, fine, continuous but with minute punctulae evident near base; scutellar seta present; dorsal elytral setae polymorphic, female with only anterior pair of setae present, male with anterior two pairs of setae present plus posterior seta present on left elytron; subapical sinuation distinct before rounded sutural apex; 13-14 lateral elytral setae.

**Pterothorax.** Metepisternum short, broad, trapezoidal, lateral margin 1.25× length of anterior margin.

**Legs.** Profemur without anteroventral setae, with 2 posteroventral setae; mesocoxa with 1 ridge seta; mesofemur with 2 anteroventral setae; metacoxa bisetose, mesal seta absent;
metafemur with 2 anteroventral setae; tarsomeres gracile but short, basal tarsomere 1.3× length of inner tibial spur; tarsomeres 1-3 with narrow, deep dorsolateral sulci, medially carinate; metaetarsomere 4 only slightly emarginate apically; basal metatarsomeres with 3 rows of sparse, elongate ventrolateral setae, medial glabrous area twice as wide as distance between rows; tarsomere 5 with two ventrolateral rows of 6 setae, each much shorter than depth of tarsomere at point of setal insertion.

Abdomen. Male with 1 apical seta each side of sternite VII, female with 3 each side.

Coloration. Head capsule brunneneous, pronotal and elytral disc slightly paler, pronotal and elytral lateral depressions paler still, flavous; palpi, antennae, and legs concolorous with pronotal margins; venter of body brunneneous, pronotal and elytral epipleura paler, concolorous with flavous femora.

Microsculpture. Vertex with isodiametric sculpticells in transverse rows, each sculpticell flat, overall surface shiny; pronotal disc with transverse mesh microsculpture, laterobasal and lateral depressions with isodiametric sculpticells in irregular transverse rows; elytral striae with distinct isodiametric microsculpture, sculpticells arranged in irregular transverse rows; venter of body covered with prominent microsculpture, transverse sculpticells arranged in irregular rows on thoracic venter, transverse rows regular on abdominal sternites.

Male genitalia. Aedeagal median lobe gracile, medioventral surface straight basad ventral excavation, apex curved downward, with tip slightly more downturned, tip extended 1.0× thickness of apex at opening of internal sac (Fig. 183A); basal sagittal crest short,
narrow; median lobe narrowed to a broadly rounded tip, right or dorsal side slightly constricted near tip (Fig. 183B).

**Female reproductive tract.** Gonocoxa basally broad, triangular gonocoxite 2 with acuminate apex (Fig. 183C); gonocoxite 1 with apical fringe of 8-9 setae in single series; gonocoxite 2 with 2 lateral ensiform setae and 1 dorsal ensiform seta; apical nematiform setae 0.21 x length of gonocoxite 2; bursa copulatrix symmetrical, subequal to length of common oviduct, with medial band of spikelike bursal microtrichia and broad dorsal bursal pouch lined with granulate microsculpture; spermatheca elongate, without basal lobe, spermathecal duct sinuous, reservoir 0.8 x length of spermathecal duct.

**Variation.** Given polymorphism in supraorbital setae and dorsal elytral setae presented above, these structures may be expected to vary in future specimens of this species.

**Holotype** 9 labeled "HI: Molokai Kamakou NCP ridge 0.8 km W Kolekole Cabin 31-V-1997 lot01 1180 m el. pyrethrum fog mossy stream bank J.K. Liebherr" (CUIC).

**Allotype** ♂ with identical data except "lot02 ... pyrethrum fog mossy seep face" (CUIC).

**Etymology.** The species epithet *platyophthalmica* refers to the flat compound eyes that distinguish this species from its syntopic cousin, *B. cheloniceps*. This species with its small eyes and presumably limited visual acuity has the dubious distinction of bearing the longest scientific name among the native Hawaiian Platynini.

**Distribution.** Known only from the type locality of *B. polhemusi* (Figs. 94, 182), the ridge and escarpment above East Kawela Gulch just west of Puu Kolekole Cabin, Molokai.

**Habits.** The two known specimens of this species were found by applying pyrethrin fog to moss mats along a small stream running off the escarpment on the south side of the ridge, and by fogging the wet seep face just below the fall line of that tiny stream. Though this site had been visited numerous times before, during day and night, in search of specimens of *B. polhemusi*, no specimens of *B. platyophthalmica* had been observed in an exposed state on any ground or plant surface. These findings suggest that *B. platyophthalmica* spends its entire life concealed within or underneath moss, sharing a secretive way of life with, among others, individuals of *B. polhemusi*.

**Phylogenetic relationships.** This species is geographically isolated from its adelphotaxon, *B. ipu* of Kipahulu Valley, East Maui (Figs. 9, 178, 182). As both species have only been discovered through use of pyrethrin insecticide on dense moss mats, it is reasonable to predict that a closely related species exhibiting the same ecological predilections will be discovered in the West Maui mountains.

Blackburnia (Metromenus) ipu Liebherr, new species
(Figs. 178, 180C, 184)

**DIAGNOSIS.** Appearing like the preceding two Molokai species—*B. cheloniceps* and *B. platyophthalmica* (Fig. 180A-B)—due to the broad basolateral extensions of the pronotum, and broad abacoid elytral humeri with broad elytral lateral depressions (Fig. 180C), but, with: 1, pronotum laterally setose, basally glabrous; 2, pronotum lacking basal marginal bead caudal laterobasal depressions; and 3, body darker, head capsule piceous, pronotal and elytral discs piceous to brunneous, though sutural interval slightly paler. Standardized body length 7.5-7.7 mm.
DESCRIPTION. Head narrow, neck with moderate dorsal impression; compound eyes slightly protruded, ocular ratio 1.40; frontoclypeal grooves shallow throughout length, lined with fine longitudinal wrinkles cephalad position of anterior supraorbital seta; anterior supraorbital setae present or absent (see Variation), posterior setae present; antennal pedicel with longer outer seta plus 2-3 shorter apical setae; labrum slightly emarginate apically, 6-setose; mentum tooth truncate to bifid.

Prothorax. Slightly obtuse pronotal hind angles produced as a slight jag, lateral margin slightly sinuate just cephalad hind angles; lateral marginal depressions broad, only slightly narrower cephalad lateral pronotal seta than behind seta, edge narrowly upraised, nearly defining a lateral bead; basal margin trisinuate, median base less pronounced than convex hind margins caudad laterobasal depressions; basal marginal bead only suggested medially by confluence of fine longitudinal wrinkles on median base, obsolete caudad laterobasal depressions; laterobasal depressions broadly elevated onto explanate basolateral margins of pronotum; median longitudinal impression finely and deeply incised onto convex disc, continued to anterior margin; anterior transverse impressions broad, shallow, traceable 3/4 of distance to tightly rounded front angles; anterior marginal bead evident mesad front angles, traceable across most of anterior margin, though discontinuous medially. Prosternal process convex ventrally, unmargined posteriorly.

Elytra. Basally broad, lateral margins broadly elevated caudad humeri; basal groove deep, sharply delimited anteriorly, tightly rounded on humeri at junction with elevated lateral margins; lateral margins gradually narrowed toward marked subapical sinuation; sutural apex broadly rounded; elytral intervals moderately convex, striae finely incised, mesal striae with minute punctulae in basal 1/3 of length; scutellar seta present; dorsal elytral setae polymorphic, posterior pair of setae always absent, anterior two pairs of setae present or absent (see Variation); 12-13 lateral elytral setae.

Pterothorax. Metepisternum short, broad, trapezoidal, lateral margin 1.2× length of anterior margin.

Legs. Profemur without anteroventral setae, with 2 posteroventral setae; mesocoxa with 1 ridge seta; mesofemur with 2 anteroventral setae; metacoxa bisetose, mesal seta absent; metafemur with 2 anteroventral setae; tarsomeres gracile, basal metatarsomere 1.7× length of inner tibial spur; tarsomeres 1-3 with deep dorsolateral sulci, medially carinate; metatarsomere 4 slightly emarginate apically, outer apical lobe 0.3× median basal tarsomere length; basal tarsomeres with 3 rows of sparse, elongate ventrolateral setae, median glabrous area 2.0× as wide as distance between lateral rows; tarsomere 5 with 2 ventrolateral rows of 4-6 setae, each much shorter than depth of tarsomere at setal insertion.

Abdomen. Males with 1 apical seta each side of sternite VII, females with 3 each side.

Coloration. Head capsule piceous, pronotal and elytral disc slightly paler, pronotal and elytral explanate lateral margins flavous, concolorous with palpi, antennae, pronotal and elytral epipleura, and femora; tibiae and tarsi darker, with smoky infuscation; thoracic and abdominal venter brunneous to piceous.

Microsculpture. Vertex of head with reduced isodiametric microsculpture; pronotal disc with transverse mesh microsculpture, laterobasal and lateral depressions with isodiametric microsculpture; elytral intervals with isodiametric sculpticells arranged in transverse rows.

Male genitalia. Aedeagal median lobe gracile, evenly curved medioventrally, ventral excavation extended to slightly downturned, bluntly rounded tip extended beyond opening of aedeagal internal sac only 0.9× width at that point (Fig. 184A); basal sagittal crest...
Fig. 184. *B. (Metromenus) ipu*, new species. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view.

moderately elongate, moderately broad; median lobe evenly tapered to a broadly rounded tip (Fig. 184B).

**Female reproductive tract.** Gonocoxa basally broad, triangular gonocoxite 2 with acuminate apex (Fig. 184C); gonocoxite 1 with apical fringe of 10 setae in an irregular double series, fifth to seventh setae from mesal edge of fringe subapical; gonocoxite 2 with 2 lateral ensiform setae and 1 dorsal ensiform seta; apical nematiform setae 0.23 × length of gonocoxite 2; bursa copulatrix symmetrical, subequal to length of common oviduct, with medial band of spikelike microtrichia and broad dorsal bursal pouch lined with sparse granulate microsculpture; spermatheca elongate, reservoir subequal to length of spermathecal duct, without basal lobe.

**Variation.** As with the related species, *B. platyophthalmica*, both supraorbital and dorsal elytral setae vary among individuals of this species. Of the three adults known, one exhibits the full complement of 4 supraorbital setae, and one lacks the anterior seta on the right side, and the third lacks both anterior setae. The dorsal elytral setae also vary, from one individual that lacks all setae, to the second that lacks the posterior pair and has the anterior seta absent from the left elytron, to the third individual that lacks only the posterior pair of setae. Finally, all individuals exhibit laterally setose pronota, though one individual
unilaterally lacks this seta on the left side. The total numbers of setae expressed on the head capsule, pronotum, and elytra are not correlated within individuals.

**Holotype** \( \sigma \) labeled “HI: Maui Haleakala N.P. Kipahulu Vy. pit crater below West Camp 19-V-1998 lot02 1845 m el. pyr. fog mossy ohia D.A. Polhemus” (NMNH).

**Allotype** ♀ from the same tree (BPBM).

**Paratype** \( \sigma \) from the same tree (CUIC).

**Etymology.** This species is named for the calabash, or ipu, used to provide percussive expression to the native hula. This name is appropriate as the beetle exhibits the rich reddish color and voluptuous curves of the ipu.

**Distribution.** Known from one pyrethrin fog sample in the upper portion of Kipahulu Valley, Haleakala National Park, East Maui (Fig. 178).

**Habits.** Like its adelphotaxon, *B. platyophthalmi ca*, this species is known only from a pyrethrin fog of dense moss mats. We can infer from its prior absence from collections that either: 1, individuals of the species do not spend much time outside of dense moss mats; or 2, more collections in its limited distributional range of Kipahulu Valley will show that it is more generalized in ecological preference. Based on information from the adelphotaxon, *B. platyophthalmica* (see above), the first alternative seems more likely.

**Phylogenetic relationships.** Based on adult morphological data, this species is geographically isolated from its adelphotaxon, *B. platyophthalmica* of Molokai (Fig. 9). This phylogenetic hypothesis is not maximally congruent with biogeographic data, as the distribution of *B. ipu* in Kipahulu Valley complements the western windward Haleakala distribution of *B. calathoides* (Fig. 178) in the same manner that the distribution of *B. kipahulu* complements that of its adelphotaxon, *B. derodera* (Fig. 129). One possible solution to this incongruence would be discovery of a deep moss-mat relative of *B. ipu* in the western portions of the Haleakala windward forest (in like manner as predicted for West Maui in the treatment of *B. platyophthalmica* above). Of course, support for a different hypothesis of relationship among the known species based on additional phylogenetic data could also remove this incongruence.

**Blackburnia (Metromenus) abax** (Sharp), new combination 
(Figs. 180D, 185, 186)

*Mesothriscus abax* Sharp, 1903: 226.

**DIAGNOSIS.** Much like *B. microps*, with quadrate, laterally setose pronotum, slightly sinuate basolateral margins cephalad distinct, obtuse hind angles (Figs. 180D, 192D), but with pronotal lateral marginal depressions very narrow and front angles less protruded; elytral humeri angulate, nearly right, but with elytral lateral depressions narrow; elytral intervals shiny, covered with partially effaced isodiametric sculpticells in transverse rows, shiny cuticular surface with irregular pitlike irregularities the size of single sculpticells. Standardized body length 6.3-7.1 mm.

**Pterothorax.** Metepisternum short, narrow, lateral margin 1.3 to 1.4× length of anterior margin.

**Male genitalia.** Aedeagal median lobe slender, slightly expanded medioventrally, ventral excavation extended onto slightly downturned apex tapered to an acuminate tip extended
in length 1.33× thickness of apex at opening of internal sac (Fig. 185A); basal sagittal crest short, moderately broad; median lobe evenly tapered to a finely rounded tip (Fig. 185B).

**Female reproductive tract.** Gonocoxa basally broad, narrowly triangular gonocoxite 2 with acuminate apex (Fig. 185C); gonocoxite 1 with apical fringe of 7-9 setae, mesal 2-4 setae near medioapical angle in double series; gonocoxite 2 with 2 short lateral ensiform setae, and 1 dorsal ensiform seta; apical nematiform setae short, 0.22× length of gonocoxite 2; bursa copulatrix symmetrical, subequal to length of common oviduct, with medial band of spikelike bursal microtrichia and rounded dorsal bursal pouch lined with sclerotized
cuticle; spermatheca ovoid, reservoir $0.75 \times$ length of spermathecal duct, without basal lobe (Fig. 185D).

**Lectotype** $\sigma$ labeled "$\sigma$ Mesothriscus abax Type D.S. 180 Molokai Mts. 4500 ft. Perkins 21.VI.1893." (BMNH) hereby designated. On this day, Perkins went upward from his Makakupaia basecamp to his tent near Pelekunu rim: "Then I went on with the intention of pushing on beyond my furthest limit" (Perkins 1893). He went down a ridge 300 to 400 ft. leading into Pelekunu Valley, but gave that up due to wind and rain, then collected "a few Carabidae." Therefore the type locality of this species appears to be the high forest near Pelekunu rim, somewhere west of Mt. Kamakou.

**Distribution.** Widely distributed across mountainous East Molokai (Fig. 186).

**Localities.** Recorded from Keopukaloa near Halawa (610 m), above Waikolu Valley, and in TNCH Kamakou Preserve including Pepeopae Bog, Puu Kolekole, and Kaunuohua. Perkins noted it as high as Molokai 6000 ft. (presumably Kamakou summit at 1512 m).

**Habits.** Like the previous several species, *B. abax* has been found by beating ferns and ohia lehua (Metrosideros polymorpha) at night, by sifting litter, and on the ground along stream beds and walking on boardwalks at night. We infer from these data that this species spends the day on the ground in terrestrial situations, and climbs vegetation at night.

**Phylogenetic relationships.** On the preferred cladogram this species is placed as the basal adelphotaxon for five species distributed on Molokai and Haleakala, West Maui: *B. latifrons* to *B. kuiki* (Fig. 9). This clade in tum is the adelphotaxon to seven other species distributed on the windward fragments of Maui Nui: *B. microps* to *B. haleakala* (Fig. 9).

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**Blackburnia (Metromenus) latifrons** (Sharpe), new combination
(Figs. 187A, 188, 189)


**Diagnosis.** Similar to *B. concolor* and *B. microps* in the distinct, obtuse pronotal hind angles and only slightly sinuate basolateral margins (Figs. 187A, 192D, 199B), but without pronotal setae; eyes convex, ocular ratio 1.57-1.60; elytral humeri distinctly angulate,
Fig. 187. Blackburnia species habitus, dorsal view. A. B. (Metromenus) latifrons. B. B. (Metromenus) calathiformis.

nearly right, lateral marginal depressions laterad humeri broadly expanded as in B. microps; elytral intervals covered with evident isodiamictric sculpticells arranged in transverse rows; basal metatarsomeres short, 1.5× length of inner tibial spur; metatarsomere 4 with slight apical emargination, outer lobe 0.25× median basal length of segment; females with 3 apical setae each side of sternite VII. Standardized body length 6.4-7.4 mm.

**Pterothorax.** Metepisternum short, narrow, lateral margin 1.3 to 1.7× length of anterior margin.

**Male genitalia.** Aedeagal median lobe slender, slightly expanded medioventrally, ventral excavation extended onto slightly downturned apex tapered to an acuminate tip extended in length 2.6× thickness of apex at opening of internal sac (Fig. 188A); basal sagittal crest short, narrow; median lobe evenly tapered to a finely rounded tip (Fig. 188B).

**Female reproductive tract.** Gonocoxa basally broad, triangular gonocoxite 2 with acuminate apex (Fig. 188C); gonocoxite 1 with apical fringe of 11-13 setae, mesal 6-8 setae near medioapical angle in double series; gonocoxite 2 with 2 short lateral ensiform setae, and 1 dorsal ensiform seta; apical nematiform setae 0.25× length of gonocoxite 2; bursa copulatrix symmetrical, subequal to length of common oviduct, with medial band of spikelike bursal microtrichia and rounded dorsal bursal pouch lined with sclerotized cuticle; spermatheca elongate, reservoir 1.30× length of spermathecal duct (Fig. 188D).
Fig. 188. B. (Metromenus) latifrons. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view. D. Female bursa copulatrix, ventral view, showing broad dorsal bursal pouch, medial band of spikelike microtrichia, and spermatheca (spermathecal gland deleted).

**Lectotype** ♀ labeled "♀ Metromenus latifrons Type D.S. Molokai. Perkins 181. // Molokai Mts. 4500 ft. Perkins VI 1893." (BMNH) hereby designated. Lot 181 was collected on 13-VI-1893 at 1365 m on Molokai (Anonymous n.d.). On this day Perkins first lost several bird specimens into dense brush after they were shot, and so, “Disgusted with the birds I now took a spell at beetle collecting” (Perkins 1893), collecting his way from Makakupaia to the forest along the rim of Pelekunu Valley.

**Distribution.** This species is known from the mountains of Molokai (Fig. 189).

**Localities.** Recorded from Pelekunu and Waikolu Valleys, and TNCH Kamakou Preserve, including Pepeopae Bog, West Kawela Gulch, and the Puu Kolekole vicinity upward to Kaunuohua.
**Habits.** This species lives in both arboreal and terrestrial microhabitats. Adults have been found on moss-covered ohia trees during daytime, and running on ferns at night. Ground-level situations include along stream banks, on mossy seep faces, and under logs, boards, and rocks.

**Phylogenetic relationships.** This species is the adelphotaxon of four species, three found on Haleakala and one on Molokai: *B. calathiformis* to *B. kuiki* (Fig. 9).

**Blackburnia (Metromenus) calathiformis** (Sharp), new combination

*Platynus calathiformis* Sharp, 1903: 229.

**DIAGNOSIS.** Among species with quadrisetose pronota, unique in the broad humeri with angulate humeral groove (Fig. 187B); pronotal base broad, basal margin expanded postolaterally mesad angulate hind angles, basolateral margins broadly sinuate before angles, lateral margin elevated above level of posterior seta; microsculpture of pronotal base and elytra very distinctly granulate, surface lustre matte; hind tarsomeres carinate medially, dorsolateral sulci of basal metatarsomere deep between median carina and carinate lateral margins of tarsomere. Standardized body length 7.1-7.8 mm.

**Pterothorax.** Metepisternum short, broad, trapezoidal, lateral margin 1.3 to 1.4× length of anterior margin.

**Male genitalia.** Aedeagal median lobe gracile, medioventral margin straight, ventral excavation extended to elongate, narrow apex ended in a finely rounded tip extended in length 2.5× thickness of apex at opening of internal sac (Fig. 190A); basal sagittal crest shallow and short; median lobe slightly constricted laterally near midlength, tapered to a finely rounded tip (Fig. 190B).

**Female reproductive tract.** Gonocoxa basally broad, triangular gonocoxite 2 with acuminate apex (Fig. 190C); gonocoxite 1 with apical fringe of 8 setae in a single row; gonocoxite 2 with 3 lateral and 1 dorsal ensiform seta; apical nematiform setae short, 0.25× length of gonocoxite 2; bursa copulatrix symmetrical, subequal to length of common
Lectotype \( \sigma \) labeled “Platynus calathiformis, Type D.S., Haleakala 5000 ft. IV1894 Perkins 385” (BMNH) hereby designated. Perkins’ lot 385 was listed as “Haleakala, Maui, contains 92 Metromeni, all under bark (mostly of Acacia) about 5,000 ft. IV. ‘94” (Anonymous n.d.) Perkins collected \( B. \) calathiformis in the company of \( B. \) erro.

**Distribution.** This species is found at higher elevations across the windward forest of Haleakala, East Maui (Fig. 191).

**Localities.** In the west found in Honomanu drainage of TNCH Waikamoi Preserve. To the east, found in Hanawi Natural Area Reserve and adjoining Hana Forest Reserve, and to the south in Haleakala National Park, found at New Greensword Bog along the northeast rift, as well as on the west rim of Kipahulu Valley near Kuiki.

**Habits.** This species has been collected only in arboreal microhabitats associated with *Metrosideros* (ohia lehua) by: 1, scraping bark, moss, and humus from trunks and crotches; 2, fogging mossy trunks with pyrethrin; and 3, beating vegetation at night. Collection localities range from 1515 to 2090 m elevation. The available evidence, therefore, suggests that adults of this species spend substantial amounts of their lifespan living on trees.

**Phylogenetic relationships.** This species is the adelphotaxon to the species triplet of \( B. \) howarthi (\( B. \) debilis + \( B. \) kuiki) (Fig. 9). Blackburnia calathiformis is sympatric in the eastern portions of its range with \( B. \) howarthi and \( B. \) kuiki, though \( B. \) howarthi is ecologically isolated in lava tube caves.
Fig. 191. Distributional records for *B. (Metromenus) calathiformis* (●), *B. (Metromenus) howarthi* (○), and *B. (Metromenus) kuiki*, new species (■).

*Blackburnia (Metromenus) howarthi* (Samuelson & Liebherr),
new combination
(Figs. 191, 192A, 193)


DIAGNOSIS. This species is easily recognized by presence of both lateral and basal pronotal setae in combination with derivations associated with cave life (Fig. 192A)—i.e., eyes much reduced, outer surface only slightly convex, a maximum of 12 ommatidia across diameter; integument pallid, elytra testaceous; legs elongate, metafemora extended beyond apex of abdomen. Standardized body length 7.5-8.0 mm.

**Pterothorax.** Metepisternum narrow, moderately elongate, lateral margin 1.6× length of anterior margin.

**Male genitalia.** Aedeagal median lobe gracile, medioventral margin slightly expanded, ventral excavation shallow, extended to elongate, narrow apex ended in an acuminate tip extended in length 3× thickness of apex at opening of internal sac (Fig. 193A); basal sagittal crest shallow and short; median lobe moderately slender basally, tapered to a finely rounded tip (Fig. 193B).

**Female reproductive tract.** Gonocoxa basally broad, triangular gonocoxite 2 with acuminate apex (Fig. 193C); gonocoxite 1 with apical fringe of 10-11 setae, 4-5 setae near medioapical angle in double series; gonocoxite 2 with 2 lateral ensiform setae and 1 dorsal ensiform seta; apical nematiform setae short, 0.24× length of gonocoxite 2; bursa copulatrix
symmetrical, subequal to length of common oviduct, with a broad dorsal pouch and a medial band of spikelike bursal microtrichia (Fig. 193D); spermatheca fusiform, reservoir 0.5× length of spermathecal duct, without basal lobe.


**Distribution.** This species is known only from a single lava tube cave in Kipahulu Valley, East Maui (Fig. 191).

**Habits.** This species appears to be troglobitic—i.e., restricted to the dark zone of the lava tube cave or caves it inhabits.

**Phylogenetic relationships.** This species is the adelphotaxon of the species pair *B. debilis* of Molokai and *B. kuiki* of Kipahulu Valley, East Maui (Fig. 9). Evolution to cave
Blackburnia (Metromenus) debilis (Perkins), new combination
(Figs. 192B, 194, 195)

DIAGNOSIS. Readily distinguishable by the reduced eyes, with outer surfaces only slightly convex, approximately 20 ommatidia across greatest diameter, and ocular ratio 1.25; pronotal basolateral margins broadly sinuate before distinct obtuse hind angles (Fig. 192B), laterobasal pronotal depressions with large median tubercle; pronotum appearing elongate, but with median length 0.93× maximum width (similar to B. kuiki, Fig. 192C); microsculpture of dorsal body surface distinct, frons covered with isodiametric sculpticells, pronotal disc with distinct transverse mesh microsculpture amid marked transverse wrinkles, elytra with granulate isodiametric microsculpture, sculpticells set in irregular transverse rows. Standardized body length 6.6 mm.
Pterothorax. Metepisternum short, broad, trapezoidal, lateral margin 1.2× length of anterior margin.
Male genitalia. Aedeagal median lobe very slender apically, evenly curved medioventrally, shallow ventral excavation extended to straight apex ended in a rounded
Fig. 195. Distributional records for *B. (Metromenus) debilis* (■), and *B. (Metromenus) tricolor* (●).

tip extended in length 1.0× thickness of apex at opening of internal sac (Fig. 194A); basal sagittal crest obsolete; aedeagal internal sac with field of large microspicules on medioapical surface; median lobe slightly tapered to a broadly rounded tip (Fig. 194B).

**Female reproductive tract.** This species is known from only a single male specimen.

**Lectotype** ♂ labeled “Mol 3000 ft.” on back of mounting card, with additional labels “Molokai 3000 ft. iii1902 RCLP // Atelothrus sp. nov. oculis parum convexis lec RCLP // Atelothrus debilis Type” // yellow card with “1321” (BPBM) hereby designated. Perkins’ (1917) description, written in England, states this species’ type locality as Haleakala, 3000 ft. (910 m). We prefer to have the specimen label take precedence in this situation, as Perkins may have written this paper without close attention to labeling of specimens collected 15 years before, and subsequently deposited in Bishop Museum. Moreover, discovery of the adelphotaxon—*B. kuiki*—on Haleakala suggests Molokai as the more likely provenance for *B. debilis*. Nonetheless, until *B. debilis* is re-collected, some uncertainty as to the actual provenance of this species must remain.

**Distribution.** For now, the label data of Molokai, 3000 ft. (910 m) remains the best indication of this species’ range. Given Perkins’ habits, this specimen most likely came from near Makakupaia, the locality of his 3000 ft. Molokai basecamp (Fig. 195).

**Habits.** Perkins makes no mention of any ecological information concerning this species. We predict that it lives in the mossy coverings on *Metrosideros* (ohia lehua).

**Phylogenetic relationships.** This species is geographically isolated from its adelphotaxon, *B. kuiki*, known from the valley rims above Kipahulu Valley, Haleakala (Figs. 9, 191). The preferred general area cladogram derived for *Blackburnia* (Fig. 10A) predicts an undiscovered relative of these two species—most closely related to *B. debilis*—in West Maui.

**Blackburnia (Metromenus) kuiki Liebherr, new species**
(Figs. 191, 192C, 196)

**DIAGNOSIS.** Easily recognized by the narrow body with shiny upper body surface (Fig. 192C)—i.e., pronotum narrow with sharply obtuse hind angles, elytral humeri narrow and
angulate, and elytra with shiny, flattened, partially effaced isodiametric sculpticells; antennal pedicel with elongate outer apical setae plus 4 apical setae from 0.5 to >1.0× as long as apical diameter of segment; elytral striae shallow, outer 5 striae interrupted along length, inner striae interrupted or not; head and elytral disc shiny brunneneous, contrasted with rufous pronotum and testaceous antennae, legs, and elytral epipleura. Standardized body length 6.1-6.3 mm.

DESCRIPTION. Head narrow, eyes moderately reduced, slightly convex, ocular ratio 1.40; frontoclypeal grooves deep at anterior margin of frons, nearly parallel throughout their length, divergent only near anterior supraorbital setae; mandibles elongate, extended more than half their length beyond anterior margin of labrum; antennal scape stout, its diameter about 0.5× diameter of compound eye, pedicel about 0.5× diameter of scape, with apical ring of 4 elongate setae; apical margin of labrum straight, 6-setose; mentum tooth apically rounded to truncate, sides subparallel.

Prothorax. Pronotum appearing narrow, median length 0.95× maximum width; lateral marginal depression of equal width from cephalad laterobasal depression to slightly protruded front angles; hind angles sharply obtuse; basolateral margin protruded at basal seta, slightly concave cephalad, and angled caudad to hind angle; laterobasal depressions with indistinct median tubercle, deepest posteromesad tubercle; basal marginal bead distinct caudad laterobasal depressions, nearly obsolete medially; median base slightly wrinkled, minute punctures along posterior margin of raised disc; median longitudinal impression fine on disc, very broad and deep toward anterior transverse impression; median apex depressed; anterior marginal bead fine but continuous across front of notum. Prosternal process flat ventrally; posterior face with median raised carina continued dorsally between procoxae.

Elytra orbicular, lateral margins evenly convex from humeri to subapical situation; humeri narrow, basal groove angulate at humeri; lateral depression moderately broad caudad humeral angles, evident to subapical situation; subapical situation marked, sutural apex broadly rounded; elytral intervals slightly convex, striae very shallow, interrupted between outer 2-3 intervals; scutellar seta present, anterior dorsal elytral seta absent, posterior 2 setae present or absent; 12-13 lateral elytral setae.

Pterothorax. Metepistemum narrow, moderately elongate, lateral margin 1.5 to 1.6× length of anterior margin.

Legs. Profemur without anteroventral setae, with 2-3 posteroventral setae; mesocoxa with 1 ridge seta; mesofemur with 2-3 anteroventral setae; metacoxa bisetose, mesal seta absent; metafemur with 2-4 anteroventral setae; tarsomeres gracile, tarsomeres 1-3 with distinct dorsolateral sulci, medially carinate; metatarsomere 4 almost straight apically, outer apical lobe 0.3× median basal tarsomere length; metatarsomere 4 with subapical setae at apical angles of segment; basal tarsomeres with 3 rows of sparse, elongate ventrolateral setae, medial glabrous area as wide as distance between lateral rows; tarsomere 5 with two ventrolateral rows of 6 setae, each as long as depth of tarsomere at point of setal insertion.

Abdomen. Males with 1 apical seta each side of sternite VII, females with 3 each side.

Coloration. Head capsule brunneneous to piceous; frons, clypeus, and mandibles rufous; maxillae, labium, and basal 3 antennomeres testaceous, outer antennomeres slightly infuscated; pronotum and elytral suture and margins rufous, paler than dark brunneneous elytral disc; femora, tibiae, and elytral epipleura testaceous, tibiae and tarsi with rufous cast, thoracic and abdominal venter rufous, the latter with flavous cast along lateral margins near elytral epipleura.
**Microsculpture.** Frons shiny, with reduced isodiametric microsculpture; pronotal disc with distinct transverse mesh microsculpture, median base and laterobasal depressions with more distinct and granulate microsculpture, a mixture of isodiametric and transverse sculpticells; elytra covered with flattened isodiametric sculpticells, their margins somewhat effaced, surface therefore shiny.

**Male genitalia.** Aedeagal median lobe apically slender, evenly curved medioventrally, shallow ventral excavation extended to elongate, narrow apex ended in a rounded tip
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extended in length 2.5× thickness of apex at opening of internal sac (Fig. 196A); basal sagittal crest shallow, short; median lobe evenly tapered to finely rounded tip (Fig. 196B).

**Female reproductive tract.** Gonocoxa basally broad, triangular gonocoxite 2 with acuminate apex (Fig. 196C); gonocoxite 1 with apical fringe of 7 setae in a single row; gonocoxite 2 with 2 lateral ensiform setae and 1 dorsal ensiform seta; apical nematiform setae moderate, 0.28× length of gonocoxite 2; bursa copulatrix symmetrical, subequal to length of common oviduct, with a medial band of spikelike bursal microtrichia (Fig. 196D); spermatheca elongate, reservoir subequal to length of spermathecal duct, without basal lobe.

**Holotype** ♂ labeled "HI: Maui Haleakala N.P. Kipahulu west rim below Kuiki sift moss ex ohia 15-V-1993 lot 01 el. 2090m / J.K. Liebherr & A.C. Medeiros collectors” (CUIC).

**Allotype** ♀ from same locality except 14-V-1995 lot 01 (CUIC).

**Paratype.** Hana For. Res., rdg. S Heleleikeoha Str. fence camp, pyr. fog moss ohia, 1785 m, 12-V-1998, Polhemus (NMNH, 1).

**Etymology.** The species epithet is derived from the type locality as a noun in apposition. Kuiki is the Hawaiian word for quilting.

**Distribution.** This species is known from the north and south rims near the head of Kipahulu Valley, on Haleakala, East Maui (Fig. 191).

**Habits.** This species has been found in moss on Metrosideros (ohia lehua) either by sifting or by pyrethrin fogging. This range of collecting situations is the same as observed in the related *B. calathiformis*. As for that species, we infer that adults of this species spend substantial portions of their adult life in arboreal moss mats.

**Phylogenetic relationships.** This is the adelphotaxon of Molokai’s *B. debilis* (Fig. 9).

*Blackburnia (Metromenus) microps* (Sharp), new combination
(Figs. 192D, 197, 198)

*Mesothriscus microps* Sharp, 1903: 226.

**DIAGNOSIS.** Recognizable by the nearly quadrate, laterally setose pronotum, hind angles distinct and slightly obtuse, basolateral margins subparallel, front angles convergent and separated by 0.75× distance between hind angles, lateral marginal depressions covered with granulate isodiametric microsculpture (Fig. 192D); elytral humeri distinctly angulate, elytral lateral depression expanded laterad seventh interval, elytral intervals covered with evident isodiametric sculpticells arranged in transverse rows; tarsomeres short, basal metatarsomere about 1.5× length of inner tibial spur; metatarsomere 4 with very short apical lobes, outer lobe 0.17× median basal length of segment. Standardized body length 6.5-7.2 mm.

**Pterothorax.** Metepisternum short, broad, trapezoidal, lateral margin 1.2 to 1.4× length of anterior margin.

**Male genitalia.** Aedeagal median lobe slender, broadly expanded medioventrally, ventral excavation extended onto evenly curved apex tapered to an acuminate tip extended in length 2.3× thickness of apex at opening of internal sac (Fig. 197A); basal sagittal crest short, narrow; median lobe slightly constricted on right side near midlength, apically tapered to a finely rounded tip (Fig. 197B).

**Female reproductive tract.** Gonocoxa basally broad, narrowly triangular gonocoxite 2 with acuminate apex (Fig. 197C); gonocoxite 1 fringed of 8-10 setae, mesal 2 setae near medioapical angle in double series; gonocoxite 2 with 2 short lateral ensiform setae, 1-2
Fig. 197. *B. (Metromenus) microps*. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view.

dorsal ensiform setae; apical nematiform setae moderately long, 0.31× length of gonocoxite 2; bursa copulatrix symmetrical, subequal to length of common oviduct, with medial band of spikelike bursal microtrichia and sclerotized region the only evidence of a dorsal pouch; spermatheca ovoid, reservoir 0.75× length of spermathecal duct, without basal lobe.

**Holotype** ♂ labeled “♂ Mesothriscus microps. Type D.S. ?W. Maui Perkins. 357.” (BMNH) hereby designated. Sharp (1903) attributed this species to the West Maui fauna even though lot 357 was listed as “Haleakala 4000 ft.” (Anonymous n.d.). Rediscovery of the species at Hanaula and Puu Kukui, West Maui, affirms Sharp’s supposition.

**Distribution.** This species is distributed throughout West Maui’s mountains (Fig. 198).

**Localities.** Known from the length of the West Maui mountains, including Mt. Eke, Puu Kukui summit, Violet Lake, unnamed 4503 ft. elevation puu on northwest flank (hill northwest of Violet Lake near camp locally known as Three Pines), and Haelau or Kualalewelewe Cabin, Lihau summit, and Hanaula summit and reservoirs.

**Habits.** Found on both *Cheirodendron* (olapa) and *Metrosideros* (ohia lehua), either under bark of dead limbs or in moss. Also collected from the ground on open cracked clay soil, and running on boardwalks at night. Therefore this species appears to be an ecological generalist, with adults active on the ground and in arboreal microhabitats.

**Phylogenetic relationships.** This species is the adelphotaxon of a clade of six species—*B. tricolor* to *B. haleakala* (Fig. 9)—distributed on the windward fragments of Maui Nui: Molokai, West Maui, and Haleakala.
Fig. 198. Distributional records for *B. (Metromenus) microps* (■), and *B. (Metromenus) abaxoides*, new species (●).

**Blackburnia (Metromenus) tricolor** (Sharp), new combination
(Figs. 195, 199A, 200)

*Mesothriscus tricolor* Sharp, 1903: 224.
*Mesothriscus tricolor* var. *rudis* Sharp, 1903: 224 (new synonymy).

**DIAGNOSIS.** Individuals of this species exhibit a generalized habitus within the context of species with broader humeri and smaller body size; standardized body length 6.1-7.1 mm. The laterally setose pronotum has obtuse-angulate hind angles, slightly sinuate basolateral margins, smooth laterobasal depressions with at most a small tubercle, and narrow lateral marginal depressions (Fig. 199A); elytral humeri tightly rounded, not angulate, elytral lateral depressions only slightly widened near anterior set of 5 lateral elytral setae; eyes moderately convex, ocular ratio 1.45; tarsomeres moderately elongate, basal metatarsomere 2× length of inner tibial spur; females with either 2 or 3 apical setae each side of sternite VII.

**Pterothorax.** Metepisternum short, broad anteriorly and narrowed behind, lateral margin 1.2 to 1.5× length of anterior margin.

**Male genitalia.** Aedeagal median lobe gracile, slightly and broadly expanded medioventrally, short apex tapered to a slightly downturned, finely rounded tip extended in length 1.5× thickness of apex at opening of internal sac (Fig. 200A); basal sagittal crest short, narrow; median lobe slightly constricted near midlength, tapered to a rounded tip (Fig. 200B).
Female reproductive tract. Gonocoxa basally broad, triangular gonocoxite 2 with acuminate apex (Fig. 200C); gonocoxite 1 with apical fringe of 8-9 setae, mesal 2 setae near medioapical angle in double series; gonocoxite 2 with 2 short lateral ensiform setae and 1 dorsal ensiform seta; apical nematiform setae moderately elongate, 0.31× length of gonocoxite 2; bursa copulatrix symmetrical, subequal to length of common oviduct, with medial band of spikelike bursal microtrichia and broad bursal pouch lined with microsculpture; spermatheca elongate, reservoir 0.90× length of spermathecal duct, without basal lobe.

Types. For Mesothriscus tricolor, lectotype ♂ labeled “♂ Mesothriscus tricolor. Type D.S. Molokai 4000 ft. VI.1896. Perkins” (BMNH) hereby designated. For Mesothriscus tricolor var. rudis, lectotype ♀ labeled “♀ Mesothriscus tricolor var? rudis D.S.” (BMNH) hereby designated.

Nomenclatural note. The form M. tricolor var. rudis is represented by two specimens that fall within the bounds of variability of this species. These cannot be geographically delimited from the nominate form; specimens of both B. tricolor and Sharp's variety are from Molokai. Nonetheless, as the variety was proposed before 1961 it is considered an available subspecific name, and therefore is synonymized.

Distribution. This species is known from the mountains of Molokai (Fig. 195).

Localities. Known from Oloku summit, Waialua Valley, Waiakuikani Gulch, Waikolu Valley, and TNCH Kamakou Preserve, including Pepeopae Bog, Puu Alii Bog Trail near Pelekunu overlook, East Kawela Gulch, Puu Kolekole vicinity upward to Kaunuohua.
**Habits.** This species is found in a variety of situations. It has been beaten from *Cibotium* (tree fern), low ferns, and *Metrosideros* (ohia lehua) at night, and retrieved from pyrethrin fog samples of moss-covered ohia during day. On the ground it has been found along stream banks, under logs, boards, and rocks, in mossy seep faces, and in tree fern litter. Thus, like its adelphotaxon, *B. concolor*, this species is an ecological generalist, being found in terrestrial and arboreal forest microhabitats as well as along streams and in wet open areas adjacent to forest. The cladistically more basal species, *B. microps*, also occupies this variety of microhabitats.

**Phylogenetic relationships.** This species is geographically isolated from its adelphotaxon, *B. concolor* of West Maui (Fig. 9).

*Blackburnia (Metromenus) concolor* (Sharp), new status, new combination
(Figs. 199B, 201, 202)

*Metromenus tricolor* var. *concolor* Sharp, 1903: 224.

**DIAGNOSIS.** Very similar to *B. tricolor* (Fig. 199A), but with pronotal lateral margins broader, hind angles more obtuse and basolateral margins therefore less sinuate (Fig. 199B), laterobasal depressions smooth or slightly wrinkled, without a median tubercle; elytral humeri subangulate, lateral depressions broad caudad humeri; females consistently with 3 apical setae each side of sternite VII. Standardized body length 6.5-7.0 mm.

**Pterothorax.** Metepisternum short, broad anteriorly and narrowed behind, lateral margin 1.2 to 1.4× length of anterior margin.

**Male genitalia.** Aedeagal median lobe gracile, slightly expanded medioventrally, ventral excavation extended onto evenly curved apex tapered to a bluntly rounded tip extended in length 1.5× thickness of apex at opening of internal sac (Fig. 201A); basal sagittal crest short, narrow to obsolete; median lobe slightly constricted near midlength, apically tapered to a rounded tip (Fig. 201B).

**Female reproductive tract.** Gonocoxa basally broad, triangular gonocoxite 2 with acuminate apex (Fig. 201C); gonocoxite 1 with apical fringe of 9-10 setae, mesal 5-6 setae near medioapical angle in double series; gonocoxite 2 with 3 short lateral ensiform setae, basal seta thinner, and 1 dorsal ensiform seta; apical nematiform setae 0.27× length of gonocoxite 2; bursa copulatrix symmetrical, subequal to length of common oviduct, with medial band of spiked bursal microtrichia and liplike bursal pouch lined with microsculpture (Fig. 201D); spermatheca ovoid, reservoir 0.80× length of spermathecal duct, without basal lobe.

**Lectotype** ♀ labeled “♂ M. tricolor concolor minor D.S. W. Maui 4000 ft. IV.94. Perkins 379.” (BMNH) hereby designated. Lot 379 is simply described as “West Maui, 4000 ft. (Coleops.) IV.49.” During the latter part of this month, Perkins collected in and around Iao Valley (Perkins 1894b).

**Distribution.** This species is broadly distributed across West Maui (Fig. 202).

**Localities.** Recorded from Mt. Eke, Puu Kukui summit and unnamed 4503 ft. elevation puu on its northwest flank (hill northwest of Violet Lake near camp locally known as Three Pines), and Hanaula. These sites are between 1210 and 1750 m elevation.
Fig. 201. *B. (Metromenus) concolor*. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view. D. Female bursa copulatrix, ventral view, showing liplike dorsal bursal pouch, medial band of spikelike microtrichia, and spermatheca.
Fig. 202. Distributional records for B. (Metromenus) concolor (■), B. (Metromenus) komohana, new name (□), B. (Metromenus) putealis (●), and B. (Metromenus) haleakala (○).

**Habits.** Like B. tricolor, this species lives in a variety of situations, including mossy Cheirodendron (olapa) and Metrosideros (ohia lehua), and terrestrial microhabitats in bogs. It has also been found running on boardwalks within forest habitats at night.

**Phylogenetic relationships.** This species is geographically isolated from its adelphotaxon, B. tricolor of Molokai (Fig. 9).

**Blackburnia (Metromenus) abaxoides** Liebherr, new species
(Figs. 198, 199C, 203, 204)

**DIAGNOSIS.** This is a morphologically heterogeneous species, with specimens from below 1000 m elevation differing from those found from 1200 to 2100 m. The higher elevation specimens (Fig. 199C) are most similar overall to B. abax (Fig. 180D) in exhibiting a trapezoidal, laterally setose pronotum, abacoid elytra with broad, angulate humeri and expanded lateral marginal depressions, but: differing by exhibiting a shinier dorsal body surface, with barely traceable isodiametric sculpticells on frons, and smooth elytral intervals without evident microsculpture on disc. Beyond that, diagnosed by pronotal basolateral margins only slightly concave to straight before distinct slightly obtuse hind angles, laterobasal margin expanded posteriorly behind laterobasal depressions, which have a broad median tubercle. Lowland specimens (455 to 970 m elevation) are more similar in overall appearance to B. tricolor of Molokai (Fig. 199A), with pronotal basolateral margins sinuate cephalad obtuse hind angles, but: 1, pronotum narrower, front angles less protruded, hind
angles more rounded; 2, eyes more convex, ocular ratio 1.44-1.60; 3, dorsal surface shiny due to reduced microsculpture—i.e., pronotal disc with partially effaced transverse sculpticells, elytral intervals with flat and shiny isodiametric sculpticells in transverse rows; 4, elytral humeri distinctly angulate, nearly right; and 5, all females with 3 apical setae each side of sternite VII. Standardized body length 5.6-7.8 mm. This description is based on all specimens, with elevationally associated variation discussed in the Variation section.

DESCRIPTION. Head. Frons broad, eyes slightly convex, ocular ratio 1.44-160; antennal pedicel with longer outer seta and 3-4 shorter apical setae; labrum apically straight to slightly emarginate; frontoclypeal grooves linearly divergent from frontoclypeal suture, curved laterad to meet anterior supraorbital setae; mentum tooth apically truncate to bifid.

Prothorax. Pronotum broad, laterally setose, slightly obtuse hind angles of almost all specimens glabrous (see Variation below), basolateral margins straight or slightly convex cephalad angles in highland specimens, slightly concave in lowland specimens; lateral marginal depressions narrow but evident, slightly wider in highland specimens, margin upraised into indistinct bead; laterobasal depressions broad with convex tubercle extended over most of surface, bordered laterally by broad indistinct convexity, bordered posteriorly by basal marginal bead best developed near border of median base and laterobasal depressions, continuous in most specimens caudad laterobasal depressions (highland specimens), just a slightly raised margin in some lowland specimens; median base covered with longitudinal wrinkles or fine punctures, bordered posteriorly by traceable marginal bead in highland specimens, obsolete medially in some lowland specimens; median longitudinal impression finely incised on disc, extended to beaded anterior margin; anterior transverse impression very shallow, difficult to trace; front angles tightly rounded, protruded anteriorly. Prosternal process convex ventrally, unmargined posteriorly.

Elytra. Basally quadrate, humeri broad, angulate, humeral angle obtuse, right, or acute (see Variation section below); basal groove carinate; humeri with elevated marginal bead extended cephalad junction with carinate basal groove in highland specimens, margin in some specimens raised as a tooth just cephalad of humeral angle; lateral elytral margin narrower in lowland specimens, raised as a tooth in a few specimens; subapical sinuation marked; sutural apex with small, blunt posterior projection; elytral intervals broadly convex, striae deep in highland specimens, intervals almost flat in lowland specimens; scutellar seta and 3 dorsal elytral setae present; 11-13 lateral elytral setae.

Pterothorax. Metepisternum short, broad, slightly narrowed posteriorly, lateral margin 1.3 to 1.5× length of anterior margin.

Legs. Profemur without anteroventral setae, with 2 posteroventral setae; mesocoxa with 1 ridge seta; mesofemur with 2 anteroventral setae; metacoxa bisetose, mesal seta absent; metafemur with 2 anteroventral setae; tarsomeres short, robust, broadened apically, basal metatarsomere 1.40 to 1.67× length of inner tibial spur; tarsomeres 1-3 with broad, shallow dorsolateral sulci, median area narrowly convex; metatarsomere 4 nearly straight apically, outer apical lobe 0.25× median basal tarsomere length in highland specimens, 0.33 to 0.45× in lowland specimens; basal tarsomeres with 3 rows of sparse, elongate ventrolateral setae, medial glabrous area twice as wide as distance between lateral rows; tarsomere 5 with two ventrolateral rows of 6 setae, each much shorter than tarsomere depth at setal insertion.

Abdomen. Males with 1 apical seta each side of sternite VII, females with 3 each side.

Coloration. Head, pronotum, and elytra shiny rufous to piceous; basal 3 antennomeres and legs testaceous, outer antennomeres and tibiae and tarsi with smoky infuscation;
Fig. 203. B. (Metromenus) abaxoides, new species. A. Male aedeagal median lobe, right lateral view, Waikamoi, 1300 m. B. Male aedeagal median lobe, euventral view, Waikamoi. C. Male aedeagal median lobe, right lateral view, Hanawi Stream, 880 m. D. Male aedeagal median lobe, euventral view, Hanawi. E. Male aedeagal median lobe, right lateral view, Kipahulu, 1200 m. F. Male aedeagal median lobe, euventral view, Kipahulu.

Thoracic and abdominal venter brunneous, pronotal and elytral epipleura paler, from only slightly so to flavor.

Microsculpture. Markedly reduced, body surface shiny in highland specimens, microsculpture better developed in lowland specimens; frons with reduced isodiametric mesh, traceable but less obvious than numerous pits the size of single sculpticells; pronotal
Fig. 204. *B. (Metromenus) abaxoides*, new species. A. Left female gonocoxa, ventral view, Kipahulu, 1200 m. B. Left female gonocoxa, ventral view, Waikamoi, 1300 m. C. Female bursa copulatrix, ventral view, showing broad dorsal bursal pouch lined with microsculpture, medial band of spikelike microtrichia, and spermatheca, Waikamoi.

disc with reduced but traceable transverse mesh microsculpture, median base and lateral reaches of laterobasal depressions with isodiamictric sculpticells; elytral intervals on disc shiny, with only indistinct isodiamictric sculpticells, outer intervals with more obvious isodiamictric microsculpture in highland specimens, intervals with flat and shiny isodiamictric sculpticells in transverse rows in lowland specimens.
Table II. Frequency distributions for configuration of pronotal lateral margins, tooth on humeral angle, and shape of humeral angle for selected samples of *B. abaxoides*. Samples represent transects up Kipahulu Valley, Waikamoi Gulch, and vicinity (*), plus a single lowland individual from Hanawi Stream.

<table>
<thead>
<tr>
<th>Locality</th>
<th>Elevation (m)</th>
<th>Pronotal lateral margin</th>
<th>Humeral tooth</th>
<th>Humeral angle</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Sinuate</td>
<td>Straight</td>
<td>-</td>
</tr>
<tr>
<td>Kipahulu Vy.</td>
<td>455</td>
<td>2</td>
<td>0</td>
<td>2</td>
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<tr>
<td>Hanawi Stream</td>
<td>880</td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Kipahulu Vy.</td>
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<td>6</td>
<td>0</td>
<td>5</td>
</tr>
<tr>
<td>Waikamoi Gulch</td>
<td>960</td>
<td>6</td>
<td>0</td>
<td>5</td>
</tr>
<tr>
<td>Waikamoi Gulch</td>
<td>1160</td>
<td>1</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Kipahulu Vy.</td>
<td>1200</td>
<td>5</td>
<td>0</td>
<td>4</td>
</tr>
<tr>
<td>Waikamoi Flume*</td>
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<td>22</td>
<td>41</td>
<td>0</td>
</tr>
<tr>
<td>Koolau Gap*</td>
<td>1325</td>
<td>1</td>
<td>6</td>
<td>0</td>
</tr>
<tr>
<td>Ukulele Pipeline*</td>
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<td>4</td>
<td>14</td>
<td>0</td>
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<tr>
<td>Kipahulu Vy.</td>
<td>1500</td>
<td>2</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>T.N.C. Waikamoi*</td>
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<td>3</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td>Kipahulu Vy.</td>
<td>2090</td>
<td>1</td>
<td>2</td>
<td>0</td>
</tr>
</tbody>
</table>

**Male genitalia.** Aedeagal median lobe slender, evenly curved to slightly convex medioventrally, ventral excavation extended onto slightly downturned apex tapered to a finely rounded tip extended in length 1.0 to 1.4× thickness of apex at opening of internal sac, longest in highland specimens (Fig. 203A versus 203C, E); basal sagittal crest various, short, broad to obsolete; median lobe moderately broad until tapered near apex to a rounded tip (Fig. 203B, D, F).

**Female reproductive tract.** Gonocoxa basally broad, narrowly triangular gonocoxite 2 with acuminate apex (Fig. 204A-B); gonocoxite 1 with apical fringe of 8-10 setae, mesal 4 setae near medioapical angle in double series; gonocoxite 2 with 2 short, thin lateral ensiform setae, and 1 dorsal ensiform setae; apical nematiform setae short, 0.19 to 0.26× length of gonocoxite 2; bursa copulatrix symmetrical, subequal to length of common oviduct, with medial band of spikelike bursal microtrichia, and rounded dorsal bursal pouch lined with microsculpture (Fig. 204C); spermatheca elongate, reservoir subequal to length of spermathecal duct, without basal lobe.
**Variation.** Conspecificity of lowland and highland populations of this species is supported by series from Waikamoi Gulch, elevation 960 to 970 m, and Kipahulu Valley, elevation 910 m, both of which exhibit variation in pronotal shape. Pronotal laterobasal margins are either straight or sinuate just cephalad the pronotal hind angles (Table 11). Individuals of these lowland series also vary in the amount of elytral microsculpture. Most individuals possess flat isodiametric sculpticells, but, several individuals have more reduced microsculpture, and therefore appear as shiny as most specimens from higher-elevation sites at 1200 to 1800 m.

Elytral humeri also vary among individuals of this species, with humeral angles ranging from obtuse, to right, to moderately acute. Many of those beetles with right and acute humeral angles exhibit a raised margin cephalad the angles that resembles a shallow tooth. It is not possible to distinguish more than one species among the specimens available due to presence of different combinations of pronotal shape and humeral configuration (Table 11). In general, individuals from higher elevations exhibit more quadrate pronotum, and acute humeral angles with a toothed margin.

It is clear that environmental variation is correlated with morphological variation in this species, with the lowland form exhibiting: 1, rounder, more laterobasally sinuate pronotum; 2, narrower pronotal and elytral lateral margins; and 3, less developed elytral microsculpture, versus highland populations with a more quadrate pronotum, broader pronotal and elytral lateral margins, and more distinct microsculpture. In exhibiting this elevational variation, this species parallels patterns observed by Gagné (1997) in *Nesiomiris swezeyi* Gagné (Hemiptera, Miridae).

Of 291 specimens examined, 1 had short setae on both hind angles. These setae were as stout as the lateral setae, but were less than half the length, a situation not unlike the short stout setae at the posterior angles of the holotype of *B. polhemusi*.

**Holotype** σ labeled “HI: Maui Haleakala N.P. Kipahulu Valley Central Pali Tr. 1200 m el. 29-IV-1991 under rocks on trail // J.K. Liebherr A.C. Medeiros Jr. collectors” (CUIC).

**Paratypes.** MAUl, Haleakala: 1515 m, 01-IV-1894, Perkins (BPBM, 1), V-1896, Perkins (BMNH, 1), V-1896, Perkins (BPBM, 3); Haleakala N.P., Kipahulu Vy., 455 m, 21-VIII-1929, Swezey (BPBM, 2), beating vegetation at night, 1500 m, 09-V-1991, Jessel & Medeiros (CUIC, 1), sifting litter (CUIC, 1), 1800 m, 08-V-1991 (CUIC, 1), Central Pali Tr., sifting leaf/moss litter, 910 m, 30-IV-1991, Liebherr & Medeiros (CUIC, 1), under boards/logs/tarps (CUIC, 5), beating vegetation at night, 1200 m, 29-IV-1991, Liebherr & Medeiros (CUIC, 4), under rocks, trail (CUIC, 4), West Camp, pyr. fog ohia w/ moss, 1950 m, 20-V-1998, Polhemus (NMNH, 1), pit crater below West Camp, pyr. fog ohia w/ moss, 1845 m, 19-V-1998 (NMNH, 1); Kipahulu west rim ESE Kuiki, ohia, sifting humus, 1850 m, 15-V-1993, Liebherr & Medeiros (CUIC, 1), Kipahulu west rim below Kuiki, ohia, beating at night, 2090 m, 14-V-1993 (CUIC, 1), ohia, sifting moss (CUIC, 1), 15-V-1993 (CUIC, 1); Hana For. Res., Heleleikeoha Str. fence camp, pyr. fog ohia + *Astillia*, 1615 m, 11-V-1998, Liebherr (CUIC, 4), pyr. fog ohia w/ moss (CUIC, 27), Polhemus (NMNH, 32), pyr. fog *Cibotium*, Liebherr (CUIC, 2); Heleleikeoha Str., ridge S fence camp, pyr. fog ohia w/ moss, 1785 m, 12-V-1998, Polhemus (NMNH, 7), Heleleikeoha Str., ridge W, under logs, 1740 m, 11-V-1998, Ewing (CUIC, 2), 12-V-1998, Liebherr (CUIC, 5); Hanawi N.A.R., Kukiwa Vy., Pouli Cabin, pyr. fog ohia w/ moss, 1590 m, 05-V-1998, Liebherr (CUIC, 1), Polhemus (NMNH, 23), 06-V-1998, Liebherr (CUIC, 6), pyr. fog ohia roots/trunk, Polhemus (NMNH, 9), middle Hanawi Str., tributary, 880 m, 12-XI-1992,
Polhemus (BPBM, 1); Koolau For. Res., Koolau Gap, Halehaku, pyr. fog Cibotium, 1325 m, 13-V-1998, Liebherr (CUIC, 1), pyr. fog Cibotium + log (CUIC, 1), pyr. fog ohia w/ moss (CUIC, 5), Polhemus (NMNH, 1); Koolau For. Res., Kula Pipeline Rd., pyr. fog ohia w/ moss, 1160 m, 15-V-1998, Polhemus (NMNH, 3); Kula Pipeline Rd. W Waikamoi Gulch, pyr. fog ohia w/ moss, 960 m, 15-V-1998, Polhemus (NMNH, 4), beating uluhe fern, 970 m, 15-V-1998, Liebherr (CUIC, 1), pyr. fog ohia + Cibotium, 970 m, 15-V-1998, Liebherr (CUIC, 1); Makawao For. Res., Maile Rd., scrape ohia bark, 1300 m, 26-V-1997, Liebherr (CUIC, 2); Waikamoi Flume, Waikamoi Gulch, beating/sifting moss, 1300 m, 09-V-1991, Liebherr (CUIC, 2), under boards/wet ohia for., 1300 m, 09-V-1991, Liebherr (CUIC, 6), under boards, 26-V-1997 (CUIC, 11), Waikamoi Gulch to Haipuaena Gulch, under boards/wet ohia for., 1300 m, 11-IV-1991, Liebherr (CUIC, 64); Waikamoi N.C.P., Honomanu drainage, Trans. 3, sifting litter, 1700 m, 10-IV-1991, Liebherr (CUIC, 1), ohia, scraping bark, 08-V-1991 (CUIC, 2), ohia, scraping humus/moss (CUIC, 5), Maile Rd., pyr. fog mossy log, 1435 m, 02-V-1998, Polhemus (NMNH, 29), Ukulele Pipeline, pyr. fog mossy ohia log, 1465-1495 m, 07-V-1998, Polhemus (NMNH, 18), under logs, 1495-1525 m, 07-V-1998, Liebherr (CUIC, 22), pyr. fog ohia w/ moss, 1525 m, 07-V-1998 (CUIC, 7), 1550 m (CUIC, 1).

**Etymology.** The species epithet *abaxoides* refers to the great similarity of this species to *B. abax* of Molokai. Both names stem from the broad, angulate humeri observed in the pterostichine carabid genus *Abax*.

**Distribution.** This species is widely distributed across a broad elevational band of windward montane forest on Haleakala, East Maui (Fig. 198).

**Habits.** This species lives predominantly on the ground, with most specimens found under boards and logs, or under rocks in wet ohia forest. In highland habitats, adults are also found in leaf and moss litter from the ground. Of the above type series, only six highland individuals were collected by beating vegetation at night, or by scraping bark on ohia lehua (*Metrosideros*) trunks. Lowland populations exhibit more varied habitat preferences, with collections from gravel substrate along Hanawi Stream, uluhe fern, or mossy ohia trunks.

**Phylogenetic relationships.** This species is the adelphotaxon of the species triplet: *B. komohana* of West Maui (*B. putealis + B. haleakala* of Haleakala) (Figs. 9, 202).

*Blackburnia (Metromenus) komohana* Liebherr & Zimmerman, new name
(Figs. 199D, 202, 205)


**DIAGNOSIS.** Recognizable by the broad, glabrous pronotum with distinct, nearly right hind angles (Fig. 199D), sinuate basolateral margins, and lateral marginal depressions lined with granulate isodiametric microsculpture sharply contrasted with reduced transverse mesh microsculpture of shiny pronotal disc; elytral basal carina markedly elevated cephalad broad and angulate humeri, elytral marginal depressions narrow throughout length; elytral apex flavous, contrasted with brunneous disc; mentum tooth bifid; dorsolateral sulci on metatarsomeres 1-3 shallow and broad, delimiting a narrowly angulate median carina; females with 2 apical setae each side of sternite VII. Standardized body length 6.5-7.3 mm.
CARABIDAE PART 1: PLATYNINI

Pterothorax. Metepisternum short, broad, trapezoidal, lateral margin 1.3× length of anterior margin.

Male genitalia. Aedeagal median lobe gracile, slightly expanded medioventrally; deep ventral excavation extended to downturned apex ended in a finely rounded tip extended in length 1.67× thickness of apex at opening of internal sac (Fig. 205A); basal sagittal crest shallow; median lobe parallel-sided at midlength, tapered to finely rounded tip (Fig. 205B).

Female reproductive tract. Gonocoxa basally broad, triangular gonocoxite 2 with rounded apex (Fig. 205C); gonocoxite 1 with apical fringe of 9-11 setae, mesal 4-6 setae near medioapical angle in double series; gonocoxite 2 with 2-3 short lateral ensiform setae and 1 dorsal ensiform seta; apical nematiform setae 0.26× length of gonocoxite 2; bursa copulatrix symmetrical, subequal to length of common oviduct, with medial band of spikelike bursal microtrichia and broad dorsal bursal pouch; spermatheca broad and elongate, reservoir length subequal to both width and length of spermathecal duct, without basal lobe.

Lectotype ♂ labeled “Mecomenus koebelei Type D.S. Lahaina Koebele” (BMNH) hereby designated.

Etymology. This replacement name is necessitated by recognition of *Atrachycnemis koebelei* Sharp as the senior name in *Blackburnia*. Komohana is the Hawaiian word for west, indicating this species’ provenance of West Maui.

Distribution. This species is known only from the vicinity of Lahaina, West Maui (Fig. 202), most likely the lower reaches of Pu‘u Kukui east of the town.

Fig. 205. B. *(Metromenus) komohana*, new name. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view.
Localities. Known from Lahaina, 910 m elevation.
Habits. Consistent with Albert Koebele’s inadequate labeling of specimens, we know nothing of this species’ habits.
Phylogenetic relationships. This species is geographically isolated from its adelphotaxon: the Haleakala species pair *B. putealis* + *B. haleakala* (Figs. 9, 202).

*Blackburnia* (*Metromenus*) *putealis* (Blackburn), new combination
(Figs. 132C-D, 202, 206A, 207)

*Anchomenus putealis* Blackburn, 1881: 227.
*Metromenus putealis*: Blackburn & Sharp, 1885: 212.
*Meconemenus putealis*: Sharp, 1903: 231.

DIAGNOSIS. Pronotum with sinuate basolateral margins and obtuse-angulate hind angles (Fig. 206A)—similar to *B. tricolor*, *B. concolor*, and lowland *B. abaxoides* (Fig. 199A-C)—but glabrous, lacking the lateral setae, lateral margin depressions narrower though lined with evident isodiametric sculpticells. Also diagnosed by: 1, mandibles elongate, projected as far beyond front angles of labrum as distance from dorsal condyle to labral
Fig. 207. *B. (Metromenus) putealis*. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view. D. Female bursa copulatrix, ventral view, showing broad dorsal bursal pouch, medial band of spikelike microtrichia, and spermatheca (spermathecal gland deleted).
margin; 2, labrum broadly emarginate apically; 3, elytral humeri obtuse-angulate, lateral
marginal depressions slightly expanded caudad humeri; 4, intervals covered with distinct
isodiametric microsculpture, sculpticells arranged in irregular transverse rows; 5, elytral
apex broadly flavous, contrasted with rufous disc; 6, metatarsomere 1 short, 1.6× length of
inner tibial spur, dorsolateral sulci deep and broad, median area narrowly convex; and 7,
females with 2 apical setae each side of sternite VII. Standardized body length 6.0-7.0 mm.

**Pterothorax.** Metepisternum moderately elongate, narrowed posteriorly, lateral margin
1.3 to 1.5× length of anterior margin.

**Male genitalia.** Aedeagal median lobe basally slender, broadly expanded medioventrally
along ventral excavation, excavation extended to broadly downturned apex tapered to
bluntly rounded tip extended 2.0× depth of apex at opening of internal sac (Fig. 207A);
basal sagittal crest extremely short and narrow; median lobe broadest at midlength, tapered
to rounded tip (Fig. 207B).

**Female reproductive tract.** Gonocoxa basally broad, triangular gonocoxite 2 with
acuminate apex (Fig. 207C); gonocoxite 1 with apical fringe of 7-8 setae, mesal 2 setae near
 medioapical angle in double series; gonocoxite 2 with 3 lateral ensiform setae, and 1 dorsal
ensiform seta; apical nematiform setae moderately elongate, 0.28× length of gonocoxite 2;
bursa copulatrix symmetrical, subequal to length of common oviduct, with median band of
spikelike bursal microtrichia, and rounded dorsal bursal pouch lined with scaly
microsculpture (Fig. 207D); spermatheca elongate, reservoir 0.90× length of spermathecal
duct, without basal lobe.

**Lectotype.** ♀ on card with 3 parallel lines, the top line thickest—Blackburn’s Oahu code
(Zimmerman 1957)—and “putealis” handwritten on reverse (BMNH) hereby designated.

**Distribution.** Known from Haleakala’s montane windward forest, East Maui (Fig. 202).

**Localities.** Recorded from Perkins’ Haleakala 4000 and 5000 ft. localities (above Olinda
and at Ukulele Camp). In this century found in the eastern reaches of Haleakala’s windward
forests: 910 to 1500 m in Kipahulu Valley, Haleakala National Park, and at 1600 m along
Heleleikeoha Stream, Hana Forest Reserve.

**Habits.** The largest series (11) of this species was collected under boards, logs, and
tarpaulins at an abandoned camp in Kipahulu Valley. Other beetles have been found in
moss mats on ohia lehua (*Metrosideros polymorpha*), in leaf litter, under decaying
vegetation along stream banks, and on vegetation at night. This species appears to be a
generalized inhabitant of the wettest habitats on the windward face of Haleakala.

**Phylogenetic relationships.** The distribution of this species is sympatric with that of its
adelphotaxon, *B. haleakala*, in the Olinda forest along the western edge of the windward
Haleakala montane forest (Figs. 9, 202).

**Blackburnia (Metromenus) haleakala** Liebherr & Zimmerman, new name
(Figs. 202, 206B, 208)

*Mecostomus perkinsi* Sharp, 1903: 229 (junior homonym of *Atrachycnemis perkinsi*
Sharp, 1903).

DIAGNOSIS. Quite unlike any of the other abacoid species, being an aggregate of
exaggerated attributes (Fig. 206B): 1, mandibles very long, extended as far past labral
angles as from dorsal condyle to labral angles; 2, labrum broadly emarginate apically;
3, vertex convex, neck markedly impressed just caudad posterior supraorbital setae; 4, pronotum with obsolete lateral marginal depressions, markedly sinuate basolateral margins, right hind angles, flat laterobasal depressions, and wrinkled median base without marginal bead; 5, parallel-sided elytra, with angulate, toothed humeri, deep basal groove lined with longitudinal wrinkles, flat disc, and narrowly flavous apex; 6, elytral intervals covered with indistinct but traceable isodiametric sculpticells arranged in irregular transverse rows, and irregularly distributed, minute pits the size of individual sculpticells; 7, metatarsomere 1 short, 1.35× length of inner tibial spur, dorsolateral sulci broad, shallow, median area broadly convex; and 8, females with 2 apical setae each side of sternite VII. Standardized body length 6.1-6.7 mm.

**Pterothorax.** Metepisternum moderately elongate, narrowed posteriorly, lateral margin 1.5× length of anterior margin.

**Male genitalia.** Aedeagal median lobe basally slender, slightly expanded medioventrally just beyond midlength, ventral excavation extended to slightly downturned apex tapered to a rounded tip extended 1.5× depth of apex at opening of internal sac (Fig. 208A); basal sagittal crest extremely short and broad; median lobe broad basally, tapered in apical half to a finely rounded tip (Fig. 208B).

**Female reproductive tract.** Gonocoxa basally broad, triangular gonocoxite 2 with acuminate apex (Fig. 208C); gonocoxite 1 with apical fringe of 7-8 setae, 1-2 smaller subapical setae near medioapical angle; gonocoxite 2 with 2 short, thin lateral ensiform
setae, and 1 dorsal ensiform seta; apical nematiform setae 0.22× length of gonocoxite 2; bursa copulatrix symmetrical, subequal to length of common oviduct, with medial band of spikelike bursal microtrichia, and rounded dorsal bursal pouch lined with scaly microsculpture; spermatheca elongate, reservoir subequal to length of spermathecal duct.

**Variation.** Of the four specimens examined, three have lateral pronotal setae present, and one lacks them.

**Lectotype** ♀ labeled “♀ Mecostomus perkinsi Type D.S. Haleakala 4000 ft. V.1895. Perkins.” (BMNH) hereby designated.

**Etymology.** Because Haleakala is the mountain that serves as the current center of carabid diversity in the Hawaiian Islands, it is also one of the few replacement names with sufficient import to stand in place of Perkins.

**Distribution.** This species is known only from the northwestern end of the windward Haleakala montane forest, East Maui (Fig. 202).

**Localities.** As with the preceding species, *B. haleakala* was collected by Perkins near his Haleakala 4000 ft. (1210 m) and 5000 ft. (1515 m) sites (above Olinda, and Ukulele Camp).

**Habits.** Perkins (1894a) stated that he collected one specimen each on 1-IV-1894 and 5-IV-1894 under dead wood on the ground, though only the latter specimen is available (BPBM) in collections examined for this study. He collected three other specimens, but made no notice of their capture in his notes. From such fragmentary information, we can only conclude that this species is an inhabitant of terrestrial microhabitats.

**Phylogenetic relationships.** This species is sympatrically distributed with its adelphotaxon, *B. putealis* (Figs. 9, 202).

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**Blackburnia (Metromenus) kilauea** Liebherr & Zimmerman, new name

(Figs. 130G-H, 134, 209A, 210, 211)

*Atelothrus hawaiiensis* Sharp, 1903: 219 (junior homonym of *Colpocaccus hawaiiensis* Sharp, 1903).

*Mesothriscus hawaiiensis* Sharp, 1903: 224 (new synonymy; junior homonym of *Colpocaccus hawaiiensis* Sharp, 1903).

*Metromenus lentus* Sharp, 1903: 235 (new synonymy; junior homonym of *Pseudobroscus lentus* Sharp, 1903).

**DIAGNOSIS.** This species confounded Sharp due to extensive variation in pronotal setation; possible setal configurations include: 1, lateral setae present and basal setae absent; 2, basal setae present and lateral setae absent; or 3, pronotum glabrous (see Variation below). As in the following 3 species, the pronotum is laterobasally sinuate (in some specimens, only slightly so). But, in this species the hind angles are rounded-angulate and situated cephalad median base (Fig. 209A); mentum tooth apically truncate, not bifid; microsculpture on outer 2 elytral intervals subgranulate, markedly contrasted with the shinier disc; tarsi short, metatarsomere 1 less than 3.0× as long as broad, and less than 2.0× as long as inner apical tibial spur; tarsomere 4 emarginate apically, outer apical lobe of fourth metatarsomere 0.7× median basal tarsomere length (Fig. 130H). Standardized body length 5.9-7.3 mm.

**Pterothorax.** Metepisternum short, narrower posteriorly, lateral margin 1.3 to 1.5× length of anterior margin.
Male genitalia. Aedeagal median lobe gracile, broadly, shallowly expanded medioventrally, ventral excavation extended to elongate apex ended in a finely rounded, downturned tip, tip extended $2.0 \times$ thickness of apex at opening of internal sac (Fig. 210A); basal sagittal crest various, broad to obsolete; median lobe moderately slender basally, tapered slightly to a broadly rounded tip (Fig. 210B).

Female reproductive tract. Gonocoxa basally broad, triangular gonocoxite 2 with acuminated apex (Figs. 134A, 210C); gonocoxite 1 with apical fringe of 6-8 setae in single row; gonocoxite 2 with 2-3 lateral ensiform setae and 1 dorsal ensiform seta (Fig. 134B); apical nematiform setae elongate, $0.32 \times$ length of gonocoxite 2; bursa copulatrix symmetrical, subequal to length of common oviduct, with a broad dorsal pouch and a medial band of spikelike bursal microtrichia; spermatheca elongate, reservoir $1.0 \times$ length of spermathecal duct, without basal lobe.

Variation. Because Sharp (1903) relied so heavily on configuration of pronotal setae for his classification, he was forced to recognize this species under several generic and specific names. Having access to substantially more material, we can obtain a far better view of variation in this feature. Most specimens lack pronotal setae (Table 12), a derived loss given presence of lateral pronotal setae in close relatives of *B. kilauea*. However, the plesiomorphic condition of lateral setae present occurs in 29% of the specimens. Rarely, lateral setae are absent, and one or both basal setae are present. Probably, beetles with 4 pronotal setae occur as representatives of this species, though none has yet been observed. No other morphological characters were observed that support distinction of pronotal setal

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Fig. 210. *B. (Metromenus) kilauea*, new name. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view.
Table 12. Configurations of pronotal setae observed among specimens of *B. kilauea*: +, setae bilaterally present; -, setae bilaterally absent; ±, seta unilaterally present. First symbol refers to lateral pronotal setae, second to basal setae.

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<tbody>
<tr>
<td>No. specimens</td>
<td>27</td>
<td>51</td>
<td>1*</td>
<td>1</td>
<td>12</td>
</tr>
</tbody>
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* Holotype of *Atelothrus hawaiiensis*.

classes as biological entities. Moreover, repeated collection of mixed syntopic series of individuals best supports interpretation of this variation as infraspecific.


**Etymology.** The replacement species epithet *kilauea* is taken from the most commonly represented locality among known specimens.

**Distribution.** This species is distributed across Hawaii Island (Fig. 211).

**Localities.** Known from all volcanoes of Hawaii Island. In the Kohala Mountains, found on Puu Pala, Puu Pohoulaula, Kawainui Stream at Upper Hamakua Ditch, and along the ditch. Perkins collected this species at his Kona 4000 ft. locality, most likely the area now accessible by Kaloko Drive. On Mauna Kea, this species has been found in Laupahoehoe Natural Area Reserve, Nauhi Gulch, and above Honomu. In the Mauna Loa/Kilauea area, it is recorded from Volcano village, Puu Makaala Natural Area Reserve, and Olaa Rain Forest and Thurston Lava Tube areas of Hawaii Volcanoes National Park.

**Habits.** Found in a variety of situations, including active at night on *Cheirodendron*, *Cibotium*, and *Metrosideros*. It has also been found in ground-level situations, including carrion pitfall traps, under logs and rocks, and in leaf litter. Adults, larvae, and pupae were found together under bark of a downed, dead *Acacia koa* branch, with larvae crawling in bark beetle galleries (3-4-VI-1997, Liebherr, eUIC). Numerous adults were collected from moss-covered ohia lehua after use of pyrethrin insecticide. Thus, in conjunction with this species being broadly distributed geographically, it is an ecological generalist within the ohia montane forest.

**Phylogenetic relationships.** This is the adelphotaxon of a Maui Nui species triplet: *B. lanaithalensis* (*B. vagans* + *B. auana*) (Fig. 9). The basal position relative to this triplet supports colonization of Hawaii Island by the ancestors of *B. kilauea* before fragmentation of Maui Nui facilitated speciation among the other three species.
Fig. 211. Distributional records for *B. (Metromenus) kilauea*, new name.

**Blackburnia (Metromenus) lanaihalensis** Liebherr & Zimmerman, new name  
(Figs. 209B, 212, 213)

*Mesothriscus lanaiensis* Sharp, 1903: 223 (junior homonym of *Colpocaccus lanaiensis* Sharp, 1903).

DIAGNOSIS. Among species with laterally setose, cordate pronota, *B. lanaihalensis* is diagnosed by reduced, angulate elytral humeri (Fig. 209B); anterior dorsal elytral seta in depression as wide as third interval; elytral disc with distinct transverse microsculpture,
differing from microsculpture of outer 2 intervals in shape of sculpticells but not roughness, therefore elytral disc scarcely shinier than lateral margins; dorsal body surfaces rufobrunneous, margins paler, prothoracic and elytral epipleura, and legs flavous, thoracic venter slightly darker; standardized body length smaller, 6.8-7.1 mm (species known only from 2 males).

**Pterothorax.** Metepisternum short, slightly narrower posteriorly, lateral margin 1.4× length of anterior margin.

**Male genitalia.** Aedeagal median lobe gracile, medioventral margin straight, ventral excavation extended to short apex ended in a bluntly rounded tip, tip extended in length subequal to thickness of apex at opening of internal sac (Fig. 212A); basal sagittal crest short, narrow; median lobe moderately slender basally, constricted on right side, tapered to a finely rounded tip (Fig. 212B).

**Female reproductive tract.** Females of this species are not known.


**Etymology.** This species was collected on Lanaihale, the large ridge north of Koele, so the name of the type locality is chosen as stem of the replacement name.

**Distribution.** This species was collected on Lanaihale, the large ridge north of Koele, so the name of the type locality is chosen as stem of the replacement name.

**Habits.** This species has not been re-collected since Perkins found the two known specimens in January and February 1894 (R.C.L.P. lot 83, Anonymous n.d.). One would predict its habits to be like that of *B. vagans* and *B. auana*; these two species comprise the adelphotaxon of *B. lanaihalensis*.

**Phylogenetic relationships.** This species is the adelphotaxon of *B. vagans* of Molokai and *B. auana* of West Maui (Fig. 9). This relationship supports initial isolation of Lanai among the four major fragments of Maui Nui, with closer historical relationships among the three windward fragments: Molokai, West Maui, and East Maui.

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Fig. 212. *B. (Metromenus) lanaihalensis*, new name. A. Male aedeagal median lobe, internal sac everted, right lateral view. B. Male aedeagal median lobe, euventral view.
Fig. 213. Distributional records for *B. (Metromenus) lanaihalensis*, new name.

**Blackburnia (Metromenus) vagans** (Sharp), new combination

*(Figs. 209C, 214, 215)*

*Mesothriscus vagans* Sharp, 1903: 222.

**DIAGNOSIS.** This species exhibits the laterally setose, cordate pronotum of the prior 2 species—i.e., *B. kilauea* and *B. lanaihalensis*. But, the basolateral pronotal margins are more sinuate (Fig. 209C); humeral angles are rounded and broad, not markedly angulate and reduced as in *B. lanaihalensis*; basal metatarsomeres are medially carinate, dorsolateral sulci deep and distinct. *Blackburnia auana* shares the medially carinate tarsomeres with this species, but it has a narrower pronotum and elytra (Fig. 209D), with humeri somewhat reduced. Standardized body length 6.4-7.6 mm.

**Pterothorax.** Metepisternum short, broad, trapezoidal, lateral margin 1.3 to 1.4× length of anterior margin.

**Male genitalia.** Aedeagal median lobe gracile, medioventral margin straight, ventral excavation extended to short apex ended in a bluntly rounded tip, tip extended 1.4× thickness of apex at opening of internal sac (Fig. 214A); basal sagittal crest shallow to obsolete; median lobe slender basally, slightly constricted on right side, tapered slightly to a finely rounded tip (Fig. 214B).

**Female reproductive tract.** Gonocoxa basally broad, triangular gonoxoite 2 with acuminate apex (Fig. 214C); gonoxoite 1 with apical fringe of 12-13 setae, 6 setae near medioapical angle in double series; gonoxoite 2 with 3 lateral ensiform setae and 1 dorsal ensiform seta; apical nematiform setae moderately elongate, 0.29× length of gonoxoite 2; bursa copulatrix symmetrical, subequal to length of common oviduct, with a narrow, rounded dorsal pouch and a medial band of spikelike bursal microtrichia; spermatheca elongate, reservoir 1.0× length of spermathecal duct, without basal lobe.

**Variation.** This species exhibits polymorphism for presence of basal pronotal setae, mirroring at least partly the setal polymorphism in *B. kilauea*. In *B. vagans* most specimens exhibit two lateral setae and glabrous pronotal hind angles (Table 13). Of specimens examined, 14, or about 3%, possessed one basal seta on one side of the body. In 12 of these
Fig. 214. *B. (Metromenus) vagans*. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view.

Table 13. Configurations of pronotal setae among specimens of *B. vagans*: + / -, lateral setae present, basal setae absent; + / ±, lateral setae present and basal setae unilaterally present; + / +, two lateral and two basal setae present.

<table>
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<th>+ / -</th>
<th>+ / ±</th>
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<td>No. specimens</td>
<td>390</td>
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<td>5</td>
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individuals, these unilateral setae are very short, being 1/8 to 1/10 the length of a normally proportioned seta, whereas the remaining 2 specimens exhibit setae of the same length as the lateral setae. In all 5 individuals with two basal setae complementing the lateral setae, the basal setae are stunted. This stunted condition appears to be identical to the condition of the posterior pronotal setae in the holotype of *B. polhemusi*, whereby the articulatory socket of the seta is of smaller diameter, and the seta is short and blunt.

**Lectotype** ♀ labeled “Mesothriscus vagans Molokai Mts. 4000 ft. Perkins. 8.6.1893.” (BMNH) hereby designated. On June 8, Perkins hiked north, then east from Makakupaa, crossing at least one gulch. *Blackburnia vagans* is found along stream banks, suggesting that this is the habitat within which he picked up the type series.

**Distribution.** This species is found across the higher portions of East Molokai (Fig. 215).

**Localities.** Known from Kalae (Perkins), Wailau Trail (790 m), and TNCH Kamakou Preserve localities of Kamakou Flats, Waikolu Valley head, Hanalilolilo Trail, east and
west forks of Kawela Gulch, Pepeopae Bog, Puu Kolekole, and Kaunuohua. Elevations of known collection sites span 395 to 1515 m.

**Habits.** Adults of *B. vagans* live in both terrestrial and arboreal situations. They have been beaten from *Melicope, Metrosideros* (ohia lehua), and low ferns at night, and have been found in moss on ohias during day. Beetles are also active on the ground at night, frequenting stream banks, open trails, and boardwalks.

**Phylogenetic relationships.** This species is geographically isolated from its adelphotaxon, *B. auana* of West Maui (Fig. 9).

**Blackburnia (Metromenus) auana Liebherr, new species**
(Figs. 209D, 216, 217)

**DIAGNOSIS.** Like *B. vagans* with cordate, laterally setose pronotum (Fig. 209C-D) and medially carinate metatarsomeres 1-3, but the pronotal base is consistently narrower, basal pronotal width 0.65 to 0.70× maximum pronotal width versus 0.70 to 0.80× in *B. vagans*; elytral humeri correspondingly narrower, moderately reduced, rounded as in *B. vagans*, not angulate as in *B. lanaihalensis*; elytral intervals slightly convex, flatter than in *B. vagans*. Standardized body length 6.3-7.4 mm.

**DESCRIPTION.** **Head.** Eyes small in diameter but convex, ocular ratio 1.54; dorsal impression distinct, neck constriction evident caudad hind supraorbital setae; antennal pedicel with 1 longer outer seta and 1 shorter apical seta dorsally; labrum straight to slightly emarginate apically; frontoclypeal grooves broad, wrinkles radiating outward from lateral edge of raised frontal area, most posterior wrinkle extended to anterior supraorbital seta; mentum tooth broadly truncate to broadly bifid apically.

**Prothorax.** Pronotum with moderate lateral marginal depressions and upraised, non-beaded border (Fig. 209D); basolateral margins sinuate before obtuse-rounded hind angles, the angles slightly cephalad median base due to anteriorly curved laterobasal margins; laterobasal depressions smooth, deepest just inside hind angles, a transverse ridge between deepest portion extended from expanded posterior portions of lateral marginal depression,
Fig. 216. B. (Metromenus) auana, new species. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view.

bordered posteriorly by a marginal bead continuous across median base; median base with longitudinal wrinkles along posterior margin of raised disc; median longitudinal impression obsolete on median base, finely incised and deep on disc, with numerous transverse wrinkles extended onto disc; anterior transverse impression shallow, broad, demarking median apical area defined by dense isodiametric microsculpture; pronotal disc with transverse microsculpture; anterior margin irregularly beaded medially, marginal bead more consistent toward rounded, slightly protruded front angles. Prosternal process convex medioventrally, not margined posteriorly.

**Elytra.** Basal groove gently recurved laterally to rounded humeri, humeri moderately reduced, lateral marginal depression narrow laterad anterior 3 lateral setae; lateral margins subparallel medially, subapical sinuation marked, sutural apex subangulate, some specimens with a broad, blunt protuberance along posterior margin of elytra; elytral intervals slightly convex, striae smooth but irregularly constricted; scutellar seta and 3 dorsal elytral setae present; 15-16 lateral elytral setae.

**Pterothorax.** Metepistemum short, broad, trapezoidal, lateral margin 1.2 to 1.4× length of anterior margin.

**Legs.** Profemur without anteroventral setae, with 2 posterovertral setae; mesocoxa with 1 ridge seta; mesofemur with 2 anteroventral setae; metacoxa bisetose, mesal seta absent; metafemur with 2 anteroventral setae; tarsomeres gracile, tarsomere 1 slightly expanded apically, tarsomeres 2 and 3 slightly more expanded; tarsomeres 1-3 with distinct
dorsolateral sulci, medially carinate; metatarsomere 4 apically emarginate, outer apical lobe 0.4 to 0.5× median basal tarsomere length; apical setae of metatarsomere 4 slightly subapical (as in Fig. 130G); basal tarsomeres with 3 rows of elongate ventrolateral setae, medial glabrous area as wide as distance between lateral rows; tarsomere 5 with two ventrolateral rows of 6 setae much shorter than depth of tarsomere at setal insertion.

**Abdomen.** Males with 1 apical seta each side sternite VII, females with 3 setae each side.

**Coloration.** Head capsule darkest, piceous; pronotal and elytral disc dark brunneous, their lateral margins narrowly paler, brunneous; femoral apex flavous, paler than dirty yellow pronotal and elytral epipleura, femoral bases slightly infuscated, tibiae and tarsi darker yet, brunneous; antennae uniformly dark brunneous except for pale scape; thoracic and abdominal venter more or less uniformly brunneous, lateral reaches of abdominal sternites slightly paler.

**Microsculpture.** Vertex and neck constriction with distinct isodiametric microsculpture; pronotal disc with distinctly developed transverse mesh microsculpture, median base and median apex contrastingly covered with isodiametric mesh, laterobasal depressions with indistinct swirled isodiametric and transverse sculpticells; median elytral intervals with distinct isodiametric sculpticells arranged in irregular transverse rows, lateral intervals with sculpticells slightly more raised, but surface shininess not greatly different.

**Male genitalia.** Aedeagal median lobe gracile, medioventral margin slightly expanded, ventral excavation extended to short apex ended in a bluntly rounded tip, tip extended 1.2× thickness of apex at opening of internal sac (Fig. 216A); basal sagittal crest very shallow to obsolete; median lobe moderately slender basally, slightly constricted at midlength, tapered to a rounded tip (Fig. 216B).

**Female reproductive tract.** Gonocoxa basally broad, triangular gonocoxite 2 with acuminate apex (Fig. 216C); gonocoxite 1 with apical fringe of 10-11 setae, 6 setae near medioapical angle in double series; gonocoxite 2 with 3 lateral ensiform setae and 1 dorsal ensiform seta; apical nematiform setae moderately elongate, 0.29× length of gonocoxite 2; bursa copulatrix symmetrical, subequal to length of common oviduct, with a rounded dorsal pouch and a medial band of spikelike bursal microtrichia; spermatheca elongate, reservoir 1.0× length of spermathecal duct, without basal lobe.

**Variation.** Just as in *B. vagans*, this species exhibits polymorphism in presence of basal pronotal setae (Table 14). The fractions of individuals for the various setational configurations is nearly identical in the 2 species (see Tables 13, 14). There is a qualitative difference, however, that supports recognition of these two species as distinct genetic entities. In most *B. vagans* specimens exhibiting basal pronotal setae, the setae are stunted; not so in *B. auana*, where all observed basal setae are of normal proportions.

**Holotype.** ²~ labeled “HI: West Maui Is. Pu‘u Kukui trail above Pu‘u 4503’ 13-V-1992 J.K. Liebherr el.1330-1365m // on ground or on boardwalk at nighttime” (CUIC).

**Paratypes.** MAUI, West Maui: Hanaula, Hanaula Springs, creekbed under rocks, 1270 m, 11-V-1993, Liebherr (CUIC, 8), reservoirs, ohia, beating/scraping, 1210 m, 10-V-1993, Liebherr (CUIC, 1); Mt. Eke N.A.R., on ground in bog, 1330-1360 m, 24-V-1997, Liebherr (CUIC, 3); Pu‘u Kukui Tr., unnamed Pu‘u 4503 ft., ground/boards at night, 1330 m, 13-V-1992, Liebherr (CUIC, 3), ohia, beating at night, 1330 m, 13-V-1992, Liebherr (CUIC, 2), Polhemus (CUIC, 2), ohia, beating during day, 1330 m, 13-V-1992, Liebherr (CUIC, 1), on ground at night, 1330 m, 22-V-1997, Liebherr (CUIC, 3), above Pu‘u 4503 ft., ground/boards at night, 1330-1365 m, 13-V-1992, Liebherr (CUIC, 92).
Table 14. Configurations of pronotal setae among specimens of B. auana: + / -, lateral setae present, basal setae absent; + / ±, lateral setae present and basal seta unilaterally present; + / +, two lateral and two basal setae present.

<table>
<thead>
<tr>
<th>Configuration</th>
<th>+ / -</th>
<th>+ / ±</th>
<th>+ / +</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. specimens</td>
<td>102</td>
<td>5</td>
<td>2</td>
</tr>
</tbody>
</table>

Etymology. The species epithet auana is the Hawaiian verb, to wander, or to go from place to place; a name that parallels the Latin vagans applied to the adelphotaxon, B. vagans.

Distribution. This species is found along streams and streamlike situations wherever they have been surveyed in the West Maui mountains (Fig. 217).

Habits. This species, like its sister B. vagans, is a generalized inhabitant of both ground-level and arboreal microhabitats. Adults have been beaten from ohia lehua (Metrosideros) during day and night, and have been collected from under rocks during day, and on open ground at nighttime. The largest series of individuals from Puu Kukui—from the unnamed 4503 ft. elevation puu (hill northwest of Violet Lake near camp locally known as Three Pines; Liebherr, CUIC)—was collected as beetles ran on open clay soil and a wooden boardwalk surface during night.

Phylogenetic relationships. This species is the adelphotaxon of B. vagans of Molokai (Figs. 9, 215).
Fig. 218. *Blackburnia* species habitus, dorsal view. A. *B. (Metromenus) epicurus*. B. *B. (Metromenus) hilaris*. C. *B. (Metromenus) metromenoides*. D. *B. (Metromenus) caliginosa*. 
**Blackburnia (Metromenus) epicurus** (Blackburn), new combination


*Anchomenus epicurus* Blackburn, 1877: 145.


**Diagnosis.** From the confusing array of color variation displayed by *B. fraterna*, this species is recognized by the marked isodiametric microsculpture on the elytra, giving the beetles a dull appearance (Figs. 14B, 218A); pronotal laterobasal depressions covered with granulate isodiametric microsculpture, the basolateral margin clearly sinuate before obtuse-rounded hind angles; eyes large and quite convex, ocular ratio 1.65-1.75. Tarsomere 4 with short apical lobes, the outer lobe of fourth metatarsomere 0.55 to 0.60× median basal length of segment (Fig. 131G). This species is also larger than many of the Oahu species that might be confused with it: standardized body length 6.7-7.8 mm.

**Pterothorax.** Metepisternum short, trapezoidal, lateral margin 1.15 to 1.45× length of anterior margin.

**Male genitalia.** Aedeagal median lobe gracile, narrow near base of shaft at basal bulb, straight medioventrally, ventral excavation extended to short, apically downturned apex with finely rounded tip (Fig. 219A); basal sagittal crest short, narrow; median lobe basally broad, constricted on right side, tapered to a finely rounded tip (Fig. 219B).

**Female reproductive tract.** Gonocoxa basally broad, triangular gonocoxite 2 with acuminate apex (Figs. 135D, 219C); gonocoxite 1 with apical fringe of 10-11 setae, mesal 5-6 at medioapical angle in double series; gonocoxite 2 with 3-4 lateral ensiform setae and 1 dorsal ensiform seta; apical nematiform setae short, 0.24× length of gonocoxite 2; bursa copulatrix symmetrical, subequal to length of common oviduct, with a broad dorsal pouch with short lateral extensions of lightly sclerotized membrane, and a medial band of spikelike microtrichia (Fig. 219D); spermatheca elongate, subequal to length of spermathecal duct, without basal lobe.

**Lectotype** ♀ on card with 2 parallel lines, the top broadest—Blackburn’s Oahu code (Zimmerman 1957)—with “epic” handwritten on reverse, and second label “Sandwich Is. 80.6.” (BMNH) hereby designated.

**Distribution.** This species is widely distributed on Oahu (Fig. 220).

**Localities.** Found along the length of the Waianae Range, including Mokuleia, Mt. Kaala (375 to 1220 m elevation), Kawiwi, Puu Kalena, Puu Kanehoa, Puu Kaua, and Palieka. Distributed throughout the Koolau Mountains: Kawaiola Gulch and Ridge, Hauula, Kaluanui and Castle Trail, Helemano, Poamoho Trail, Punalu'u, Wahiawa, Puu Kaaumakua, Waimano Trail, Aiea Ridge, Puu Keahiakahoe massif at Tripler Ridge, Halawa Valley, Moanalua Valley, Puu Lanihuli, Kaumualihina, Nuuanu Valley and Pali including Moole Stream, Pacific Heights, Konahuanui, Maunawili, Pauoa Valley, Tantalus, Manoa Valley, Mt. Olympus, Palolo Valley and Kaa Crater, Waialae Iki, Wiliwilinui Ridge, Waiulua Gulch, and Niu Valley. This species has been found from 150 to 1220 m elevation.

**Habits.** This species is active on plant surfaces and on the ground. Substrate plant genera include *Acacia* (koa), *Byronia*, *Cheirodendron*, *Cibotium*, *Dubautia*, *Freyvinetia*, and *Metrosideros* (ohia lehua), with beetles recorded from under koa bark, and under mosses on ohia. Adults also live on the ground in dense uluhe fern (IX-1935, UHEM), found via Williams' (1936) arduous search for the immatures of *Megalagrion oahuense* (Blackburn).
Fig. 219. B. (Metromenus) epicurus. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view. D. Female bursa copulatrix, ventral view, showing broad dorsal pouch with lateral extensions, medial band of spikelike bursal microtrichia, and spermatheca.
Terrestrial situations in which this species has been found include rotten logs, under rocks, boards, and wet roadside debris, and walking on open trails at night.

**Phylogenetic relationships.** This is the adelphotaxon to a clade of 13 species—*B. hilaris* to *B. perpolita* (Fig. 9)—distributed on either Oahu or Kauai.

**Blackburnia (Metromenus) hilaris** (Perkins), new combination  
(Figs. 218B, 221, 222)


**Diagnosis.** Superficially very similar to *B. fraterna* specimens with intermediately dark coloration—i.e., head brunneous, contrasted with flavous, glabrous pronotum, elytra with smoky infuscation on disc and basal, lateral, and apical margins broadly paler, testaceous. Metatarsomere 4 similar, with apical lobes about 2/3 median basal tarsomere length. But, diagnosed by: 1, basal metatarsomere shorter, less than 2.0× length of inner tibial spur, with evident outer dorsolateral sulcus but only fine inner sulcus, median raised area broad, flat; 2, pronotal lateral margins more sinuate, basolateral margin more broadly elevated (Fig. 218B); 3, elytra narrower, not broadly ovoid (compare to Figs. 231D, 237), intervals more
convex; 4, elytral microsculpture consisting entirely of transversely stretched sculpticells producing an alutaceous sheen over entire disc; 5, male aedeagal median lobe with very short apex (Fig. 221A). Standardized body length 5.1-6.6 mm.

**Pterothorax.** Metepisternum quadrate, lateral margin 1.2 to 1.7× length of anterior margin.

**Male genitalia.** Aedeagal median lobe gracile, broad medioventral expansion (Fig. 221A); ventral excavation extended onto extremely short, bluntly rounded apex extended about as far beyond articulation with internal sac as thickness of apex at that point; basal sagittal crest short, shallow; median lobe basally broad, slightly constricted on right side, tapered to a finely rounded tip (Fig. 221B).
CARABIDAE PART 1: PLATYNINI

Fig. 222. Distributional records for B. (Metromenus) hilaris.

Female reproductive tract. Gonocoxa basally broad, triangular gonocoxite 2 with acuminate apex (Fig. 221C); gonocoxite 1 with apical fringe of 8 setae, third and fourth setae from medioapical angle in double series; gonocoxite 2 with 3-4 lateral ensiform setae and 1 dorsal ensiform seta; apical nematiform setae short, 0.20× length of gonocoxite 2; bursa copulatrix symmetrical, subequal to length of common oviduct, with a broad, rounded dorsal pouch with lateral extensions (Fig. 221D), and a medial band of spikelike microtrichia; spermatheca ovoid, 0.75× length of spermathecal duct, without basal lobe.

Lectotype ♀, the right specimen of 2 mounted together on a card, left specimen dissected, with genitalia in glass vial, right one above label “Type R.C.L.P.,” with reverse side of card labeled “Waianae Kaala 2000 ft. // Metromenus hilaris. Type.” // yellow card with “1310” (BPBM) hereby designated.

Distribution. This species is restricted to the Waianae Mountains of Oahu (Fig. 222).

Localities. Known from Mt. Kaala (summit bog and Makaha Stream west of the summit), Puu Kalena, and Palikea. Collections have been made at elevations from 365 to 1210 m.

Habits. This species occupies terrestrial and arboreal microhabitats. Substrate plants include Astelia, Broussaisia, Cheirodendron, Cibotium chamissoi and C. menziesii, and Metrosideros (ohia lehua). On the ground, it occurs in leaf and log litter. It has also been found under piles of debris washed along the edge of the Mt. Kaala road.
**Phylogenetic relationships.** This species is the adelphotaxon of the sympatrically distributed *B. metromenoides* (Figs. 9, 222, 224). These two species apparently differ in their elevational preference. *Blackburnia hilaris* is known from the Waianae summits downward as low as 365 m elevation, and *B. metromenoides* has been recorded from Waianae summits ranging 900 to 1200 m elevation.

*Blackburnia (Metromenus) metromenoides* (Perkins), new combination
(Figs. 218C, 223, 224)


**DIAGNOSIS.** Having the indeterminate look of a pale *B. fraterna* from the Waianae, but immediately separable by presence of basal pronotal seta (Fig. 218C). This diagnosis is not based on polymorphism for presence of this seta, as the species is also diagnosed by: 1, metatarsomere 4 with apical lobes longer than in *B. fraterna* or *B. hilaris*, outer lobe 0.75 to 0.85× median basal tarsomere length; 2, tarsomeres broader, dorsolateral sulci broad and shallow, median area convex; 3, elytral disc less convex, almost as flat as *B. palmae* (Fig. 266D); 4, elytral microsculpture consisting of rough-sided isodiametric sculpticells, arranged in irregular transverse rows; 5, abdominal sternites laterally flavous, the pale band as wide as metepisternum, contrasted against the darker median portions of venter. Standardized body length 5.4-6.7 mm.

**Pterothorax.** Metepisternum quadrate, broad, lateral margin 1.3 to 1.6× length of anterior margin.

**Male genitalia.** Aedeagal median lobe gracile, medioventral margin straight (Fig. 223A); ventral excavation extended onto straight, short, bluntly rounded apex extended 1.33× beyond articulation with internal sac as thickness of apex at that point; basal sagittal crest short, shallow; median lobe narrow basally, slightly constricted on right side, tapered to a finely rounded tip (Fig. 223B).

**Female reproductive tract.** Gonocoxa basally broad, triangular gonocoxite 2 with acuminat apex (Fig. 223C); gonocoxite 1 with apical fringe of 8-10 setae, mesal 3-5 setae on medioapical angle in double series; gonocoxite 2 with 3-4 lateral ensiform setae and 1 dorsal ensiform seta; apical nematiform setae short, 0.24× length of gonocoxite 2; bursa copulatrix symmetrical, 0.7× length of common oviduct, with a small, rounded dorsal pouch with lateral extensions, and a medial band of spikelike microtrichia; spermatheca ovoid, 0.75× length of spermathecal duct, without basal lobe.

**Lectotype ♀ mounted on card with “Waianae Mts. Kaala” handwritten by Perkins on reverse, second label “Atelothrus metromenoides Type.,” and the third label a yellow card with “1310” (BPBM) hereby designated.

**Distribution.** This species is restricted to the Waianae Mountain Range of Oahu (Fig. 224), with the only specific elevation noted on labels being the summit of Mt. Kaala, 1210 m elevation.

**Localities.** Recorded only from Mt. Kaala, Puu Kalena, and Palikea.

**Habits.** All records for this species indicate an arboreal life style, with adults of this species beaten from *Astelia*, *Cibotium chamissoi*, and *Gunnera*. 
Phylogenetic relationships. This species is the adelphotaxon of *B. hilaris* (Fig. 9), with chorological consequences discussed above in that species' treatment.

*Blackburnia (Metromenus) caliginosa* (Blackburn), new combination
(Figs. 131C-D, 218D, 224, 225)

*Dyscolus caliginosus* Blackburn, 1877: 148.


DIAGNOSIS. This species is distinguishable by the narrow glabrous prothorax, head capsule with markedly constricted, elongate neck and bulging eyes, narrow humeri (Fig. 218D), and small size, standardized body length 4.8-6.3 mm. Additionally, diagnosed by: 1, head and pronotal disc nearly concolorous, piceous to brunneous; 2, dorsal elytral setae set in depressions whose diameter may approach the breadth of the third elytral interval; 3, tarsomeres very short, metatarsomere 1 less than 2× length of inner apical tibial spur; and 4, tarsomere 4 with elongate apical lobes, metatarsomere 4 with outer lobe 1.3 to 1.6× median basal tarsomere length (Fig. 131C).

**Pterothorax.** Metepisternum short, broad, trapezoidal, lateral margin 1.3 to 1.5× length of anterior margin.

**Male genitalia.** Aedeagal median lobe gracile, with slight medioventral expansion (Fig. 225A); ventral excavation extended onto short, bluntly rounded apex extended beyond
articulation with internal sac subequal to thickness of apex at that point; basal sagittal crest short, moderately broad; median lobe basally broad, slightly constricted on right side, tapered to a finely rounded tip (Fig. 225B).

**Female reproductive tract.** Gonocoxa basally broad, triangular gonocoxite 2 with acuminate apex (Fig. 225C); gonocoxite 1 with apical fringe of 9-10 setae, mesal 3 setae on medioapical angle in double series; gonocoxite 2 with 2-3 lateral ensiform setae and 1 dorsal ensiform seta; apical nematiform setae short, 0.24× length of gonocoxite 2; bursa copulatrix symmetrical, subequal to length of common oviduct, with a broad, rounded dorsal pouch with lateral extensions, and a medial band of spikelike microtrichia (Fig. 225D); spermatheca elongate, 0.9× length of spermathecal duct, without basal lobe.

**Lectotype.**  $\sigma$ on card with 3 parallel lines, the top thickest—Blackburn’s Oahu code (Zimmerman 1957)—and “caliginosus” written on reverse (BMNH) hereby designated.

**Distribution.** Found throughout the entire length of the Koolau Range, Oahu (Fig. 224).


**Habits.** Recorded from both arboreal and terrestrial microhabitats. Substrate plant genera include *Astelia, Broussaisia, Cibotium, Freycinetia, Ilex, Machaerina, Acacia koa*, and *Metrosideros polymorpha*. This species is commonly beaten from mossy ohias or dead tree fern fronds and stipes. At night, adults of this species walk on the ground on open trails or other open areas; daytime terrestrial records come via sifting litter.
Fig. 226. Blackburnia species habitus, dorsal view. A. B. (Metromenus) mutabilis. B. B. (Metromenus) meticulosa.

Phylogenetic relationships. This species is the adelphotaxon of the sympatrically distributed B. mutabilis (Fig. 9). These two species exhibit the extreme sympathy of other Koolau species complexes, such as B. fossipennis (B. fugitiva + B. proterva) (Figs. 162, 166, 168), and B. fractistriata and B. fordi (Figs. 233, 235). The possible causes for such a pattern are discussed under the treatments of the former clade.

Blackburnia (Metromenus) mutabilis (Blackburn), new combination
(Figs. 131E-F, 136A, 226A, 227, 228)
Dyscolus mutabilis Blackburn, 1877: 148.
Metromenus mutabilis: Blackburn & Sharp, 1885: 211; Sharp, 1903: 232.

DIAGNOSIS. Somewhat varied in coloration, but the only species with the elytral disc flavous and the lateral and apical margins dark, with smoky infuscation; head brunneous to piceous, much darker than flavous pronotum; pronotum glabrous, sinuate basolateral margins elevated before hind angles (Fig. 226A). Additionally, B. mutabilis has markedly lobate tarsomere 4, outer apical lobe of fourth metatarsomere 1.6 to 1.7× median basal tarsomere length (Fig. 131E). Standardized body length 4.9-6.6 mm.

Pterothorax. Metepisternum short, broad, trapezoidal, lateral margin 1.3 to 1.5× length of anterior margin.
CARABIDAE PART I: PLATYNNINI

Fig. 227. B. (Metromenus) mutabilis. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view.

**Male genitalia.** Aedeagal median lobe gracile, with slight medioventral expansion (Fig. 227A); ventral excavation extended onto short, slightly downturned apex extended beyond articulation with internal sac 1.5× thickness of apex at that point; basal sagittal crest short, shallow; median lobe narrow throughout length; slightly constricted near midlength, tapered to a rounded tip (Fig. 227B).

**Female reproductive tract.** Gonocoxa basally broad, triangular gonocoxite 2 with acuminate apex (Fig. 227C); gonocoxite 1 with apical fringe of 10-11 setae in single series; gonocoxite 2 with 3 lateral ensiform setae and 1 dorsal ensiform seta; apical nematiform setae short, 0.26× length of gonocoxite 2; bursa copulatrix symmetrical, subequal to length of common oviduct, with broad, rounded dorsal pouch with lateral extensions, and a medial band of spikelike microtrichia; spermatheca ovoid, 0.7× length of spermathecal duct.

**Lectotype** ♀ on blank card with “mutabilis” handwritten on reverse (BMNH) hereby designated.

**Distribution.** This species is found throughout the Koolau Mountains, Oahu (Fig. 228).

**Localities.** Having a range almost identical to that of *B. caliginosa*, including: Pupukea, Kawailoa Gulch and Ridge, Kaipapau, Kaluanui, Poamoho Trail, Punalu'u, Kahana, Puu Ohulehule, Wahiawa, Waiawa Trail, Waiahole Ditch, Puu Kaaumakua, Eleao, Aiea Heights, Moanalua, Puu Keahiakaohe at Tripler Ridge, Puu Lanihuli, Konahuanui, Tantalus, Mt. Olympus, Manoa Valley, Palolo Valley and Kaau Crater, Wailupe Gulch, and Kuliouou Trail summit. These sites range in elevation from 455 to 910 m.
Fig. 228. Distributional records for *B. (Metromenus) mutabilis*.

**Habits.** Like *B. caliginosa*, found in both arboreal and terrestrial situations. Host plant genera associated with this species include *Astelia, Cibotium* (tree fern), *Freycinetia* (*ieie*), *Machaerina*, and *Metrosideros* (*ohia lehua*). Adults walk on open trails at night, and in *Oreobolus furcatus* litter during day. Perkins (1913, cxlii) noted that this species occupies *Astelia* flowers during day, as well as hiding among the leaf bases.

**Phylogenetic relationships.** This is the adelphotaxon of the sympatric *B. caliginosa* (Fig. 9), with a discussion of chorology presented in that species’ treatment.

**Blackburnia (Metromenus) meticulosa** (Blackburn), new combination (Figs. 226B, 229, 230)

*Anchomenus meticulosus* Blackburn, 1877: 146.

*Metromenus meticulosus*: Blackburn & Sharp, 1885: 212; Sharp, 1903: 234.

**DIAGNOSIS.** With the distinct microsculpture, narrow pronotal lateral marginal depressions (Fig. 226B), and small body, standardized body length 4.9-6.0 mm, these remind of a *Bradycellus* of the tribe Harpalini. The non-setose pronotum has the laterobasal depressions very shallow, with a median longitudinal raised tubercle connected cephalad
Fig. 229. *B. (Metromenus) meticulosa.* A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view.

with the elevated disc; vertex shiny, with isodiametric microsculpture, pronotal disc with distinct transverse mesh, elytra with very distinct transversely stretched sculpticells in transverse rows; metatarsomere 4 with short apical lobes, outer lobe 0.7× median basal length of segment; head and elytral disc bruneous, pronotum slightly paler, especially along margins, which are flavous; legs, and prothoracic and elytral epipleura testaceous, contrasted with bruneous thoracic ventrites and metacoxae.

**Pterothorax.** Metepisternum very short, broad, trapezoidal, lateral margin 1.0 to 1.2× length of anterior margin.

**Male genitalia.** Aedeagal median lobe gracile, straight medioventrally (Fig. 229A); ventral excavation extended onto short, evenly downturned apex extended beyond articulation with internal sac from 1.5 to 2.0× thickness of apex at that point; basal sagittal crest short, almost obsolete; median lobe moderately broad basally; slightly constricted near midlength, tapered to a finely rounded tip (Fig. 229B).

**Female reproductive tract.** Gonocoxa basally broad, triangular gonocoxite 2 with acuminate apex (Fig. 229C); gonocoxite 1 with apical fringe of 10-11 setae, mesal 6 near medioapical angle in double series; gonocoxite 2 with 3 lateral ensiform setae and 1 dorsal ensiform seta; apical nematiform setae short, 0.22× length of gonocoxite 2; bursa copulatrix symmetrical, subequal to length of common oviduct, a rounded dorsal pouch with lateral extensions, and a medial band of spikelike microtrichia; spermatheca ovoid, 0.8× length of spermathecal duct, without basal lobe.
Lectotype ♀ on card with 2 parallel lines, the top thickest—Blackburn’s Oahu label (Zimmerman 1957)—and “meticulosus” handwritten on reverse (BMNH) hereby designated.

Distribution. This species is known from the Mt. Kaala massif, and isolated northern and southern Koolau localities, Oahu (Fig. 230).

Localities. In the Waianae known from Mt. Kaala summit and upper Haleauau Gulch. One record from the S Waianae Mountains, 9-XI-1919 (Bridwell, NMNH), suggests a broader historical distribution. Koolau records are concentrated south of Nuuanu Pali on Konahuanui, Tantalus, Mt. Olympus, Puu Lanipo, and Wailupe Gulch. Perkins collected a single specimen at Helemano, II-1893 (BPBM), again suggesting a broader historical distribution than seen today.

Habits. As with B. caliginosa and B. mutabilis, B. meticulosa lives in both terrestrial and arboreal microhabitats. Adults walk on trails at night, and rest during day under boardwalks and rocks, and in Berlese samples of rotted wood. Substrate plant genera for this species include: Cheirodendron (olapa), Cibotium (tree fern), Freycinetia (ieie), and Metrosideros (ohia lehua).

Phylogenetic relationships. This species is the adelphotaxon of a species triplet composed of two Koolau species, plus a third that lives on Haleakala, East Maui (Figs. 9, 217, 230, 233, 235). Blackburnia meticulosa sympatrically occupies the Koolau Mountain
Range with the Oahu species of its adelphotaxon, but it also lives allopatrically in the Waianae Mountains. If broad-scaled allopatric speciation brought about divergence in this complex, *B. meticulosa* would have possessed a primordial range restricted to the Waianaeas.

**Blackburnia (Metromenus) fractistriata** (Perkins), new combination  
*(Figs. 231A, 232, 233)*  

**DIAGNOSIS.** Immediately recognizable by the foveate dorsal elytral punctures (Fig. 231A), setose pronotal hind angles, and dark coloration, with head and elytra piceous, and pronotum, ventral body surface, antennae, and legs bruneous. The eyes are prominent, ocular ratio 1.60; pronotum broad with evident lateral marginal depressions, and laterobasal depression with evident median tubercle; tarsomere 4 with elongate apical lobes, metatarsomere 4 with outer lobe about 1.1× median basal tarsomere length. Standardized body length 5.2-6.6 mm.

**Pterothorax.** Metepisternum short, broad, trapezoidal, lateral margin 1.1 to 1.4× length of anterior margin.

**Male genitalia.** Aedeagal median lobe gracile, slightly curved medioventrally based ventral excavation (Fig. 232A); ventral excavation extended onto short, evenly downturned apex extended beyond articulation with internal sac subequal to thickness of apex at that point; basal sagittal crest short, almost obsolete; median lobe moderately broad basally, tapered to a finely rounded tip (Fig. 232B).

**Female reproductive tract.** Gonocoxa basally broad, triangular gonocoxite 2 with acuminate apex (Fig. 232C); gonocoxite 1 with apical fringe of 7-8 setae, mesal 4 near medioapical angle in double series; gonocoxite 2 with 3 lateral ensiform setae and 1 dorsal ensiform seta; apical nematiform setae short, 0.17× length of gonocoxite 2; bursa copulatrix symmetrical, subequal to length of common oviduct, with a small rounded dorsal pouch and a medial band of spikelike microtrichia; spermatheca ovoid, 0.7× length of spermathecal duct, without basal lobe.

**Lectotype** ♂ on card, separate label “Honolulu Mts. 2500+ ft // Atelothrus fractistriatus Type” // yellow card with “1314” (BPBM) hereby designated.

**Distribution.** This species is known from Kahana south to Kulepiaamoa Ridge east of Lanipo, Koolau Mountains, Oahu (Fig. 233).

**Localities.** The most northerly locality is Poamoho Trail, with other localities including Puu Kaaumakua, Waikane, Waipio Ridge, Kipapa Gulch, north peak of Eleo massif, Puu Kahauapi, Puu Lanihuli, Konahuani, Nuuanu-Manoa Ridge, Tantalus, Palolo Valley above Kaau Crater, Mt. Olympus, Puu Lanipo, Wiliwilinui Ridge, and Kulepiaamoa Ridge. Known localities are 695 to 940 m elevation.

**Habits.** Almost all records of this species are in association with plant surfaces: *Astelia*, *Cibotium*, *Freycinetia*, *Machaerina*, *Metrosideros*, and an unidentified palm. One adult was found walking on a wet rock face at night on Eleo during a windstorm associated with a shear line moving over the islands (Liebherr, CUIC). As this lone terrestrial collection is associated with extreme conditions, we infer that this species is restricted to arboreal microhabitats.
Fig. 232. *B. (Metromenus) fractistriata*. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view.

**Phylogenetic relationships.** This species is sympatric with one member species of its adelphotaxon, *B. fordi*, and distantly isolated from the other, *B. foveolata* of Haleakala, East Maui (Fig. 9).

*Blackburnia (Metromenus) fordi* Liebherr, new species  
(Figs. 231B, 234, 235)

**DIAGNOSIS.** Body size, head, and pronotum reminding of *B. caliginosa*, due to the bulging eyes and constricted neck, and narrow pronotum (Figs. 218D, 231B), but, with pronotum exhibiting wider lateral marginal depressions and lateral setae; dorsal elytral setae in foveate depressions associated with constriction of the third elytral interval; antennal pedicel with 6 setae around apex; elytral basal groove angulate at humerus, disc shiny brunneous to piceous, apex flavous; elytral surface covered with transverse sculpticells in transverse rows. Standardized body length 4.6-5.1 mm. The only other species with foveate elytra and lateral pronotal setae—*B. foveolata* of East Maui—differs by the more rounded pronotal hind angles (Fig. 231C), rounded humeri, entirely flat elytral intervals, much reduced elytral microsculpture, and larger body size.
DESCRIPTION. **Head.** Eyes convex, moderately protruded, ocular ratio 1.55 appearing larger due to markedly constricted neck; frontoclypeal region broadly depressed, consisting of 2 deeper depressed areas, with indistinct wrinkles posteriorly near anterior supraorbital seta; antennal pedicel with apical ring of 6 elongate setae plus longer outer seta; labrum very shallowly emarginate; mentum tooth broadly truncate to slightly bifid.

**Prothorax.** Pronotum broadly convex, with moderate lateral marginal depressions, elevated and sinuate basolateral margins, and distinct, obtuse hind angles; lateral pronotal setae present in most specimens, though absent or unilaterally present in a few specimens; laterobasal depressions broad, flat-bottomed without median tubercle, with minute transverse wrinkles, bordered behind by elevated margin not quite so large as basolateral margin; median base with indistinct longitudinal wrinkles, marginal bead complete medially; median longitudinal impression fine on disc, obsolete on median base and before broad and shallow anterior transverse impression; anterior marginal bead complete medially, taller toward tightly rounded front angles. Prosternal process flat medioventrally, unmargined.

Fig. 233. Distributional records for *B. (Metromenus) fractistriata.*
Fig. 234. *B. (Metromenus) fordii*, new species. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view.

**Elytra.** Ovoid with narrow, distinctly angulate humeri, basal groove curved forward to humerus; subapical sinuation reduced, elytral margin straight to slightly concave toward sutural apex; elytral striae smooth, second and third closer to each other at the 3 foveate dorsal elytral setae; scutellar seta present; elytral intervals moderately convex; 12-13 lateral elytral setae.

**Pterothorax.** Metepisternum short, variously broad, lateral margin 1.1 to 1.6× length of anterior margin.

**Legs.** Profemur without anteroventral setae, with 2 posteroventral setae; mesocoxa with 1 ridge seta; mesofemur with 2 anteroventral setae; metacoxa bisetose, mesal seta absent; mesofemur with 2 anteroventral setae, glabrous dorsoapically; tarsomeres gracile, short, basal metatarsomere 1.5× length of inner apical tibial spur; metatarsomeres 1-3 with broad dorsolateral sulci, median area narrow; metatarsomere 4 emarginate, apical lobes short, 0.6× median basal tarsomere length; tarsomeres 1-4 with 3 ventrolateral rows of sparsely distributed, elongate setae; tarsomere 5 with ventrolateral rows of 6 setae shorter than depth of tarsomere at point of setal insertion.

**Abdomen.** Sternite VII with 2 apical setae each side in males, 6 setae in females.

**Coloration.** Head, pronotum, and elytra nearly concolorous, shiny brunneous to piceous, the paler lateral margins of pronotum and elytra may make those structures appear paler; elytral apicolateral and apical areas broadly paler, flavous; palpi, antennal scape, pronotal and elytral epipleura, trochanters, and femora palest underneath, testaceous, contrasted with the darker, smoky antennomeres 2-11, tibiae, and tarsi.
Fig. 235. Distributional records for *B. (Metromenus) fordi*, new species.

**Microsculpture.** Head capsule with shallow microlines in form of isodiametric mesh on vertex, microlines somewhat more distinct on constricted neck; pronotal disc shiny, but with evident transverse mesh, laterobasal and lateral marginal depressions and median base with distinct isodiametric microsculpture; elytral surface shiny, but covered with evident transversely stretched sculpticells, sculpticells more isodiametric in foveate dorsal impressions, elytral microsculpture more developed along lateral and apical margins.  

**Male genitalia.** Aedeagal median lobe gracile, medioventrally expanded basad ventral excavation (Fig. 234A); excavation extended onto blunt, broad, downturned apex barely extended beyond articulation with internal sac; basal sagittal crest short, almost obsolete; median lobe basally broad, constricted on right side, tapered to rounded tip (Fig. 234B).  

**Female reproductive tract.** Gonocoxa basally broad, triangular gonocoxite 2 with acuminate apex (Fig. 234C); gonocoxite 1 with apical fringe of 10-11 setae, mesal 5-6 near medioapical angle in double series; gonocoxite 2 with 2-3 lateral ensiform setae and 1 dorsal ensiform seta; apical nematiform setae short, 0.27× length of gonocoxite 2; bursa copulatrix symmetrical, subequal to length of common oviduct, with a rounded dorsal pouch with lateral extensions, and a medial band of spikelike microtrichia; spermatheca ovoid, 0.6× length of spermathecal duct, without basal lobe.  

**Variation.** Of all paratypes examined, one individual bore a unilateral pronotal seta.
Holotype ♂ labeled "HI: Oahu Keahiakawoe massif Tripler Rdg. summit 9-V-1995 lot 09 835 m beating ohia w/moss J.K.Liebherr // beating ohia at nighttime" (CUIC).

Paratypes. OAHU, Koolau Range: Castle Tr., Kaluanui, 760 m, 03-IV-1938, Valentine (BPBM, 1); Eleao massif, north peak, beating ohia w/ moss, 805 m, 08-V-1995, Liebherr (CUIC, 6); Kaipapau, 12-IX-1939, Kondo (BPBM, 1), head of valley, ohia, under moss, 12-IX-1939, Anderson (BPBM, 3); Kawailoa Rdg., IX-1953, Ford (BPBM, 2); Keahiakawoe massif, Tripler Rdg. summit, beat mossy ohia at night, 835 m, 09-V-1995 Asquith (CUIC, 1), Liebherr (CUIC, 5), beating ohia 790-835 m, 09-V-1995, Asquith (CUIC, 1); Poamoho Tr., X-1953, Ford (BPBM, 3), VI-1955, Ford (BPBM, 1), IX-1958, Ford (BPBM, 10), I-1959, Ford (BPBM, 5), sifting ground litter, 750 m, 02-VI-1977, Howarth (BPBM, 4), summit, beating vegetation at night, 760 m, 05-V-1995, Asquith (CUIC, 1), Asquith & Polhemus (CUIC, 1), beating Freycinetia 760 m, 06-V-1995, Polhemus (BPBM, 1), beating ferns at night 700-760 m, 05-V-1995, Liebherr (CUIC, 1), beating ohia at night 700-760 m, 05-V-1995, Liebherr (CUIC, 4), beating ohia, 700-775 m, 23-IV-1991, Liebherr (CUIC, 13) summit, 0.2 km N, beating ohia in day, 760-800 m, 06-V-1995, Liebherr (CUIC, 1); Puu Kaumakua 760 m, 28-IV-1938, Valentine (BPBM, 1), summit, beating vegetation, 760-810 m, 06-07-V-1996, Polhemus, Asquith & Ewing (NMNH, 1); Schofield-Waikane Tr., moss, 760 m, 28-IV-1938, Zimmerman (BPBM, 3).

Etymology. This species honors the extensive collections of carabid beetles made by Everett J. Ford during his career as a U.S.D.A.-A.P.H.I.S. entomologist on Oahu. Mr. Ford’s collections, chiefly made during the 1950s, provide a valuable benchmark between Perkins’ 1890s surveys, and the 1990s surveys by JKL (e.g., Liebherr & Polhemus 1997b).

Distribution. This species exhibits a moderately sparse distribution in the northern two-thirds of the Koolau Mountain Range, Oahu (Fig. 235).

Habits. This species has been beaten from ferns (1 specimen), ohia (35 specimens), and Freycinetia (1 specimen) both during day and night. A small number (4 specimens) have been discovered by sifting ground litter. Therefore, this species appears to be predominantly an arboreal species; however, adults are also active on the ground.

Phylogenetic relationships. This species is geographically isolated from its adelphotaxon, B. foveolata of Haleakala, East Maui (Figs. 9, 217, 235).

Blackburnia (Metromenus) foveolata Liebherr, new species
(Figs. 217, 231C, 236)

Diagnosis. A dark shiny beetle with dorsal elytral setae set in foveate impressions; pronotum with lateral setae present, basal seta absent, basolateral margins straight to slightly sinuate before obtuse-rounded hind angles (Fig. 231C); elytral basal groove rounded on humerus, elytral intervals almost flat, extremely shiny due to reduced isodiametric microsculpture; femora with smoky median band and dark apex, basally and anteapically testaceous. Standardized body length 6.5-7.0 mm.

Description. Head broad, eyes prominent, ocular ratio 1.60; neck moderately constricted just caudad hind supraorbital setae; antennal pedicel with longer outer seta and 1 dorsal apical seta; labrum broadly and shallowly emarginate; frontoclypeal grooves broadly and shallowly extended from frontoclypeal suture to just before anterior supraorbital setae; mentum tooth broadly rounded apically.


**Prothorax.** Pronotum broad, convex disc extended to very narrow lateral marginal depressions, marginal depressions slightly wider caudad broadly rounded front angles; basolateral margins straight to slightly sinuate before obtuse-rounded hind angles; laterobasal depressions deepest on mesal edge adjacent to elevated median base, with median raised area elevated to meet disc, bordered laterally and posteriorly by evenly curved, elevated margin; median base smooth, with indistinct longitudinal wrinkles along hind portion of elevated disc, bordered behind by complete basal marginal bead; median longitudinal depression fine, with transverse wrinkles extended laterally onto disc; anterior transverse impression broad and shallow, most evident due to presence of isodiametric microsculpture in its deepest portions; anterior marginal bead complete. Prosternal process convex medioventrally.

**Elytra.** Ovoid, humeri moderately broad, basal elytral groove rounded on humerus; subapical sinuation present, margin sinuate before broadly rounded sutural apex; elytral intervals flat, striae deeply incised; scutellar seta present; 3 dorsal elytral setae set in foveate depressions associated with constriction of third interval, a few irregularities in third and fourth striae may also occur in some specimens; 12-14 lateral elytral setae.

**Pterothorax.** Metepisternum moderately short, broad, quadrate, lateral margin 1.2 to 1.6× length of anterior margin.

**Legs.** Profemur without anteroventral setae, with 2 posteroventral setae; mesocoxa with 1 ridge seta; mesofemur with 2 anteroventral setae; metacoxa bisetose, mesal seta absent; metafemur with 2 anteroventral setae; tarsomeres slightly expanded apically, metatarsomers 1-3 with distinct outer dorsolateral sulcus, fine, shallow inner sulcus; metastarsomere 4 emarginate, outer lobe 0.5 to 0.6× median basal tarsomere length; tarsomeres 1-4 with 2-3 ventrolateral rows of elongate setae, broadly glabrous medioventrally; tarsomere 5 with ventrolateral rows of 6 setae, each shorter than depth of tarsomere at point of setal insertion.

**Abdomen.** Males with 1 seta each side of sternite VII, female with 3 setae each side.

**Coloration.** Head capsule, pronotal disc, and elytra concolorous, shiny rufopiceous to piceous, margins of pronotum paler, brunneous; all antennomeres with smoky infuscation on ventral surfaces; prothoracic and elytral epipleura pale, testaceous, contrasted with brunneous thoracic sternites; femora with a medial dark infuscated band, bordered by basal and anteapical testaceous bands, apex dark, especially at hind margin near femoral-tibial articulation; tibiae dark, rufopiceous, tarsi slightly paler, rufous; abdominal sternites medially piceous, paler laterally.

**Microsculpture.** Vertex of head shiny, with shallow microlines in form of isodiametric mesh, constricted neck with more evident microsculpture, sculpticells slightly transverse; pronotal disc with evident transverse mesh microsculpture, laterobasal and lateral marginal depressions, and anterior transverse impression with isodiametric sculpticells; elytral intervals shiny, but with shallow microlines in form of isodiametric mesh visible, striae and foveate punctures lined with isodiametric sculpticells.

**Male genitalia.** Aedeagal median lobe gracile, slight medioventral expansion based ventral excavation (Fig. 236A); ventral excavation extended onto blunt, broad, evenly curved apex barely extended beyond articulation with internal sac; basal sagittal crest short, almost obsolete; median lobe basally broad, tapered to finely rounded tip (Fig. 236B).
Female reproductive tract. Gonocoxa basally broad, triangular gonocoxite 2 with acuminate apex (Fig. 236C); gonocoxite 1 with apical fringe of 8-9 setae, mesal 4 near medioapical angle in double series; gonocoxite 2 with 3 lateral ensiform setae and 1 dorsal ensiform seta; apical nematiform setae short, 0.23× length of gonocoxite 2; bursa copulatrix symmetrical, subequal to length of common oviduct, with a broad dorsal pouch and a medial band of spikelike microtrichia; spermatheca ovoid, 0.6× length of spermathecal duct, without basal lobe (Fig. 236D).

Holotype ♂ labeled “HI: Maui Haleakala NW slope, Waikamoi Flume nr. Waikamoi Gulch 9-V-1991 el. 1300 m J.K. Liebherr // under boards in wet ohia rain forest” (CUIC).

Paratypes. MAUI, Haleakala: Haleakala N.P., 1300 m, 21-IV-1997, Takumi (HALE, 1), Kekuewa Hill, 0.7 km N Puu Ahulili, vegetation at night, 1600 m, 16-V-1993, Liebherr &
Medeiros (CUIC, 1), beating vegetation at night, 1500 m, 09-V-1991, Jessel & Medeiros (CUIC, 1), sifting litter 1800 m, 08-V-1991, Jessel & Medeiros (CUIC, 1), Kipahulu west rim ESE Kuiki, ohia, sifting humus, 1850 m, 15-V-1993, Liebherr & Medeiros (CUIC, 1); Waikamoi Gulch, V-1967, Krauss (BPBM, 1), 1365 m, 14-I-1926, Swezey (BPBM, 1); Hana For. Res., Heleleikeoha Str. fence camp, pyr. fog ohia + Astelia, 1615 m, 11-V-1998, Liebherr (CUIC, 1), pyr. fog ohia w/ moss (CUIC, 7), Polhemus (NMNH, 1), Heleleikeoha Str., ridge S fence camp, pyr. fog ohia w/ moss, 1785 m, 12-V-1998, Polhemus (NMNH, 2); Hanawi N.A.R., Kopiliula Str., pyr. fog Cibotium+Clermontia, 1120 m, 03-V-1998, Polhemus (NMNH, 2), pyr. fog ohia w/ moss, 1160 m, 04-V-1998, Polhemus (NMNH, 1); Koolau For. Res., Kula Pipeline Rd. W Waikamoi Gulch, pyr. fog ohia w/ moss, 960 m, 15-V-1998, Polhemus (NMNH, 8), pyr. fog ohia + Cibotium, 970 m, 15-V-1998, Liebherr (CUIC, 4); Waikamoi Gulch to Haipuaena Gulch, under boards in wet ohia for., 1300 m, 09-V-1991, Liebherr (CUIC, 3), Waikamoi Gulch to Haipuaena Gulch, under boards in wet ohia for., 1300 m, 11-IV-1991, Liebherr (CUIC, 30), under boards in wet ohia for., 1300 m, 09-V-1991, Liebherr (CUIC, 21); Waikamoi N.C.P., Ukulele Pipeline, pyr. fog mossy ohia, log, 1465 m, 07-V-1998, Polhemus (NMNH, 1).

Etymology. The species epithet foveolata refers to the foveate punctures associated with the dorsal elytral setae.

Distribution. This species has been found in wet forest from 960 to 1800 m elevation across windward Haleakala, East Maui (Fig. 217).

Habits. This species has been usually encountered on the ground, either by sifting litter, or looking under boards in wet ohia forest. Of 59 specimens with microhabitat information, only 2 were otherwise found by beating vegetation at night. Thus available data suggest that this species predominantly inhabits terrestrial microhabitats.

Phylogenetic relationships. This species is geographically isolated from its adelphotaxon, B. fordi of Oahu (Fig. 9). This relationship can be explained by a recent dispersal to Maui by the ancestor of this species, those colonists derived from ancestors of present-day B. fordi. This pattern of colonization does not differ from the overall biogeographic pattern summarized from data across the entire radiation (Fig. 10); the only anomaly is the apparent absence of related species on other Maui Nui fragments. Another geographically isolated singleton apically nested within a diversifying clade is observed in B. palmae (Fig. 9) of Oahu, which is the lone phylogenetic element to return to an older island from the slopes of Maui Nui (Liebherr 1997).

**Blackburnia (Metromenus) fraterna** (Blackburn), new combination

(Figs. 231D, 237, 238, 239, 240)

*Anchomenus fraternus* Blackburn, 1877: 145.

*Metromenus fraternus*: Blackburn & Sharp, 1885: 212; Sharp, 1903: 236.

*Anchomenus scrupulosus* Blackburn, 1877: 145 (new synonymy).

*Metromenus scrupulosus*: Blackburn & Sharp, 1885: 212; Sharp, 1903: 235.

*Metromenus aequalis* Sharp, 1903: 233 (new synonymy).

*Metromenus velox* Sharp, 1903: 236 (new synonymy).

**DIAGNOSIS.** This is the most morphologically heterogeneous platynine species in Hawaii. The pronotum lacks setae, is narrowed behind with lateral margins slightly sinuate before
rounded hind angles (Figs. 231D, 237); eyes convex, ocular ratio 1.64-1.66; frons and vertex with evident isodiametric microsculpture; elytra ovoid, evenly convex, not flat medially, with tightly rounded to slightly angulate humerus, slightly convex elytral intervals, dorsal elytral setae not set in depressions more than 1/2 width of third elytral interval, and all intervals with slightly transverse sculpticells in transverse rows, surface shiny or with slight alutaceous reflection; length of metatarsomere 1 more than 3.25× its apical width, and more than 2.0× length of inner tibial spur, with distinct inner and outer dorsolateral sulci; tarsomere 4 lobate, outer lobe of metatarsomere 4 about 2/3 median basal length of segment. Standardized body length 5.6-6.6 mm.

Pterothorax. Metepisternum short and quadrate to longer, trapezoidal, lateral margin 1.0 to 1.5× length of anterior margin, this ratio larger in larger individuals.

Male genitalia. Aedeagal median lobe gracile, elongate, with broad medioventral expansion, and ventral excavation extended onto elongate apex with bluntly rounded tip, apex variously extended beyond opening of internal sac from 2.0 to 2.5× thickness of apex at sac opening, this variation not correlated with variation in color (Fig. 238A, C); basal sagittal crest elongate, narrow; median lobe moderately broad basally, evenly tapered to a finely rounded tip (Fig. 238B, D).

Female reproductive tract. Gonocoxa basally broad, with small, triangular gonocoxite 2 (Fig. 239A-C); gonocoxite 1 with apical fringe of 7-11 setae, inner 3-6 at medioapical angle in double series; gonocoxite 2 with 2-3 lateral ensiform setae and 1 dorsal ensiform seta; apical nematiform setae short, 0.23 to 0.25× length of gonocoxite 2; bursa copulatrix symmetrical, short, about 0.8 to 1.0× length of common oviduct, with a round, unsclerotized dorsal pouch near vagina, and a medial band of spikelike microtrichia; spermatheca somewhat variously ovoid, from 0.67 to 1.0× length of spermathecal duct.

Variation. Extensive variation exists in coloration, resulting in redescription of this species by both Blackburn and Sharp. Most commonly, B. fraterna specimens have a piceous head capsule, a pronotum with the disc infuscated and margins paler, and elytra dark on the disc and paler along anterior, lateral, and in some specimens, the apical margins. Ventrally the elytral epipleura and legs are palest, testaceous, and contrast with the darker, brunneous thoracic ventrites. The basal three antennomeres, and glabrous portion of antennomere 3 are testaceous, slightly darker than the setose, brunneous outer antennomeres.

Blackburn differentiated his A. scrupulosus by the broad, pale apex of the elytra on his unique specimen of the taxon. However, specimens he attributed to A. fraternus also exhibit paler elytral margins. The holotype of A. scrupulosus is larger than all specimens Blackburn possessed of his A. fraternus, but this discontinuity has been erased through collection of more material.

Sharp added the name velox for a series of dark specimens from the lee side of the Waianaes, considering it allied to B. epicurus. The velox form is darker than most B. fraterna because the apical elytral margin is as dark as the disc, unlike the usual situation with the apex slightly paler to much paler—i.e., testaceous. Nonetheless, specimens assigned to velox by Sharp are indistinguishable from the darkest Koolau Range specimens he identified as Metromenus fraternus, as well as from the darkest Koolau Range specimens collected since. Characters of pronotal and elytral shape, also used to diagnose Sharp’s M. velox, are within the range of variation of his specimens identified as M. fraternus. Therefore, we must conclude that the velox form simply represents color variation.
Fig. 237. *B. (Metromenus) fraterna* habitus, dorsal view. A. Specimen described as *Anchomenus scrupulosus* by Blackburn. B. Specimen described as *Metromenus aequalis* by Sharp. C. Specimen described as *Metromenus velox* by Sharp.
The most distinctive variation within this species involves pallid coloration of the entire body observed in many of the specimens from the Waianae Mountain Range, and a smaller percentage in the northern Koolaus. Specimens of this form look teneral, with the head brunneous instead of piceous, elytral disc flavous and concolorous with the margins instead of contrastingly darker, and thoracic and abdominal venter flavous instead of brunneous. Leg color tends to vary less, however, with femora testaceous in all specimens regardless of body coloration. Antennal coloration also does not differ, with antennomeres 4-11 darker than the basal 3. Sharp named this form *M. aequalis*, based on specimens from Halemano in the Koolaus, and from 605 m elevation in the Waianaes. This variation in color is not correlated with seasonality—i.e., collection of samples just after eclosion so that some individuals are not fully sclerotized and melanized—as series from November and April exhibit a similar range in coloration (D. A. Polhemus series from Mt. Kaala, 16-XI-1993 and JKL series from Mt. Kaala, 22-IV-1991; CUIC). Sclerotization of the male aedeagus is similar in all specimens regardless of whether the dorsal body coloration is dark or pale.
Fig. 239. Female gonocoxa of *B. (Metromenus) fraterna*. A. Specimen with darker coloration. B. Specimen with paler coloration used to diagnose *aequalis* form. C. Specimen identified as *M. scrupulosus* by Sharp.

Therefore we conclude that coloration of this species is markedly variable—the most heterogeneous in the Waianaes—and that the underlying basis for such variation is not yet fully understood.

**Types.** For *Anchomenus fraternus*, ♂ lectotype on 3-line card, top line thickest—Blackburn’s Oahu code (Zimmerman 1957)—and “fraternus” handwritten on reverse (BMNH) hereby designated. For *Anchomenus scrupulosus*, ♀ holotype on 3-line card, top line thickest, with “scrupulosus” handwritten on reverse (BMNH). For
Metromenus aequalis, $\varphi$ lectotype, left specimen on 3 specimen card, labeled “$\varphi$ Metromenus aequalis Types D.S. Halemano. 240. Perkins. // specimen at left designated Lectotype, det. by E. C. Zimmerman” (BMNH) hereby designated. For Metromenus velox, $\varphi$ lectotype on blank card with “542” handwritten on reverse // “Waianae Mts. Oahu Lee side Perkins. II. 1896” (BMNH) hereby designated.

**Distribution.** Both *B. epicurus* (Fig. 220) and this species (Fig. 240) exhibit extremely broad distributions across the island of Oahu.

**Localities.** In the Waianae Mountains known from Mt. Kaala, including Haleauau Gulch, Waianae Gulch, Makaha Gulch, Dupont Trail, and the summit, Kawiwi, Puu Kalena, Puu Kanehoa, Puu Kaua, and Palikea. Recorded from the length of the Koolau Range, including Pupukea, Kawaiolua, Kaipapau, Castle Trail, Punaluu, Kahana, Puu Ohulehule, Helemano, Poamoho, Wahiawa, Puu Kaumakua, north peak of Eleao massif, Waipio Ridge, Waimano Trail, Schofield-Waikane Trail, Puu Kehiakohoe massif at Tripler Ridge, Kalihi Valley, Puu Lanihuli, Pauoa Valley, Pacific Heights, Konahuanui, Tantalus, Makiki, Palolo Valley, Haiku Valley, Mt. Olympus, Waiulu Gulch, and Puu O Kona. The species has been historically found at elevations as low as 365 m on Tantalus, but can also be found along the Koolau crest and on the summit of Mt. Kaala (1210 m).
Habits. This species is a generalist, found both on plant surfaces and on the ground. Genera of plants upon which beetles have been found include Astelia, Broussaisia, Cheirodendron, Cibotium (tree fern), Dubautia, Eleocarpus, Freycinetia (ieie), Gunnera, Ilex, Metrosideros (ohia lehua), Pritchardia, and Psychotria. Adult beetles are on vegetation, including mossy ohia during day or night, or on ferns at night. They also venture across the ground at night, and live in tree fern litter, or under logs, or other rotten wood and boards.

Phylogenetic relationships. This species is the adelphotaxon of four species, two distributed on Kauai, and two on Oahu (Fig. 9). The present cladistic analysis places this species and its adelphotaxon as an apical clade within one of the two more speciose clades of Division 2: B. epicurus to B. filipes (Fig. 9). Our earlier analysis, which included a slightly different set of ingroup taxa (see Cladistic Analysis), placed B. fraterna and this same adelphotaxon near the base of Division 2 (Liebherr & Zimmerman 1998, Figs. 88, 90). Many of the relationships among the various closely related species are identical within the cladograms derived from each analysis, including the relationships of B. fraterna and its adelphotaxon. The different positions of this clade in the overall cladogram of Division 2 is caused mostly by different rootings of the entire Division 2 on the cladogram: a basal split of clades rooted at the B. fraterna clade plus B. kahili + B. asquithi clade (Liebherr & Zimmerman 1998), versus rooting at B. kahili alone in this analysis. These different results, given only slightly different included taxa, point to the overall ambiguity of character support for basal relationships among Division 2. We prefer the present hypothesis, because rooting of Division 2 at B. kahili: 1, recognizes the cristate setae of the bursa copulatrix in that species as a derivation evolved in concert with the taxa in Division 1, then lost in the remainder of Division 2; and 2, supports transformation of tarsomeres from the smooth condition, lacking dorsolateral sulci as observed in taxa of Division 1, to slightly developed sulci observed in B. kahili, to more distinct sulci as in many of the other taxa of Division 2. As such, we present the relationships as they are derived from our present, and presumably most complete, analysis, cognizant that the incorporation of phylogenetic data from other taxa, and sources such as other life stages and DNA molecules, may produce a more robust hypothesis.

We included the pale “aequalis” form of B. fraterna in the analysis to test whether the different coloration of the pale form would justify its placement other than as a synonym of B. fraterna. Their placement together on the cladogram (Fig. 9), coupled with the spectrum of coloration seen in individuals from sites with the pale form, justifies synonymization of the “aequalis” form under B. fraterna.

Blackburnia (Metromenus) limbata (Sharp), new combination
(Figs. 241A, 242, 243)

Metromenus limbatus Sharp, 1903: 241.

DIAGNOSIS. Much like B. fraterna, in glabrous pronotum with slightly sinuate basolateral margins and rounded hind angles (Fig. 241A); convex eyes, ocular ratio 1.58; and slightly lobate tarsomere 4, outer lobe of fourth metatarsomere 2/3 median basal length of segment.
But, this species is easily diagnosed by: 1, elytral intervals 5-7 slightly carinate basally, angulate midway between striae; and 2, elytral margins broadly paler than disc, with sutural stria, elytral base, lateral 2-3 intervals, and apex beyond posterior dorsal elytral seta flavous, disc darker, piceous to brunneous. The inner elytral intervals are very convex, almost carinate, to flatter and more rounded. Standardized body length 5.8-6.9 mm.

**Pterothorax.** Metepisternum short, trapezoidal, lateral margin 1.5 to 1.6× length of anterior margin.

**Male genitalia.** Aedeagal median lobe gracile, elongate, slightly expanded medioventrally (Fig. 242A); ventral excavation extended onto short, nearly straight apex with bluntly rounded tip; basal sagittal crest very small to obsolete; median lobe narrow throughout length, slightly tapered to a rounded tip (Fig. 242B).

**Female reproductive tract.** Gonocoxa basally broad, triangular gonocoxite 2 with acuminate apex (Fig. 242C); gonocoxite 1 with apical fringe of 9 setae, inner 2-4 at medioapical angle in double series; gonocoxite 2 with 2-3 lateral ensiform setae and 1 dorsal ensiform seta, lateral setae long and broad, longest 0.23× length of gonocoxite 2; apical nematiform setae short, 0.28× length of gonocoxite 2; bursa copulatrix symmetrical, 1.2× length of common oviduct, with a broadly rounded, un sclerotized dorsal pouch near vagina, and a medial band of spikelike microtrichia; spermatheca somewhat elongate, subequal to length of spermathecal duct, without basal lobe.

**Lectotype** ♀ labeled “Koholuamano, Kauai, 4000 ft. Perkins. iv.1895” with “511” handwritten on reverse of card (BMNH) hereby designated. Perkins’ lot 511 consisted of “Coleop. 28 spec. 12 IV ‘95” (Anonymous n.d.). That day Perkins hiked to Kaholuamano from Waimea in the morning, and collected in the vicinity of the mountain house at Kaholuamano (Perkins 1895a).

**Distribution.** This species is distributed from Kahili to Kalalau in the montane forest of Kauai (Fig. 243).

**Localities.** Known from Mt. Kahili, Koholuamano, the high plateau along Mohihi-Waialae Trail, Keaku Cave in the deep Alakai Swamp, Alakai Swamp Trail at Pihea Trail, Waineke Swamp, and Kilohana, and Kokee State Park, including Kumuwela Ridge, Halemanu, Ka Uno o Hua Ridge, and Kalalau lookout. Localities range in elevation from 850 to 1515 m.

**Habits.** Records from March include under logs and moss mats on logs. In May, beetles were observed climbing on Clermontia, low fern, and ohia lehua (Metrosideros) at night. June records include collection on Sadleria and in rotting fern stipes. The lone July record is from under logs and rocks. Therefore, this species appears to spend the cool, wet winter season on the ground secreted under logs and moss mats. In spring, the time when the beetles become active and start breeding, they spend substantial periods on plant surfaces, especially at night, where they forage and presumable meet conspecific individuals.

**Phylogenetic relationships.** This species is the adelphotaxon of the sympatrically distributed B. pavida plus the Oahu species B. cuneipennis and B. perpolita (Figs. 9, 243, 245). As noted in the treatment of B. fraterna, the cladistic relationships determined by adult morphological data consistently support close relationships among these four species plus their adelphotaxon, B. fraterna (Liebherr & Zimmerman 1998 versus cladistic analysis herein). The overall cladistic position of this five-species clade, however, varies based on the overall rooting of Division 2 relative to Division 1. These various hypotheses of relationship will be tested as more data are brought to bear.
Blackburnia (Metromenus) pavida (Sharp), new combination
(Figs. 131A-B, 135C, 241B, 244, 245)

Metromenus pavidus Sharp, 1903: 238.
Mesothriscus truncatus Sharp, 1903: 225 (new synonymy).

DIAGNOSIS. This species is characterized by the shiny piceous dorsum, testaceous legs and antennae, and quadrate elytra with distinct subapical sinuation and truncate apex (Fig. 241B). Pronotum glabrous in most specimens, though rare individuals express lateral setae either unilaterally or bilaterally. Blackburnia pavida shares with its adelphotaxon—the following 2 species, B. cuneipennis and B. perpolita of Oahu—complete or at least traceable pronotal basal marginal bead, beadlike lateral pronotal margin, broad humeri, very short apical lobes on tarsomere 4 (Fig. 131A), and presence of only 2 setae each side of the female sternite VII. The last is an evolutionary reversal from the trisetose condition observed throughout much of the rest of the subgenus. This species is diagnosed from its Oahu adelphotaxon by: 1, presence of a lateral depression inside lateral pronotal marginal bead; 2, sinuate pronotal basolateral margin (Fig. 241B); 3, marked subapical sinuation and medially flattened, truncate elytra; and 4, elytral microsculpture of isodiametric to transverse sculpticells arranged in transverse rows. Standardized body length 6.0-8.1 mm.
**Pterothorax.** Metepisternum broad, trapezoidal, lateral margin 1.3 to 1.5× length of anterior margin.

**Male genitalia.** Aedeagal median lobe gracile, elongate, slightly expanded medioventrally (Fig. 244A); elongate ventral excavation extended onto slightly downturned apex with finely rounded tip; basal sagittal crest narrow; median lobe basally broad, somewhat constricted laterally beyond midlength, with rounded tip (Fig. 244B).

**Female reproductive tract.** Gonocoxa basally broad, triangular gonocoxite 2 with finely rounded apex (Figs. 135C, 244C); gonocoxite 1 with apical fringe of 8-12 setae, mesal 2-3 at medioapical angle in double series; gonocoxite 2 with 2 lateral ensiform setae and 1 dorsal ensiform seta; apical nematiform setae short, 0.23× length of gonocoxite 2; bursa copulatrix symmetrical, subequal to length of common oviduct, with a rounded, unsclerotized dorsal pouch near vagina, and a medial band of spikelike microtrichia; spermatheca somewhat elongate, 0.85× length of spermathecal duct, without basal lobe.
Variation. Most individuals of this species have a glabrous pronotum. But, of 338 specimens examined, 3 had lateral pronotal setae present, and another 3 specimens had a lateral seta unilaterally present. This rare condition was what Sharp (1903) recognized as *Mesothriscus truncatus*.

Lectotypes. For *Metromenus pavidus*, lectotype ♂ labeled “Metromenus pavidus D.S. Waimea. Perkins. 267.” (BMNH) hereby designated. For *Mesothriscus truncatus*, lectotype ♀ labeled “Mesothriscus truncatus Type D.S. Khlm. Kauai Perkins iv.95.” (BMNH) hereby designated. The lectotype has lateral pronotal setae on both sides; a ♀ paralectotype has the lateral pronotal setae unilaterally on right side.

Distribution. This species exhibits a distribution anchored at Mt. Waialeale summit and extended across the high Alakai plateau and the upper reaches of Waimea Canyon, Kauai (Fig. 245).

Habits. Winter season records in January and March are from tree moss litter, and under bark, logs, and moss mats. During the breeding season in May and June, beetles of this species are active in a variety of nighttime situations, including climbing trees, running on open trails, and walking along stream banks. Plant associations include *Metrosideros*, *Acacia koa*, *Cheirodendron*, *Clermontia*, *Elaeocarpus*, *Pritchardia*, *Pouteria*, and *Tetraplasandra*. Therefore, much like the other Kauai species, such as the closely related *B. limbata* and the less closely related *B. alternans*, these beetles alternate between terrestrial microhabitats in winter and use of arboreal microhabitats in spring.

Phylogenetic relationships. This species is the adelphotaxon of the sympatric *B. limbata* (Fig. 9).
CARABIDAE PART I: PLATYNINI

Blackburnia (Metromenus) cuneipennis (Blackburn), new combination
(Figs. 241C, 246, 247)

Anchomenus cuneipennis Blackburn, 1877: 146.


DIAGNOSIS. This species is immediately recognizable by the distinct microsculpture, isodiametric on frons, and a transverse mesh on pronotal and elytral disc producing an alutaceous lustre (Fig. 241C); glabrous pronotum without lateral marginal depression mesad lateral bead, marginal bead continuous and distinct around obtusely rounded hind angles; elytral disc markedly convex, body deep, tubular; subapical sinuation of elytra reduced, lateral margin straight to convex near sutural angles. Standardized body length 6.2-8.3 mm.

Pterothorax. Metepisternum short, somewhat narrowed behind, lateral margin 1.3 to 1.6× length of anterior margin.

Male genitalia. Aedeagal median lobe gracile, elongate, broadly expanded medioventrally (Fig. 246A); elongate ventral excavation extended onto short, straight apex with a bluntly rounded tip; basal sagittal crest elongate, moderately broad; median lobe basally broad, tapered evenly to a finely rounded tip (Fig. 246B).

Female reproductive tract. Gonocoxa basally broad, triangular gonocoxite 2 with acuminate apex (Fig. 246C); gonocoxite 1 with apical fringe of 11 setae, mesal 4-6 at medioapical angle in double series; gonocoxite 2 with 2-3 lateral ensiform setae and 1 dorsal ensiform seta; apical nematiform setae short, 0.25× length of gonocoxite 2; bursa copulatrix symmetrical, subequal to length of common oviduct, with a broad, rounded
dorsal pouch with sclerotized margins near vagina, and a medial band of spikelike microtrichia; spermatheca elongate, $1.2 \times$ length of spermathecal duct, without basal lobe.

**Lectotype** ♀ on 2-line card, the top line thickest—Blackburn's Oahu code (Zimmerman 1957)—with "cuneip" handwritten on reverse of card (BMNH) hereby designated.

**Distribution.** This species' distribution includes both Mt. Kaala and the Koolau Mountain Range, Oahu (Fig. 247).

**Localities.** Mt. Kaala, and Koolau Range localities of Helemano, Poamoho Trail, Wahiawa, Waimano Stream, Halawa Valley, Puu Lanihuli, Nuuanu Valley, Konahuanui, Tantalus and the Honolulu Mountains of Perkins, and Waialae Iki. These localities span 365 to 820 m elevation, though the only collection during the last 50 years is from the latter elevation at Puu Lanihuli summit (Asquith, Ewing & Polhemus, CUIC).

**Habits.** The recent Puu Lanihuli collection was a single individual collected from open ground at night. Perkins (1906) also considered it to be a strictly terrestrial species.

**Phylogenetic relationships.** This species is broadly sympatric with its adelphotaxon, *B. perpolita*, in the Koolau Mountains (Figs. 9, 247, 249), consistent with broad levels of sympatry observed in other closely related complexes of species inhabiting the Koolau Range: e.g., the species triplet *B. fossipennis (B. fugitiva + B. proterva)* (Figs. 162, 166, 168), and the species pairs *B. caliginosa* plus *B. mutabilis* (Figs. 224, 228), and *B.
fractistriata plus B. fordi (Figs. 233, 235). One possible underlying history to such a pattern is discussed in the treatment of B. fossilispennis. For B. cuneipennis, however, its occurrence on Mt. Kaala suggests an original provenance in the Waianae, with allopatric speciation between B. cuneipennis and B. perpolita followed by the former colonizing the Koolau Range. This hypothesis recalls that proposed for B. meticulosa versus B. fractistriata and B. fordi (Figs. 9, 230, 233, 235). In both of these hypotheses, the patterns of allopatric and sympatric populations support colonization from the older Waianae volcano to the younger Koolau volcano.

Blackburnia (Metromenus) perpolita (Sharp), new combination
(Figs. 241D, 248, 249)
Metromenus perpolitus Sharp, 1903: 241.

DIAGNOSIS. This striking species is immediately recognizable by the extremely shiny body (Fig. 241D), which has microsculpture reduced to extremely indistinct transverse lines associated with irregularities in the cuticular surface. Like B. cuneipennis, the elytra are convex, the body deep, tubular; the glabrous pronotum has the convex disc extended to lateral bead without intervening lateral depression; the elytral striae are absolutely smooth, intervals broadly convex. This species has the dorsolateral sulci of basal tarsomeres quite reduced; the outer or anterior sulcus is fine and shallow, posterior inner sulcus evidenced by longitudinally flattened dorsolateral surfaces of tarsomeres 1-3. The femora have a basal smoky band, contrasted with the testaceous apex; coxae and tibiae are piceous. Blackburnia perpolita is also one of the few species of the Hawaiian fauna in which the anterior supraorbital setae are consistently absent; among species of subgenus Metromenus, individuals of the broadly abacoid species B. calathoides lack these setae in most individuals; B. platyophthalmica from Molokai, and B. ipu from Kipahulu Valley, East Maui, are polymorphic for these setae; and both known individuals of B. lihau of West Maui lack these setae. Standardized body length 6.7-8.8 mm.

Pterothorax. Metepisternum moderately elongate, lateral margin 1.5× length of anterior margin.

Male genitalia. Aedeagal median lobe gracile, elongate, broad, shallow medioventral expansion (Fig. 248A); ventral excavation extended onto short, evenly curved apex tapered to an acuminate tip, tip extended 2.5× thickness of apex at opening of internal sac; basal sagittal crest elongate, moderately broad; median lobe basally broad, constricted on right side, tapered to a finely rounded tip (Fig. 248B).

Female reproductive tract. Gonocoxa basally broad, triangular gonocoxite 2 with acuminate apex (Fig. 248C); gonocoxite 1 with apical fringe of 8 setae, mesal 2 at medioapical angle in double series; gonocoxite 2 with 2 lateral ensiform setae and 1 dorsal ensiform seta; apical nematiform setae short, 0.20× length of gonocoxite 2; bursa copulatrix symmetrical, subequal to length of common oviduct, with a broad, rounded dorsal pouch sclerotized on its medial surface, and a medial band of spikelike microtrichia (Fig. 248D); spermatheca elongate, 1.1× length of spermathecal duct, without basal lobe.

Lectotype ♂ labeled “♂ Metromenus perpolitus Type D.S. Oahu, Wahiawa 750. Perkins.” (BMNH) hereby designated.
**Fig. 248.** *B. (Metromenus) perpolita.* A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view. D. Female bursa copulatrix, ventral view, showing broadly quadrate dorsal pouch near vagina, medial band of spikelike bursal microtrichia, and spermatheca.

**Distribution.** This species is known from throughout the Koolau Mountains, Oahu (Fig. 249).

**Localities.** Known from the length of the Koolaus, including Kawailoa Ridge and Gulch, Helemano, Poamoho Trail, Wahiawa, Schofield-Waikane Trail, Puu Kaaumakua, Kipapa Gulch, Waiahole Ditch, Puu Keahiakahoe massif at Tripler Ridge, Kalihi Valley, Puu Lanihuli, Tantalus, Manoa Valley, Palolo Valley, and Mt. Olympus. These sites range from 395 to 840 m elevation. The collection from 395 m was made on Tantalus in 1906, but other lowland collections have been made—e.g., Kalihi Valley, 1967, 455 to 760 m (CNC).

**Habits.** This species has been recorded from a variety of plant substrates throughout the year, including *Astelia, Cibotium, Freycinetia,* and mossy ohia lehua (*Metrosideros polymorpha*). A series of nine individuals (IX-1935, HDAC, UHEM) was found under uluhe fern during Williams' (1936) herculean search for the terrestrial immature stages of *Megalagrion oahuense.* Beetles have also been found in leaf litter (January), and walking
on the ground at night (May). Therefore, this species appears to be an ecological generalist, at home in terrestrial and arboreal microhabitats within its range.

**Phylogenetic relationships.** This species is sympatric with its adelphotaxon, *B. cuneipennis* (Fig. 9), with chorological ramifications discussed in that species’ treatment.

**Blackburnia (Metromenus) hakeakapa** Liebherr, new species  
(Figs. 250A, 252, 253)

**DIAGNOSIS.** This is the only species of subgenus *Metromenus* with trisetose metacoxae (i.e., 2 lateral setae and 1 mesal seta present on each coxa), elytral disc dark (distinctly darker than paler margins and sutural interval), and pronotum with basal seta present, lateral seta absent (Fig. 250A). *Blackburnia hakeakapa* is superficially similar to *B. transiens* (Fig. 149B) of Kauai, but lacks the costate elytral intervals so characteristic of the Kauaian fauna. Standardized body length 6.3-7.5 mm.

**DESCRIPTION.** Head elongate, eyes small, as convex as elongate genae, ocular ratio 1.50; frontoclypeal grooves very short, broad, disappearing mesad anterior supraorbital setae; neck constriction marked, situated just caudad hind supraorbital setae; antennal pedicel with
1 longer outer seta and 2 dorsoapical setae; labrum very shallowly emarginate; mentum
tooth broadly rounded to slightly bifid.

**Prothorax.** Pronotal lateral margin slightly explanate, translucent laterad epipleura;
larval seta absent, basal seta present, situated in raised lateral margin with a flat-topped
expansion at the seta; convex disc extended to explanate lateral margins, lateral marginal
depression obsolete; laterobasal depressions broad, flat, bordered by markedly elevated
lateral margin at hind setae, a narrower margin behind; median base slightly rugose due to
minute wrinkles, basal marginal bead effaced; median longitudinal impression extended
from slightly wrinkled base all the way to anterior margin, finely incised, with fine
transverse wrinkles extended onto disc; anterior transverse impression shallow, traceable
to rounded front angles along line where cervical membrane attaches to pronotum; anterior
marginal bead obsolete medially, at most slightly irregular due to fine longitudinal wrinkles
along margin. Prosternal process flat medioventrally.

**Elytra.** With very narrow humeri, basal groove angulate on humerus; elytra widest behind
middle, subapical situation present though reduced, sutural apex rounded, sutural margin
divergent before apex; elytral intervals slightly convex; elytral striae smooth, slightly
wavering; scutellar seta and 3 dorsal elytral setae present; 13-16 lateral elytral setae.

**Pterothorax.** Metepisternum short, trapezoidal, lateral margin 1.2 to 1.5× length of
anterior margin.

**Legs.** Profemur without anteroventral setae, with 2 posteroventral setae; mesofemur with
1 ridge seta; mesocoxa with 2 ridges setae; mesofemur in most specimens with 2, in some with 3-4 anteroventral setae;
metacoxa trisetose; metafemur with 2 or 3 anteroventral setae; tarsomeres gracile,
tarsomeres 1-3 with distinct dorsolateral sulci, medial area dorsally angulate; tarsomere 4
emarginate, metatarsomere 4 with apical lobes 0.5× median basal tarsomere length;
tarsomeres 1-3 with 2 ventrolateral rows of elongate setae, medially glabrous; tarsomere
5 with 2 rows of 6 ventrolateral setae, each less than tarsomere depth at point of setal
insertion.

**Abdomen.** Males with 1 seta each side of sternite VII, females with 3 setae each side.

**Coloration.** Head capsule brunneous, pronotum slightly paler, rufous; elytra broadly
darker on brunneous disc, basal, lateral, and apical margins testaceous, translucent;
prothoracic and elytral epipleura and femora concolorous with elytral dorsolateral margins,
 thoracic and abdominal venter, and coxae, tibiae, and tarsi slightly darker, rufotestaceous.

**Microsculpture.** Vertex of head with isodiametric microsculpture, slightly more
developed on neck constriction; pronotal disc with distinct transverse mesh microsculpture,
median base, median apex, and laterobasal depressions covered with irregularly oriented
isodiametric sculpticells; elytral intervals covered with slightly transversely stretched
sculpticells arranged in irregular transverse rows; elytral striae with irregular, minute
punctulae the diameter of one sculpticell.

**Male genitalia.** Aedeagal median lobe gracile, with broad medioventral expansion,
ventral excavation extended to short, straight apex with rounded tip extended 1.1× thickness
of apex at opening of internal sac (Fig. 252A); basal sagittal crest moderately elongate,
narrow to obsolete; median lobe moderately broad basally, slightly constricted on right side,
tapered to a finely rounded tip (Fig. 252B).

**Female reproductive tract.** Gonocoxa basally broad, triangular gonocoxite 2 with
acuminate apex (Fig. 252C); gonocoxite 1 with apical fringe of 10-13 setae in single series;
gonocoxite 2 with 2 lateral ensiform setae and 1 dorsal ensiform seta; apical nematiform
Fig. 252. *B. (Metromenus) hakeakapa*, new species. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view. D. Female bursa copulatrix, ventral view, showing rounded dorsal pouch with lateral extensions, medial band of spikelike bursal microtrichia, and spermatheca.

setae short, 0.27× length of gonocoxite 2; bursa copulatrix symmetrical, subequal to length of common oviduct, with a rounded dorsal pouch with short lateral extensions of lightly sclerotized membrane, and a medial band of spikelike microtrichia (Fig. 252D); spermatheca elongate, subequal to length of spermathecal duct, without basal lobe.


**Paratypes.** MOLOKAI, Kamakou: Kainalu, 605-910 m, 28-VII-1927, Bryan (BPBM, 1); Kamakou N.C.P., Hanalilolilo Tr., sifting litter, tree fern, 1210 m, 26-IV-1991, Liebherr (CUIC, 5), Hanalilolilo Tr., NW of peak, sifting litter, tree fern, 1180 m, 04-V-1993, Liebherr (CUIC, 1), Kaunuhua, 0.5 km SW, scraping ohia w/ moss, 1280-1380 m, 29-V-1997, Liebherr (CUIC, 1), beating ferns & *Melicope* at night 1380 m, 29-V-1997, Liebherr
Fig. 253. Distributional records for B. (Metromenus) hakeakapa, new species.

(CUIC, 9), Kawela Gulch, mv light trap, 1140 m, 04-I-1981, Gagné & Gagné (BPBM, 1), Pepeopae Bog Trailhead, ferns, beating at night, 1180 m, 06-V-1993, Liebherr (CUIC, 2), Pepeopae Bog woods W of bog boardwalk, at night, 1150-1210 m, 26-IV-1991, Liebherr (CUIC, 1), Puu Kolekole, VII-1952, Tamashiro (BPBM, 1), Kolekole Cabin 1200 m, 15-V-1992, Polhemus (BPBM, 6), beating vegetation at night, 1180 m, 04-V-1993, Liebherr (CUIC, 1), Polhemus (CUIC, 1), beating ferns, 1200 m, 15-V-1992, Liebherr (CUIC, 55), beating ferns at night, 1200 m, 28-V-1997, Liebherr (CUIC, 2), beating ohia at night, 1200 m, 27-V-1997, Liebherr (CUIC, 2), dead Cibotium fronds, 1190 m, 21-X-1997, Polhemus (NMNH, 1), 0-0.5 km W Kolekole Cabin, beating tree fern, 1180 m, 05-V-1993, Liebherr (CUIC, 17), moss on ground, 1180 m, 05-V-1993, Liebherr (CUIC, 3), beating ferns at night, 1210 m, 27-V-1997, Liebherr (CUIC, 11), ridge 0.8 km W, pyrethrin fog mossy seep face, 1180 m, 31-V-1997, Liebherr (CUIC, 1), transect 7 N cabin, 1200-1250 m, 16-V-1992, Liebherr (CUIC, 4); Waikolu Valley, above, 02-V-1955, Ford (BPBM, 5).

**Etymology.** The species epithet *hakeakapa* combines Hawaiian words for pale, hakea, with margin, kapa, indicating the pale margins of the elytra.

**Distribution.** Found across the higher elevations of East Molokai, from above Waikolu to Kainalu (Fig. 253).

**Habits.** This species is most commonly encountered by beating ferns and tree ferns at night (98 of 115 specimens with collecting information in this situation). Adults have also been found on the ground during daytime in tree fern litter and mosses. It appears that this species rests on the forest floor during the day, and then climbs actively on ferns during nighttime. This climbing behavior is very dependent on weather conditions. The night must be relatively dry, without active rain or raindrops standing on the fern fronds, and relatively warm, above 17°C or so, for these beetles to be active on vegetation.

**Phylogenetic relationships.** This species is the adelphotaxon for a large complex of species—*B. moerens* to *B. filipes* (Fig. 9)—that constitute many of the most numerically abundant native platynine species. Though individuals likely live on the ground for parts of their lives, individuals of all of these species are usually found in arboreal microhabitats, either actively climbing on tree trunks or ferns, resting in leaf axils, or secreted inside epiphytic moss mats. All of these species save one—*B. palmae* of Oahu (Figs. 9, 272)—are distributed on the fragments of Maui Nui.
CARABIDAE PART I: PLATYNINI

Blackburnia (Metromenus) moerens (Sharp), new combination
(Figs. 250B, 254, 255)

Metromenus moerens Sharp, 1903: 237.

DIAGNOSIS. This species is very distinctive due to the glabrous pronotum with posteriorly expanded laterobasal margins, obtuse hind angles, and very narrow lateral margins (Fig. 250B); humeri broad, angulate; elytral intervals with granulate isodiametric microsculpture. The tarsi are somewhat broadened apically, metatarsomes 1-3 with shallow dorsolateral sulci, median area broadly convex; metatarsomere 4 emarginate, outer apical lobe 0.5 to 0.7 x median basal tarsomere length. Standardized body length 7.4-8.7 mm.

Pterothorax. Metepisternum short, broad, lateral margin 1.3 x length of anterior margin.

Male genitalia. Aedeagal median lobe gracile, abruptly curved near midlength, with broad medioventral expansion (Fig. 254A); ventral excavation extended to short, slightly downturned apex with finely rounded tip extended 1.6 x thickness of apex at opening of internal sac; basal sagittal crest various, long and very broad to almost obsolete; median lobe basally broad, slightly constricted at midlength, tapered to a rounded tip (Fig. 254B).

Female reproductive tract. Gonocoxa basally broad, triangular gonocoxite 2 with narrow, acuminate apex (Fig. 254C); gonocoxite 1 with apical fringe of 14-15 setae, mesal 6-8 setae near medioapical angle in double series; gonocoxite 2 with 2-3 lateral ensiform setae and 1 dorsal ensiform seta; apical nematiform setae moderate, 0.31 x length of gonocoxite 2; bursa copulatrix symmetrical, subequal to length of common oviduct, with a slightly developed transverse dorsal pouch; bursa with medial band of spikelike microtrichia; spermatheca elongate, 0.9 x length of spermathecal duct, without basal lobe.

Lectotype ♂ labeled “♂ Metromenus moerens Type D.S. Molokai Perkins 594” (BMNH) hereby designated. Perkins’ lot 594 is described as being collected in “VI.1894” (Anonymous n.d.) without further explanation.

Distribution. This species is distributed in the mountains of Molokai, from at least Kamakou Peak to Waikolu overlook and Kaunakakai Gulch (Fig. 255).

Localities. Perkins collected this species in the Molokai mountains at 910 to 1365 m elevation. More recent and specific localities include above Waikolu Valley, and Waaiakuianui Gulch.

Habits. This species has been collected on Pipturus, and by sifting moss from tree trunks. Perkins collected it repeatedly in 1893 (29-V, 9-VI, 12-VI, 13-VI, and 22-VI), accounting for 6 of 33 known specimens. The species has been seen only twice since 1912: one specimen each in 1955 (Gressitt, BPBM) and 1973 (Gagne, BPBM). What little we know about this species is consistent with habits of related species—i.e., it mostly occupies arboreal microhabitats.

Phylogenetic relationships. Our preferred cladogram places this species as the adelphotaxon to a clade comprising the most abundant species on Maui Nui: B. sphodriformis to B. erro (Fig. 9). This placement is highly provisional, as nearly all possible cladistic relationships are observed in various of the equally parsimonious cladograms (e.g., Liebherr & Zimmerman 1998, Fig. 88). We place B. moerens basally in this fivesome based on: 1, its habitation of Molokai, the oldest fragment of Maui Nui; 2, the great overall similarity of B. constricta, B. longula, and B. erro, suggesting that they represent a species triplet distributed across the three windward fragments of Maui Nui (Molokai, West, and East Maui, respectively).
Fig. 254. *B. (Metromenus) moerens*. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view.

Blackburnia (Metromenus) sphodriformis (Sharp), new combination
(Figs. 133A-B, 136B, 250C-D, 256, 257, 258)

*Metromenus sphodriformis* Sharp, 1903: 238.
*Atelothrus limbatus* Sharp, 1903: 217 (new synonymy).
*Atelothrus longicollis* Sharp, 1903: 217 (new synonymy).
*Mesothriscus collaris* Sharp, 1903: 225 (new synonymy).
*Metromenus cinctus* Sharp, 1903: 239 (new synonymy).

**DIAGNOSIS.** Easily distinguished by the elongate, cordate pronotum, with distinct obtuse hind angles (Fig. 250C-D); dorsal body coloration paler and redder than *B. longula, B. erro, B. moerens*, and *B. constricta*, rufobrunneous with an alutaceous lustre on elytra due to distinct transverse rows of slightly transverse sculpticells, antennae and legs contrastingly paler, testaceous, elytral epipleura rufotestaceous, paler than brunneous thoracic lateral and ventral sclerites; tarsomeres with fine dorsolateral sulci and a broadly convex median area (Fig. 133A), metatarsomeres 1-3 with fine outer sulci and obsolete inner sulci. Standardized body length 8.1-9.8 mm. The basal pronotal setae are variously present—i.e., almost always absent on Molokai, almost always present in West Maui, and present or absent on Haleakala (see Variation below).
Pterothorax. Metepisternum moderately elongate, lateral margin 1.3 to 1.5× length of anterior margin. This species has wing vestiges, longer than in related species, represented by micropterous straps extended slightly past metanotum to approximately position of fourth or fifth lateral elytral seta. (Given the status of flight wings in related species and phylogenetic relationships implicit in the cladogram of the Hawaiian platynine radiation [Fig. 9], the larger size of these micropterous straps is a reversal from a more reduced state.) Wing venation little more than curved costa plus 4 radiating longitudinal fields of melanization, corresponding to radial, medial, cubital, and anal veins (see Sharp 1903, plate VI).

Male genitalia. Aedeagal median lobe gracile, straight to slightly expanded medioventrally (Fig. 256A, C); ventral excavation extended to short, evenly curved apex ended in a finely rounded to rounded tip extended 1.0 to 1.3× thickness of apex at opening of internal sac; basal sagittal crest various, moderately broad and elongate to narrow and short; median lobe moderately broad, evenly tapered to a rounded tip (Fig. 256B, D).

Female reproductive tract. Gonocoxa basally broad, triangular gonocoxite 2 with acuminate apex (Fig. 256E, G); gonocoxite 1 with apical fringe of 8-10 setae, mesal 3 setae near medioapical angle in double series; gonocoxite 2 with 3-4 lateral ensiform setae (Fig. 136B) and 1 dorsal ensiform seta, lateral setae broad, elongate, 0.24× length of gonocoxite 2; apical nematiform setae short, 0.24× length of gonocoxite 2; bursa copulatrix symmetrical, subequal to length of common oviduct, with a broad dorsal pouch with lateral extensions and a medial band of spikelike microtrichia; spermatheca elongate, reservoir subequal to length of spermathecal duct, with a basal lobe opposite entrance of spermathecal gland duct (Fig. 256F).

Variation. Pronotal shape and setation vary rather greatly in this species, resulting in Sharp’s redescription of it under 4 different names. The increase in material available shows that the discrete differences he perceived and attempted to represent nomenclaturally were symptomatic of inadequate sampling. The larger amount of material now available, moreover, permits analysis of geographic variation in pronotal setation (Table 15). When present, the basal pronotal setae are positioned before the angulate hind angles about 0.07×
Fig. 256. *B. (Metromenus) sphodriformis*. A. Male aedeagal median lobe, right lateral view; Molokai. B. Male aedeagal median lobe, euventral view; Molokai. C. Male aedeagal median lobe, right lateral view; East Maui. D. Male aedeagal median lobe, euventral view; East Maui. E. Left female gonocoxa, ventral view; Molokai. F. Female spermatheca, ventral view; Molokai. G. Left female gonocoxa, ventral view; East Maui.
Table 15. Numbers of individuals of *B. sphodriformis* (fraction in parentheses) exhibiting various configurations of pronotal basal setae, for each island portion of this species' distribution. Variation significant at $P < 0.001$, Chi-squared test.

<table>
<thead>
<tr>
<th>Island</th>
<th>Both setae absent</th>
<th>One seta present</th>
<th>Both setae present</th>
</tr>
</thead>
<tbody>
<tr>
<td>Molokai</td>
<td>188 (0.97)</td>
<td>5 (0.03)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>West Maui</td>
<td>21 (0.09)</td>
<td>30 (0.13)</td>
<td>183 (0.78)</td>
</tr>
<tr>
<td>East Maui/Haleakala</td>
<td>112 (0.48)</td>
<td>30 (0.13)</td>
<td>92 (0.39)</td>
</tr>
</tbody>
</table>

median pronotal length. The fraction of specimens exhibiting these setae is associated with island of origin, with populations on Molokai nearly fixed for absence of the setae, West Maui populations consisting mostly of individuals that are setose, and Haleakala populations composed of a mixture of both (Table 15). The cells contributing most to the significant $\chi^2$ value are those representing the glabrous and setose conditions in the Molokai and West Maui samples. As West Maui is geographically intermediate, yet most skewed toward the setose condition, this polymorphism does not appear to be significantly influenced by gene flow.

**Types.** For *Metromenus sphodriformis*, lectotype $\sigma$ labeled “$\sigma$ Metromenus sphodriformis Type D.S. Molokai, Perkins. 12.VI.1893,” with “345” on reverse of card (BMNH) hereby designated. For *Atelothrus limbatus*, lectotype $\sigma$ labeled “$\sigma$ Atelothrus limbatus Type D.S. West Maui Mts., 4000 ft. Perkins. IV.1894” (BMNH) hereby designated. For *Atelothrus limbatus var? concolor*, lectotype $\varphi$ labeled “$\varphi$ Atelothrus limbatus var. concolor D.S. West Maui Mts. 4000 ft. Perkins. IV.1894” (BMNH) hereby designated. For *Atelothrus longicollis*, lectotype $\varphi$ labeled “$\varphi$ Atelothrus longicollis Type D.S. Haleakala 5000 ft. III.94. Perkins. 384.” (BMNH) hereby designated. For *Mesothriscus collaris*, holotype $\varphi$ labeled “Mesothriscus collaris Type D.S. Molokai Mts. 4000+ ft. Perkins. 15.VII.1893. // No. 1240 examined by Prof. Thaxter for Laboulbeniaceae” (BMNH). For *Metromenus cinctus*, lectotype $\sigma$ labeled “$\sigma$ Metromenus cinctus Type D.S. Molokai Mts. 4,500 ft. Perkins 21.VI.1893,” with “180.” on reverse of card (BMNH) hereby designated. Perkins collected the lectotype of *M. sphodriformis* in a deep gulch at Makakupua, Molokai (Perkins 1893). The types of *M. collaris* and *M. cinctus* were collected near the pali, or cliff face overlooking Pelekunu Valley, possibly in the vicinity of Pepeopae Bog, TNCH Kamakou Preserve. The type of *A. longicollis* was collected along with *B. erro* and *B. putealis* under moss, bark, and logs (Anonymous n.d.).

**Nomenclatural note.** Sharp (1903) dubiously recognized the variety “concolor” of his *Atelothrus limbatus* based on more uniform coloration, though he had only three specimens each of the typical form and his dubious variant. As the variety *concolor* was published before 1961, it is granted subspecific status, and thereupon designated a junior synonym.

**Distribution.** This species is widespread in areas that would have constituted the windward side of Maui Nui: Molokai, West Maui, and Haleakala (Figs. 257, 258).
Localities. On Molokai, recorded from Olokui summit, above Waikolu Valley, Kainaule Gulch, and TNCH Kamakou Preserve, including Hanalilolilo Trail, Pepeopae Bog, Puu Alii Bog Trail, East and West Forks of Kawela Gulch, Puu Kolekole, and Kaunuohua (Fig. 257). These localities range from 910 to 1515 m elevation.

Widespread across West Maui, including Honokohau Stream, Mt. Eke, Iao Valley, Puu Kukui, including the summit, Violet Lake, unnamed 4503 ft. elevation puu (hill northwest of Violet Lake near camp locally known as Three Pines), Haelaau or Kualalewelewe Cabin, Lihau summit, and Hanaula summit, springs, and reservoirs (Fig. 258). These sites span 890 to 1750 m elevation.

Haleakala localities include Olinda, Kailiili, Kula Pipeline Road, Waikamoi Flume, Waikamoi Gulch, Haipuaena Gulch, Honomanu Gulch, Koolau Stream, Kopiliula Stream, Hanawi Stream, and Haleakala National Park, including Waianapanapa, Upper Hana Forest, Kipahulu Valley, Kekuewa Hill N Puu Ahulili, and Manawainui Stream. Elevations on Haleakala span 880 to 2150 m elevation.

Habits. This species can most often be found by beating Cibotium tree ferns at night, as it much prefers running on fronds of these large ferns. It is also common under moss on Metrosideros (ohia lehua), or running on ohia branches at night. Adults have also been collected on Acacia (koa), Cheirodendron (olapa), Clermontia, Freycinetia (ieie), and Pipturus. At night, beetles are active on the ground, often running on boardwalks in native forest, but also on clay soil, mud stream banks, or open trails in bog situations.

In more lowland situations on Maui, from 900 to 1300 m elevation, this species is often the most common carabid species active on plant surfaces or on the ground at night. It is much less commonly encountered above 1400 m elevation, an elevational zone dominated by B. erro on Haleakala, and B. longula on West Maui. On Molokai, B. sphodriformis is uncommon above 1300 m elevation, where the most common nighttime plant climber is B. constricta. Somewhat lower, B. sphodriformis is the dominant nighttime climber, with B. vagans most common on the forest floor.

Phylogenetic relationships. Based on our preferred cladogram (Fig. 9), this species is the adelphotaxon to B. constricta (B. longula + B. erro). This hypothesis proposes that
populations of *B. sphodriformis* have not diverged to species-level status on Molokai and Maui during the same time that populations of the adelphotaxon have passed through two speciation events. Habitat isolation associated with elevation cannot explain this disparity, as *B. sphodriformis* is known from habitats as low as 880 m elevation, whereas populations of the other species occupy habitats from 455 to 910 m minimal elevation (Liebherr 1997).

**Blackburnia (Metromenus) constricta** (Sharp), new combination
(Figs. 135A-B, 251A, 259, 260)

*Atelothrus constrictus* Sharp, 1903: 217.

**DIAGNOSIS.** As *B. longula* and *B. erro* in: 1, basally setose pronotum with sinuate basolateral margins and tightly rounded hind angles (Fig. 251A-C); 2, distinct dorsal microsculpture; 3, gracile tarsomeres and emarginate metatarsomere 4; and 4, legs and antennae testaceous, contrasted with concolorous, brumneous to piceous body. But, differing from both by narrowness of body, with pronotal lateral marginal depressions obsolete mesad lateral bead, hind angles nearly angulate due to sinuate basolateral margins and narrow base, elytral humeri distinctly angulate, elytral margins subparallel medially. Standardized body length 6.4–8.0 mm.

**Pterothorax.** Metepisternum short, somewhat narrower in association with reduced humeri, lateral margin 1.4 to 1.7× length of anterior margin (this larger ratio due to narrowness of metepisternum, not greater length).
Male genitalia. Aedeagal median lobe gracile, slightly expanded medioventrally (Fig. 259A); ventral excavation extended to short, blunt apex ended in a rounded tip extended 1.0× thickness of apex at opening of internal sac; basal sagittal crest short, moderately broad; median lobe moderately broad, evenly tapered to a finely rounded tip (Fig. 259B).

Female reproductive tract. Gonocoxa basally broad, triangular gonocoxite 2 with acuminate apex (Figs. 135A, 259C); gonocoxite 1 with apical fringe of 10-11 setae, mesal 4 setae near medioapical angle in double series; gonocoxite 2 with 3 lateral ensiform setae and 1 dorsal ensiform seta; apical nematiform setae somewhat elongate, 0.32× length of gonocoxite 2; bursa copulatrix symmetrical, subequal to length of common oviduct, with a rounded dorsal pouch with lateral extensions and a medial band of spikelike microtrichia; spermatheca elongate, subequal to length of spermathecal duct, without basal lobe.

Lectotype ♂ labeled “♂ Atelothrus constrictus. Type D.S. Molokai, 197. Perkins 1893” (BMNH) hereby designated. Perkins’ lot 197 is described as “Molokai, odd specimens 1893” (Anonymous n.d.).

Distribution. This species is broadly distributed in the mountains of East Molokai from Kalae to Oloku (Fig. 260).
Localities. Recorded from Kalae, Olokui summit, above Waikolu Valley, and TNCH Kamakou Preserve, including Pepeopae Bog, Puu Alii Bog Trail at Pelekunu overlook, East Kawela Gulch, Puu Kolekole, and Kaunuohua. Localities span 910 to 1515 m elevation.

Habits. Recorded from Cibotium tree ferns and moss-covered Metrosideros (ohia lehua), as well as forest-floor ferns at night. Active at night on the forest floor as well, often running along boardwalks. Adults have also been collected from tree fern litter, ohia litter, and under logs and rocks.

Phylogenetic relationships. Based on our preferred cladogram, this species is the adelphotaxon of the Maui species pair *B. longula* and *B. erro* (Figs. 9, 262). This hypothesis proposes that Molokai is less closely related than West and East Maui are to each other. Hypotheses advanced by phylogenetic relationships proposed for Division 1 that bear on this issue can be found under treatments of *B. frigida*, *B. longipes*, *B. sharpi*, and *B. anomala*.

**Blackburnia (Metromenus) longula** (Sharp), new combination
(Figs. 251B, 261, 262)

Atelothrus longulus Sharp, 1903: 218.

DIAGNOSIS. This species from West Maui, *B. constricta* of Molokai, and *B. erro* of East Maui are diagnosed by: 1, dorsum of body covered with distinct microsculpture; 2, pronotum basally setose, with basolateral margins sinuate before obtuse-rounded hind angles, basal marginal bead present (Fig. 251A-C); 3, elytral humeri moderately broad to narrow, intervals slightly convex, non-carinate; 4, tarsomeres gracile, not expanded apically, metatarsomere 4 emarginate, outer apical lobe 0.4 to 0.5× basal median tarsomere length; 5, head capsule, pronotum, elytral disc and epipleura, and thoracic and abdominal venter concolorous, brunneous to piceous, contrasted with testaceous antennae and legs; 6, standardized body length ranging from 6.4 to 8.3 mm. These three species are among the most abundantly encountered species on their respective Maui Nui islands, and occur in a variety of microhabitats. Only the larger species, *B. sphodriformis*, is likely to be confused
Fig. 261. *B. (Metromenus) longula*. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view. D. Female bursa copulatrix, dorsal view, showing rounded dorsal pouch with distinctly developed lateral extensions, a medial band of spikelike microtrichia, and spermatheca.
Fig. 262. Distributional records for *B. (Metromenus) longula* (■), and *B. (Metromenus) erro* (●).

with these three species in the field, but, most specimens of that species: 1, lack the basal pronotal seta; 2, have the pronotal hind angles more angulate; 3, have the pronotal basal marginal bead effaced (Fig. 250C-D); and 4, are 8.1 to 9.8 mm in standardized body length. From *B. constricta* and *B. erro, B. longula* (Fig. 251B) is diagnosed by: 1, broader pronotal base with less sinuate basolateral margins, broader lateral marginal depressions, and more broadly elevated, slightly translucent marginal bead cephalad hind pronotal seta; and 2, humeri more rounded, carina cephalad elytral basal groove angulate or not at humerus, but convex surface of intervals 6 and 7 rounded basally. Standardized body length 6.7-8.3 mm.

**Pterothorax.** Metepisternum short, broad, trapezoidal, lateral margin 1.2-1.5× length of anterior margin.

**Male genitalia.** Aedeagal median lobe gracile, slightly expanded medioventrally (Fig. 261A); ventral excavation extended to short, straight apex with rounded tip extended 1.2-1.3× thickness of apex at opening of internal sac; basal sagittal crest short and narrow; median lobe basally broad, evenly tapered to a finely rounded tip (Fig. 261B).

**Female reproductive tract.** Gonocoxa basally broad, apex of triangular gonocoxite 2 narrow, acuminate (Fig. 261C); gonocoxite 1 with apical fringe of 12-13 setae, mesal 6 setae near medioapical angle in double series; gonocoxite 2 with 3 lateral ensiform setae and 1 dorsal ensiform seta; apical nematiform setae short, 0.29× length of gonocoxite 2; bursa copulatrix symmetrical, subequal to length of common oviduct, with a rounded dorsal pouch with well-sclerotized lateral extensions (Fig. 261D); bursa with medial band of spikelike microtrichia; spermatheca elongate, 0.9× length of spermathecal duct.
Lectotype ♂ labeled “♂ Atelothrus longulus Type D.S. West Maui Mts., 4000 ft. Perkins. IV.1894.” (BMNH) hereby designated.

**Distribution.** This species is found throughout the montane forests of West Maui (Fig. 262).

**Localities.** Known from Mt. Eke, above Mahinahina, Puu Kukui, including the summit, Violet Lake, and the unnamed 4503 ft. elevation puu (hill northwest of Violet Lake near camp locally known as Three Pines), above Lahaina, Lihau summit, and Hanaula summit, springs, and reservoirs. Recorded localities span 910 to 1750 m elevation.

**Habits.** These beetles live on a variety of substrate plants of the genera *Broussaisia*, *Cheirodendron* (olapa), *Cibotium* (hapuu), *Clermontia*, *Melicope*, *Metrosideros* (ohia lehua), as well as various low ferns. Adults can be commonly beaten or fogged from moss-covered ohia lehua and olapa. Adults are also active on the ground, on open trails or banks of streams, as well as resting under logs during daytime. From this diversity of collections, it is surmised that this species is a broad ecological generalist within the montane forests of West Maui.

**Phylogenetic relationships.** This species is the adelphotaxon of *B. erro* of Haleakala, East Maui (Figs. 9, 262).

*Blackburnia* (*Metromenus*) *erro* (Blackburn), new combination

(Figs. 251C, 262, 263)

*Anchomenus erro* Blackburn, 1878a: 121.

*Metromenus erro*: Blackburn & Sharp, 1885: 211.

*Atelothrus erro*: Sharp, 1903: 216.


*Atelothrus politus* Sharp, 1903: 216 (new synonymy).

**DIAGNOSIS.** As *B. longula* and *B. constricta*, but of intermediate form (Fig. 251C). Pronotal lateral margins are very narrow but discernibly lined with isodiametric microsculpture; raised pronotal margin near hind seta covered with microsculpture, not broad and translucent as in *B. longula*; humeri distinctly angulate, but elytra broader than in *B. constricta*; apex of male median aedeagal lobe slightly longer than in *B. constricta* and similar to *B. longula*, tip projected 1.2× thickness of apex at opening of internal sac (Fig. 263A). Standardized body length 7.3-8.3 mm.

**Pterothorax.** Metepisternum short, broad, trapezoidal, lateral margin 1.3 to 1.5× length of anterior margin.

**Male genitalia.** Aedeagal median lobe gracile, expanded medioventrally (Fig. 263A); ventral excavation extended to short, blunt apex ended in a rounded tip extended 1.2× thickness of apex at opening of internal sac; basal sagittal crest various, broad and elongate to narrow and short; median lobe moderately broad, evenly tapered to a rounded tip (Fig. 263B).

**Female reproductive tract.** Gonocoxa basally broad, triangular gonocoxite 2 with finely rounded apex (Fig. 263C); gonocoxite 1 with apical fringe of 11-12 setae, mesal 2-3 setae near medioapical angle in double series; gonocoxite 2 with 2-3 lateral ensiform setae and 1 dorsal ensiform seta; apical nematiform setae short, 0.22× length of gonocoxite 2; bursa copulatrix symmetrical, subequal to length of common oviduct, with a rounded dorsal
pouch with lateral extensions and a medial band of spikelike microtrichia (Fig. 263D); spermatheca elongate, 1.2× length of spermathecal duct, without basal lobe.

Lectotypes. For Anchomenus erro, lectotype ♂ on card with 3 parallel lines, top thickest, and perpendicular ink slash—Blackburn’s Maui code (Zimmerman 1957)—with “erro” handwritten on reverse (BMNH) hereby designated. For Platynus planus, lectotype ♀ labeled “Type. No.: 60818// Olinda, Finsch planus Karsch” (MNHU) hereby designated.
For *Atelothrus politus*, lectotype ♂ labeled “♂ Atelothrus politus Type D.S. Haleakala 5000 ft. IV.94. Perkins 385.” Perkins’ lot 385 is described as “Haleakala, Maui, contains 92 Metromeni, all under bark (mostly of Acacia) about 5.000 ft. IV. ‘94.”

**Distribution.** This species forms dense populations across the montane forests of Haleakala, East Maui (Fig. 262).

**Localities.** Found anywhere within native montane forest, including Olinda, Ukulele Camp, Kula Pipeline Road, Waikamoi Flume, Waikamoi Gulch, Haipuaena Gulch, Honomanu Gulch, Keanae Valley, Hanawi Stream, Kahiwa Stream, Nahiku, Waiohi Valley, and Haleakala National Park, including Big Bog, New Greensword Bog, and Midcamp Bog on Northeast Rift, Kipahulu Valley, Kuiki, Kekuewa Hill N of Puu Ahulili, and Manawainui Stream. These localities span 455 to 2090 m elevation: among the larger elevational spans due to the stature of Haleakala combined with the catholic tastes of this species.

**Habits.** The most abundant species of Hawaiian Platynini, found on a wide variety of substrate plants, including *Acacia* (koa), *Argyroxyphium* (greensword), *Astelia*, *Cibotium* (hapuu), *Clermontia*, *Freycinetia* (ieie), *Metrosideros* (ohia lehua), and *Styphelia*. On ohia, adults and larvae can be commonly found amongst moss and moss mats on trunks. Adults also hide during day under bark flaps on large *Acacia koa* trees, or under logs or boards.

**Phylogenetic relationships.** This species is the adelphotaxon of the allopatric West Maui species, *B. longula* (Figs. 9, 262).

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*Blackburnia (Metromenus) bartletti* Liebherr, new species

(Figs. 251D, 264, 265)

**Diagnosis.** Sharing with a similar West Maui species, *B. kauwa*, the somber piceous body and dark legs, slightly sinuate pronotum (Figs. 251D, 273B), and shiny elytra, but diagnosed by: 1, eyes less convex, ocular ratio 1.45-1.50; 2, pronotal lateral marginal depressions broader, margin upraised, not markedly beaded; 3, humeri distinctly angulate; 4, elytral intervals 2-5 flat in caudal view, elytra appearing flat; and 5, tarsomere 4 with moderate apical lobes, metatarsomere 4 with outer apical lobe 0.60 to 0.65× median basal tarsomere length. Standardized body length 6.5-7.5 mm.

**Description.** Head. Eyes moderately convex, head gracile but not elongate; slight dorsal impression slightly visible behind posterior supraorbital setae; antennal pedicel with longer outer seta and 2 shorter apical setae; apical labral margin straight medially; frontoclypeal grooves shallow, broad, extended toward supraorbital setae as fine, parallel wrinkles; apex of mentum tooth rounded.

**Prothorax.** Pronotum flat medially, lateral marginal depressions of moderate width, lateral margin upraised but not beadlike; basolateral margins slightly sinuate before obtuse-rounded hind angles; laterobasal depressions with diagonal wrinkles extended from hind angles, bordered laterally by gradually raised side margin, bordered posteriorly by more defined bead that is slightly traceable across median base; median base slightly irregular due to transverse wrinkles; median longitudinal impression finely incised on depressed disc, abundant transverse wrinkles extended on disc; anterior transverse impression very shallow, best evidenced as posterior border of irregularly wrinkled median apex; anterior marginal bead distinct medially, present across front, even inside tightly rounded front angles.
Elytra broad, ovoid, depressed, basal elytral groove markedly recurved to angulate humeri; elytral lateral margins convex, subapical sinuation present but reduced, lateral marginal bead thickened cephalad sinuation, dorsal view; intervals 2-4 slightly depressed, almost flat, fifth interval more convex; striae smooth but with slightly irregular sides; scutellar seta and 3 dorsal elytral setae present; 14-16 lateral elytral setae.

Pterothorax. Metepisternum short, broad, trapezoidal, lateral margin 1.4 to 1.5× length of anterior margin.

Legs. Profemur without anteroventral setae, with 2 posteroventral setae; mesocoxa with 1 ridge seta; mesofemur with 2 anteroventral setae; metacoxa bisetose, mesal seta absent; metatibia 2 anteroventral setae; tarsomeres gracile, tarsomeres 1-3 with very fine dorsolateral sulci, tarsomeres medially convex; tarsomere 4 emarginate, metatarsomere 4 with apical lobes 0.60 to 0.75× median basal tarsomere length; tarsomeres 1-3 with 3 sparsely distributed ventrolateral rows of elongate setae, glabrous medially; tarsomere 5 with 2 rows of 6 ventrolateral setae, each less than tarsomere depth at setal insertion.

Abdomen. Males with 1 apical seta each side of sternite VII, females with 3 each side.

Coloration. Head, pronotum, and elytral somber piceous, due to combination of color and microsculpture, pronotal margins slightly paler or not, rufopiceous; legs except tarsi, and thoracic and abdominal venter concolorous with dorsal surface; basal 3 antennomeres and basal 1/3 of fourth antennomere slightly paler, brunneous, compared to outer segments with a smoky infuscation.
Fig. 265. Distributional records for *B. (Metromenus) bartletti*, new species (□), *B. (Metromenus) gracilis* (●), and *B. (Metromenus) dyscolea* (○).

**Microsculpture.** Vertex with distinct isodiametric microsculpture; pronotal disc with transverse mesh microsculpture, most visible along transverse wrinkles, laterobasal depressions, median base, and median apex with granulate isodiametric microsculpture slightly more distinct than on dorsal neck impression of head; elytral intervals with distinct isodiametric sculpticells arranged in irregularly transverse rows; thoracic and abdominal venter with distinct transverse mesh microsculpture.

**Male genitalia.** Aedeagal median lobe gracile, with broad medioventral expansion, ventral excavation extended to short, evenly curved apex with rounded tip extended in length subequal to thickness at opening of internal sac (Fig. 264A); basal sagittal crest obsolete; median lobe moderately broad basally, with slight expansion on right side, tapered to a finely rounded, slightly acuminate tip (Fig. 264B).

**Female reproductive tract.** Gonocoxa basally broad, triangular gonocoxite 2 with acuminate apex (Fig. 264C); gonocoxite 1 with apical fringe of 8-9 setae, mesal 2-3 setae near medioapical angle in double series; gonocoxite 2 with 2 lateral ensiform setae and 1 dorsal ensiform seta; apical nematiform setae slightly elongate, 0.31× length of gonocoxite 2; bursa copulatrix symmetrical, subequal to length of common oviduct, with a rounded dorsal pouch with lateral extensions and a medial band of spikelike microtrichia; spermatheca elongate, reservoir 1.2× length of spermathecal duct, without basal lobe.

**Holotype** ♂ labeled "HI: West Maui Is. Pu‘u Kukui summit 11-V-1992 el. 1725-1750 m J.K. Liebherr // beating and scraping ohia during day" (CUIC).

**Paratypes.** Puu Kukui summit, ohia, beating/scraping, 1725-1750 m, 11-V-1992,
Liebherr (CUIC, 1), Polhemus (CUIC, 1); Puu Kukui, Astelia, 20-XII-1928, Swezey (BPBM, 3).

**Etymology.** This species is named after Mr. Randy Bartlett of West Maui Land and Pineapple Co., who has assisted numerous scientists exploring the biota of West Maui.

**Distribution.** This species is so far known only from Puu Kukui summit, and the vicinity of Kualalewelewe Cabin, West Maui (Fig. 265).

**Habits.** Adult beetles have been collected from Astelia and moss-covered ohia lehua (Metrosideros polymorpha). Combining this limited information with the nearly absolute fidelity to arboreal microhabitats of all patristically adjacent species—*B. gracilis*, *B. dyscolea*, *B. depressa*, and *B. kauwa* (Fig. 9)—we predict that further, more extensive collections of *B. bartlettii* will show it to be restricted to similar arboreal microhabitats.

**Phylogenetic relationships.** This species is partially sympatric with its adelphotaxon, the species quartet spanning *B. gracilis* to *B. palmae* (Figs. 9, 265). *Blackburnia bartlettii* is ecologically separated from the sympatric *B. gracilis*, as it lives on ohia and *Astelia*, and *B. gracilis* is largely restricted to ieie (*Freycinetia*).

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**Blackburnia (Metromenus) gracilis** (Sharp), new combination

(Figs. 133G-H, 265, 266A, 267)


**Diagnosis.** This and the 3 species following—*B. dyscolea*, *B. platynoides*, and *B. palmae* (Fig. 266B-D)—are similar based on: 1, elytra with flattened disc; 2, metatarsomere 4 with apical lobes subequal or longer to median basal length of segment; 3, pronotum with variously sinuate basolateral margins and rounded hind angles. This species is recognized by: 1, narrow, basally setose pronotum with barely sinuate basolateral margins (Fig. 266A); 2, vertex of head with isodiametric microsculpture much reduced, the surface shiny and sculpticells untraceable, though sculpticells are distinct on dorsal neck impression; and 3, metatarsomere 4 with moderately elongate apical lobes, outer lobe 1.20 to 1.35 x median basal tarsomere length (Fig. 133G). Standardized body length 5.9-6.8 mm.

**Pterothorax.** Metepistemum short, broad, lateral margin 1.3 to 1.5 x length of anterior margin.

**Male genitalia.** Aedeagal median lobe gracile, with broad medioventral expansion, ventral excavation extended to short, evenly curved apex with rounded tip extended in length 1.0 to 1.2 x thickness at opening of internal sac (Fig. 267A); basal sagittal crest short, broad to narrow; median lobe basally broad and for much of length, tapered near apex to an angulate tip (Fig. 267B).

**Female reproductive tract.** Gonocoxa basally broad, triangular gonocoxite 2 with acuminate apex (Fig. 267C); gonocoxites 1 with apical fringe of 11-13 setae, mesal 6 setae near medioapical angle in double series; gonocoxite 2 with 3 lateral ensiform setae and 1 dorsal ensiform seta; apical nematiform setae short, 0.26 x length of gonocoxite 2; bursa copulatrix symmetrical, subequal to length of common oviduct, with a triangular dorsal pouch with lateral extensions and a medial band of spikelike microtrichia; spermatheca elongate, reservoir subequal to length of spermathecal duct, without basal lobe.

**Lectotype** ♀ labeled "♂ Atelothrus gracilis Type D.S. West Maui? Perkins 357." (BMNH) hereby designated. Perkins’ lot 357 is described as “Haleakala, Maui, Coleops.,
Fig. 266. Blackburnia species habitus, dorsal view. A. B. (Metromenus) gracilis. B. B. (Metromenus) dyscolea. C. B. (Metromenus) platynoides. D. B. (Metromenus) palmae.
Fig. 267. *B. (Metromenus) gracilis*. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view.

4000 ft. IV. "94" (Anonymous n.d.). Sharp (1903) noted problems with labeling of this lot, properly suspecting that his *A. gracilis* was from West Maui. Collection of subsequent material affirms his suspicions.

**Distribution.** This species lives at a variety of elevations throughout the West Maui mountains (Fig. 265).

**Localities.** Distributed throughout the West Maui mountains, from Honokohau Gulch, Wailuku, Puu Kukui, including the summit, the unnamed 4503 ft. elevation puu (hill northwest of Violet Lake near camp locally known as Three Pines), Haelau or Kualalewelewelelelele Cabin, Lihaun summit, and Hanaula Springs. Localities range from 890 to 1750 m elevation.

**Habits.** Specimens of this species are almost always found in association with *Freycinetia* (158 of 169 specimens with ecological label data), though a few specimens have been encountered beating ohia lehua (*Metrosideros polymorpha*), and one beetle was found walking on a boardwalk at night. Two collections have come via Malaise traps, indicating good climbing abilities in adults of this species.

**Phylogenetic relationships.** Our preferred cladogram places this species as the adelphotaxon of the biogeographically unlikely species triplet *B. dyscolea* (*B. platynoides* + *B. palmae*) (Fig. 9), with all four species defining the hypothesis of area relationship: West Maui (East Maui (Molokai + Oahu)). The apical position of *B. palmae* is the best documented example in this radiation of a back-dispersal event from Maui Nui to Oahu (Liebherr 1997). The remaining area relationships are quizzical. Nonetheless, the cladistic
support for this species quartet monophyletically groups the four species of Division 2 that are predominantly restricted to living in leaf axils of ieie vines (*Freycinetia*). Levels of specificity to this microhabitat are described under the species treatments below.

**Blackburnia (Metromenus) dyscolea** (Sharp), new combination

(Figs. 133C-D, 136C, 265, 266B, 268)

*Atelothrus dyscoleus* Sharp, 1903: 220.

**Diagnosis.** Similar to *B. gracilis* and *B. platynoides* in flattened elytral disc, basally setose and sinuate pronotum with rounded hind angles, and lobate tarsomere 4, but, differing in: 1, pronotal basolateral margins markedly sinuate, pronotal base narrow, distance between basal seta 0.70 to 0.75× maximum width (Fig. 266B); 2, elytra broad, clearly broadest behind middle; 3, elytral intervals flat, surfaces shiny though transversely stretched sculpticells are visible; and 4, outer apical lobe of fourth metatarsomere 0.70 to 0.90× basal median tarsomere length (Fig. 133C). Standardized body length 6.4-8.6 mm.

**Pterothorax.** Metepisternum moderately elongate, lateral margin 1.5 to 1.9× length of anterior margin.

**Male genitalia.** Aedeagal median lobe gracile, with slight, broad medioventral expansion, ventral excavation extended to short, bluntly rounded apex extended in length subequal to thickness at opening of internal sac (Fig. 268A); basal sagittal crest various, broad to narrow; median lobe basally broad, evenly tapered to a finely rounded tip (Fig. 268B).

**Female reproductive tract.** Gonocoxa basally broad, triangular gonocoxite 2 with acuminate apex (Fig. 268C); gonocoxite 1 with apical fringe of 11-13 setae, mesal 4-7 setae near medioapical angle in double series; gonocoxite 2 with 3-4 lateral ensiform setae and 1 dorsal ensiform seta, lateral ensiform setae elongate, 0.24× length of gonocoxite 2; apical nematiform setae moderately elongate, 0.30× length of gonocoxite 2; bursa copulatrix symmetrical, subequal to length of common oviduct, with a narrow dorsal pouch with elongate lateral extensions and a medial band of spikelike microtrichia (Fig. 268D); spermatheca elongate, reservoir subequal to 0.8× of spermathecal duct, without basal lobe.

**Lectotype** ♀ labeled "♀ Ateelothrus dyscoleus Type D.S. Haleakala 3000 ft. Perkins 845." (BMNH) hereby designated. Perkins' lot 845 was collected in 1900, and the notes associated with these lots have been lost.

**Distribution.** This species is broadly distributed in the lower-elevation montane forests of Haleakala, East Maui (Fig. 265).

**Localities.** In the western reaches of windward Haleakala known from Kailua, and Waikamoi and Honomanu Gulches. To the east, recorded from Kipahulu Valley. Localities span 600 to 1210 m elevation.

**Habits.** Like *B. gracilis*, this species is commonly associated with *Freycinetia*, where adults hide by day in leaf axils (19 of 23 specimens with ecological data from this microhabitat). Adults have also been beaten from ohia lehua (*Metrosideros*) forest vegetation at night, and one individual was found on the ground under logs and boards.

**Phylogenetic relationships.** In our preferred cladogram this species is placed as the adelphotaxon of the allopatric species pair *B. platynoides* of Molokai and *B. palmae* of Oahu (Figs. 9, 265, 270, 272).
Fig. 268. *B. (Metromenus) dyscolea*. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view. D. Female bursa copulatrix, dorsal view, showing narrow dorsal pouch with lateral extensions, medial band of spikelike microtrichia, and spermatheca.
**Blackburnia (Metromenus) platynoides (Sharp), new combination**  
(Figs. 266C, 269, 270)

*Atelothrus platynoides* Sharp, 1903: 221.

*Atelothrus platynoides var. flavipes* Sharp, 1903: 221 (new synonymy).

**Diagnosis.** Much like *B. dyscolea* (Fig. 266B) in the basally narrowed and setose pronotum (Fig. 266C), and like *B. gracilis* and *B. palmae* in the flattened elytra, but *B. platynoides* has the apical lobes of tarsomere 4 longer, and the outer apical lobe of fourth metatarsomere 1.65 to 1.80× median basal length of segment; length slightly longer than in *B. palmae* (Fig. 133E), but apical lobes are narrower, more pointed apically. Even the darkest specimens, which are rufopiceous above, have pronotal and elytral epipleura paler than thoracic and abdominal venter, versus epipleura in *B. dyscolea* that are darker than bordering sternites. Standardized body length 6.0-6.8 mm.

**Pterothorax.** Metepisternum short, narrow, lateral margin 1.3 to 1.6× length of anterior margin.

**Male genitalia.** Aedeagal median lobe gracile, expanded on dorsal surface, straight medioventrally, ventral excavation extended to short, bluntly rounded apex extended in length 1.0 to 1.3× thickness at opening of internal sac (Fig. 269A); basal sagittal crest obsolete; median lobe moderately broad basally, evenly tapered to a finely rounded tip (Fig. 269B).

**Female reproductive tract.** Gonocoxa basally broad, triangular gonocoxite 2 with acuminate apex (Fig. 269C); gonocoxite 1 with apical fringe of 13-15 setae, mesal 6-8 setae near medioapical angle in triple series; gonocoxite 2 with 4 lateral ensiform setae and 1 dorsal ensiform seta, lateral ensiform setae elongate, 0.26× length of gonocoxite 2; apical nematiform setae moderately elongate, 0.30× length of gonocoxite 2; bursa copulatrix symmetrical, subequal to length of common oviduct, with a broad dorsal pouch with elongate lateral extensions and a medial band of spikelike microtrichia (Fig. 269D); spermatheca elongate, reservoir subequal to 1.0× of spermathecal duct, without basal lobe.


**Nomenclatural note.** Sharp (1903, 221) diagnosed the variety *flavipes* based on the paler color of the legs, stating “I see no distinction in it except the colour of the legs, and in this group of *Atelothrus* this character does not appear to me to indicate specific distinctness.” The availability of more material permits dismissal of this character as nothing beyond individual variation. As the variety was proposed before 1961, it is considered a subspecific name and synonymized.

**Distribution.** This species is found in the mountains of Molokai from Waikolu overlook east as far as Kainalu (Fig. 270).

**Localities.** Known from across eastern Molokai, including above Waikolu Valley, Kawela Gulch, Kainalu Gulch, and TNCH Kamakou Preserve localities of Pepeopae Bog and Puu Kolekole. Localities lie from 575 to 1210 m elevation.
**Habits.** Most specimens of this species have been collected from ieie (*Freycinetia*; 26 of 35 specimens with ecological data), with a few beaten from *Pipturus, Metrosideros* (ohia lehua), and ferns, and one individual found under a board. Perkins (1913, cxliii) considered it to have exclusively arboreal habits.

**Phylogenetic relationships.** This species is geographically isolated from its adelphotaxon, *B. palmae* of Oahu (Fig. 9).
Blackburnia (Metromenus) palmae (Blackburn), new combination
(Figs. 133E-F, 136D, 266D, 271, 272)

Dyscolus palmae Blackburn, 1877: 147.

DIAGNOSIS. The only species of the subgenus with elongate apical lobes on metatarsomere 4 (Fig. 133E), and a glabrous pronotum. The outer lobe of metatarsomere 4 ranges from \(1.40 \text{ to } 1.75 \times \) median basal length of segment. Except for lack of basal pronotal setae, this species is very similar to B. platynoides, though the elytra are widest behind the middle in that species (Fig. 266C), and more evenly ovoid in this one (Fig. 266D). The darkest B. palmae have a piceous head and elytra, rufopiceous pronotum, and infuscated legs. Many specimens, however, either have not melanized as completely, or darken less at maturity, for very many specimens are brunneous above, with testaceous pronotal and elytral epipleura and femora. Standardized body length 5.3-7.0 mm.

Pterothorax. Metepisternum short, broad, lateral margin 1.3 to 1.4 \times \) length of anterior margin.

Male genitalia. Aedeagal median lobe gracile, expanded on dorsal surface, straight to slightly recurved medioventrally, ventral excavation extended to short, bluntly rounded apex extended in length subequal to thickness of apex at opening of internal sac (Fig. 271A); basal sagittal crest short and shallow to obsolete; median lobe basally broad, constricted on right surface, then evenly tapered to a rounded tip (Fig. 271B).

Female reproductive tract. Gonocoxa basally broad, triangular gonocoxite 2 with acuminate apex (Fig. 271C); gonocoxite 1 with apical fringe of 11 setae, mesal 2-4 setae near medioapical angle in double series; gonocoxite 2 with 3-4 lateral ensiform setae and 1 dorsal ensiform seta, lateral ensiform setae broad, elongate, 0.24 \times \) length of gonocoxite 2; apical nematiform setae short, 0.26 \times \) length of gonocoxite 2; bursa copulatrix symmetrical, subequal to length of common oviduct, with a rounded dorsal pouch with slightly developed lateral extensions and a medial band of spikelike microtrichia; spermatheca ovoid, reservoir 0.7 \times \) length of spermathecal duct, without basal lobe.
Variation. Of the 604 specimens of this species examined from many localities in Oahu, 3 had a basal pronotal seta unilaterally present. These were not concentrated in a single series or locality, qualifying them as sports in the classical sense of the word.

Lectotype ♂ on card with 2 parallel lines, the top line thickest—Blackburn’s Oahu code (Zimmerman 1957)—and “palmae” handwritten on reverse (BMNH) hereby designated.

Distribution. This species is widely distributed along the length of the Koolau Mountain Range of Oahu, and has also been found on Mt. Kaala in the Waianae Range (Fig. 272).

Localities. In the Waianae Range, known only from 760 to 1120 m elevation on Mt. Kaala, with one other record from south Waianae Mountains (Bridwell, NMNH). Known from the entire length of the Koolau Range, including Pupukea, Kawaiola Ridge, Castle Trail, Punalu'u, Helemano, Poamoho Trail, Wahiawa, Puu Kaaumakua, Waiau Trail, north peak of Eleao massif, Waipio Ridge, Puu Keahiakahoe massif at Tripler Ridge, Puu Lanihuli, Nuuanu Valley and Pali, Kaumuohana, Konahuanui, Tantalus, Manoa Valley, Pauoa Valley and Ridge, Palolo Valley including Kaau Crater, Haiku Valley, Mt. Olympus, Puu Lanipo, Waialae Nui, Wiliwilinui Ridge, Niu Valley, Kuliouou Trail summit at Puu o Kona, and Hawaii Kai. Recorded elevations are as low as 395 m. This species was abundant on Tantalus at 500-m elevation in 1991.

Habits. Like the preceding three species, most specimens (132 of 174 with ecological data) of B. palmae are recorded from ieie (Freycinetia). Other substrate plant genera include Astelia, Cibotium, Gahnia, Metrosideros (ohia lehua), and uluhe fern. The sole terrestrial associations include two individuals found under an Astelia plant, and one found while clearing uluhe fern during studies on Megalagrion oahuense (Williams 1936).
Phylogenetic relationships. This species is geographically isolated from its adelphotaxon, *B. platynoides* of Molokai (Fig. 9). Based on quantititative items of error biogeographic analysis (Liebherr 1997), this species most parsimoniously arose through dispersal of its ancestors from Molokai followed by speciation.

**Blackburnia (Metromenus) depressa** (Sharp), new combination
(Figs. 273A, 274, 275)

*Atelothrus depressus* Sharp, 1903: 220.
*Atelothrus depressus* var. *fuscipes* Sharp, 1903: 220 (new synonymy).

DIAGNOSIS. Similar to *B. constricta* of Molokai, this Lanai species has a dark body contrasted with testaceous legs and basal antennomeres, narrow and angulate humeri, and basally narrow pronotum with sinuate basolateral margins (Fig. 273A), but *B. depressa* differs by: 1, elytral intervals 2-5 depressed (visible in caudal view); 2, pronotal basal bead complete; and 3, metatarsomeres 1-3 with inner and outer sulci equal, fine, tarsomeres broadly convex medially. This species also might be confused with the flattened species above—*B. gracilis, B. dyscolea, B. platynoides,* and *B. palmae*—but *B. depressa* has only...
moderately emarginate fourth tarsomeres, the outer apical lobe of fourth metatarsomere 0.60 to 0.75× basal median tarsomere length. Standardized body length 6.2-7.3 mm.

**Pterothorax.** Metepisternum somewhat shortened, narrow, lateral margin 1.4 to 1.8× length of anterior margin.

**Male genitalia.** Aedeagal median lobe gracile, straight to slightly expanded medioventrally (Fig. 274A); ventral excavation extended to short, evenly curved apex ended in a finely rounded tip extended 1.1× thickness of apex at opening of internal sac; basal sagittal crest various, elongate and narrow to obsolete; median lobe moderately broad, evenly tapered to a finely rounded tip (Fig. 274B).

**Female reproductive tract.** Gonocoxa basally broad, triangular gonocoxite 2 with acuminate apex (Fig. 274C); gonocoxite 1 with apical fringe of 7-8 setae, mesal 4 setae near medioapical angle in double series; gonocoxite 2 with 4-5 lateral ensiform setae and 1 dorsal ensiform seta, lateral setae broad, elongate, 0.25× length of gonocoxite 2; apical nematiform setae short, 0.23× length of gonocoxite 2; bursa copulatrix symmetrical, subequal to length of common oviduct, with a broad dorsal pouch with lateral extensions and a medial band of spikelike microtrichia; spermatheca elongate, reservoir 0.8× length of spermathecal duct, without basal lobe.

**Lectotypes.** For Atelothrus depressus, lectotype ♀ labeled “♀ Atelothrus depressus Type D.S. Lanai, 2-3000 ft. Perkins. VI+VII.1894” (BMNH) hereby designated. For *Atelothrus*
depressus var. fuscipes, lectotype ♂ labeled "♀ Atelothrus depressus var. fuscipes D.S. Lanai, 86. 2000+ ft. Perkins I.1894" (BMNH) hereby designated.

**Distribution.** Found along the length of Lanaihale, Lanai (Fig. 275).

**Nomenclatural note.** Sharp diagnosed the variety *fuscipes* based on 4 specimens, all of which had darker legs than typical *A. depressus*, and 3 of which had deeper striae. The availability of more material permits us to ascribe this to individual variation. As the variety was proposed before 1961, it is considered a subspecific name to be synonymized.

**Localities.** Known from across Lanaihale, including the summit (1020 m), Halepaakai, and Waiakeakua. Also recorded from Hauola Trail (750 m).

**Habits.** Known only from arboreal situations, including native vegetation (mostly *Metrosideros polymorpha*), and in dead stipes of *Sadleria* ferns.

**Phylogenetic relationships.** This species is the adelphotaxon of a clade of five species—*B. kauwa* to *B. filipes* (Fig. 9)—distributed on all fragments of Maui Nui that support forest—i.e., Molokai, Maui, and Lanai.
CARABIDAE PART 1: PLATYNINI

Fig. 275. Distributional records for *B. (Metromenus) depressa*.

**Blackburnia (Metromenus) kauwa** Liebherr, new species
(Figs. 273B, 276, 277)

**DIAGNOSIS.** This species, and the following 4—*B. fulgida, B. insociabilis, B. fraudator,* and *B. filipes*—have shiny bodies with reduced microsculpture, lateral pronotal setae absent and basal pronotal setae present (polymorphic in *B. fraudator*), and legs contrastingly paler than dorsal body surface. Tarsomeres are gracile, narrow, with distinct outer dorsolateral sulci and fine inner sulci; tarsomere 4 emarginate, metatarsomere 4 with apical lobes 0.2 to 0.5 × median basal tarsomere length. *Blackburnia kauwa* is differentiated by the most distinct microsculpture of the 4, with vertex of head bearing distinct isodiametric microsculpture; pronotal disc shiny with reduced transverse mesh microsculpture, but with sculpticells distinct in transverse wrinkles; elytral intervals with irregular transverse mesh, producing an alutaceous lustre. The prothorax (Fig. 273B) differs from that of *B. fulgida* (Fig. 278A), and *B. fraudator* (Fig. 278C) by the sinuate basolateral margins, and placement of basal pronotal seta in the broadly elevated margin. Standardized body length 6.9-7.2 mm.

**DESCRIPTION.** Head broad, eyes large, convex, ocular ratio 1.60; slight dorsal impression, or neck, caudad hind supraorbital setae; antennal pedicel with 1 longer outer seta and 2 shorter apical setae; labrum broadly, shallowly emarginate; frontoclypeal grooves very broad, vague, extended laterally as shallow area cephalad anterior supraorbital setae; mentum tooth apically rounded.

**Prothorax.** Pronotum somewhat flattened on disc, lateral marginal depressions moderate, bordered by lateral bead; laterobasal depressions broad, bordered laterally by widely elevated margin within which the basal seta is inserted (Fig. 273B); median base smooth, with fine longitudinal wrinkles along edge of elevated discal area; basal marginal bead effaced medially, in some specimens only narrowly so; median longitudinal impression fine, evident on disc and extended almost to anterior marginal bead; anterior transverse impression broad, shallow, crossed by numerous longitudinal wrinkles; front angles rounded, barely protruded. Prosternal process convex medioventrally.
Fig. 276. *B. (Metromenus) kauwa*, new species. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view. D. Female bursa copulatrix, dorsal view, showing rounded dorsal pouch with well-developed lateral extensions, medial band of spikelike microtrichia, and elongate spermatheca.

**Elytra** broadly ovoid, slightly flattened medially, laterally depressed; basal groove recurved to tightly rounded to angulate humeri (largest female has broadest elytra and roundest humeri); subapical sinuation reduced but present, lateral margin slightly sinuate before rounded sutural apex; elytral intervals slightly convex, striae slightly wavering but distinctly incised; scutellar seta and 3 dorsal elytral setae present; 14-15 lateral elytral setae.
Pterothorax. Metepistemum short, broad, trapezoidal, lateral margin 1.5 to 1.6× length of anterior margin.

Legs. Profemur without anteroventral setae, with 2 posteroventral setae; mesocoxa with 1 ridge seta; mesofemur with 2 anteroventral setae; metacoxa bisetose, mesal seta absent; metafemur with 2 anteroventral setae; tarsomeres gracile, tarsomeres 1-3 with dorsolateral sulci, outer sulcus broader than inner; tarsomere 4 emarginate, metatarsomere 4 with apical lobes 0.4× median basal tarsomere length; tarsomeres 1-3 with 3 ventralateral rows of elongate setae, glabrous medially; tarsomere 5 with 2 rows of 6 ventralateral setae, each less than tarsomere depth at point of setal insertion.

Abdomen. Males with 1 apical seta each side of sternite VII, females with 3 each side.

Coloration. Head capsule, pronotal disc, and elytra concolorous, shiny piceous; clypeus, frons, and mandibles paler, rufous; pronotal lateral margins and sutural stria rufous; palpi and basal 3 antennomeres palest, rufotestaceous; legs and outer antennomeres with smoky infuscation over rufotestaceous ground color, contrasted with piceous pronotal and elytral epipleura, and thoracic and abdominal venter.

Microsculpture distinct even though body surface shiny; frons and vertex with distinct isodiametric mesh; pronotal disc with transverse mesh that is somewhat reduced in medial flat area, but evident in transverse wrinkles; pronotal lateral marginal and laterobasal depressions covered with a combination of isodiametric and transverse sculpticells; pronotal base and apex with slightly transverse sculpticells; elytral intervals with transverse sculpticells arranged in irregular transverse rows; abdominal sternites covered with distinct transverse mesh microsculpture.

Male genitalia. Aedeagal median lobe gracile, with broad medioventral expansion, ventral excavation extended to short, straight apex with rounded tip extended 1.25× thickness of apex at opening of internal sac (Fig. 276A); basal sagittal crest moderately elongate, narrow; median lobe moderately broad basally, slightly constricted on right side, tapered to a finely rounded tip (Fig. 276B).

Female reproductive tract. Gonocoxa basally broad, triangular gonocoxite 2 with acuminate apex (Fig. 276C); gonocoxite 1 with apical fringe of 8-11 setae, mesal 4 setae near medioapical angle in double series; gonocoxite 2 with 2-3 lateral ensiform setae and 1 dorsal ensiform seta; apical nematiform setae short, 0.29× length of gonocoxite 2; bursa copulatrix symmetrical, subequal to length of common oviduct, with a rounded dorsal pouch with lateral extensions of lightly sclerotized membrane (Fig. 276D), and a medial band of spikelike microtrichia; spermatheca elongate, 1.3× length of spermathecal duct.

Holotype ♂ labeled “HI: West Maui Is. Pu‘u Kukui Tr. @ Kualalewelewe Cabin 14-V-1992 el. 890 m. J.K. Liebherr // beating sabah palm” (CUIC).

Paratypes. MAUI: same data as holotype (CUIC, 5).

Etymology. The species epithet kauwa is the Hawaiian word for outcast or pariah, signifying similarity of this species and B. insociabilis.

Distribution. This species is known only from the type locality on the leeward side of the West Maui mountains (Fig. 277).

Habits. The type series was beaten from the palm tree planted just behind the Kaulalewelewe Cabin of the Maui Land and Pineapple Co.

Phylogenetic relationships. Based on our preferred cladogram, this species is the adelphotaxon of four species—B. fulgida to B. filipes (Fig. 9)—distributed on Molokai, Haleakala, and Lanai.
FIG. 277. Distributional records for B. (Metromenus) kauwa, new species (■), B. (Metromenus) fulgida, new species (○), and B. (Metromenus) insociabilis (●).

**Blackburnia (Metromenus) fulgida** Liebherr, new species
(Figs. 277, 278A, 279)

**DIAGNOSIS.** This species is diagnosed by: 1, upper body surface shiny; 2, only basal pronotal seta present; 3, apical lobes on metatarsomere 4 short; and especially 4, pronotum quadrate (Fig. 278A), basolateral margins only slightly sinuate before obtuse hind angles. The elytra are very shiny, intervals lacking discernible sculpticells in the single, teneral holotype female specimen. Standardized body length 7.7 mm.

**DESCRIPTION.** Head broad, eyes large, convex, ocular ratio 1.61; slight dorsal impression caudad hind supraorbital setae; antennal pedicel with longer outer seta and 1 shorter apical seta; frontoclypeal grooves shallowly extended to anterior supraorbital setae, frons with medial triangular depression, apex pointing caudad; labrum only slightly emarginate apically; mentum tooth rounded apically.

**Prothorax.** Pronotum almost quadrate, hind angles obtuse-rounded (Fig. 278A); lateral marginal depressions narrow, slightly widened toward slightly protruded, rounded front angles; laterobasal depressions broad, smooth, bordered laterally by elevated margin that is thicker behind basal pronotal setae; median base smooth, basal marginal bead complete except at very middle where it is obsolete; median longitudinal impression very fine, almost obsolete; anterior transverse impression shallow, diffuse, diamond-shaped, not extended toward front angles; anterior marginal bead complete.
Fig. 278. *Blackburnia* species habitus, dorsal view. A. *B. (Metromenus) fulgida*, new species. B. *B. (Metromenus) insociabilis*. C. *B. (Metromenus) fraudator*. D. *B. (Metromenus) filipes*. 
Fig. 279. *B. (Metromenus) fulgida*, new species. A. Left female gonocoxa, ventral view. B. Female bursa copulatrix, ventral view, showing rounded dorsal pouch with lateral extensions, medial band of spikelike bursal microtrichia, and spermatheca.

**Elytra** subparallel, humeri broad, basal groove markedly recurved laterad scutellum, angulate at humerus; subapical sinuation reduced but present, lateral margin sinuate before rounded sutural apex; elytral intervals slightly convex, striae distinctly incised; scutellar seta and 3 dorsal elytral setae present; 15-16 lateral elytral setae.

**Pterothorax.** Metepisternum short, broad, trapezoidal, lateral margin $1.4\times$ length of anterior margin.
Legs. Profemur without anteroventral setae, with 2 posteroventral setae; mesocoxa with 1 ridge seta; mesofemur with 2 anteroventral setae; metacoxa bisetose, mesal seta absent; metafemur with 2 anteroventral setae; tarsomeres gracile, tarsomeres 1-3 with fine dorsolateral sulci, tarsomeres medially convex; tarsomere 4 emarginate, metatarsomere 4 with apical lobes 0.35× median basal tarsomere length; tarsomeres 1-3 with 3 sparsely distributed ventrolateral rows of elongate setae, glabrous medially; tarsomere 5 with 2 rows of 6 ventrolateral setae, each less than tarsomere depth at point of setal insertion.

Abdomen. Female with 3 setae each side of sternite VII.

Coloration. The single specimen is teneral; head and pronotum concolorous, brunneous; elytral base brunneous, apex paler, testaceous; thoracic and abdominal venter brunneous; legs testaceous; basal 3 antennomeres testaceous, apical antennomeres darker, brunneous. Given the cladistic relationship of this species to other darkly colored species (Liebherr & Zimmerman 1998), mature specimens are likely to have piceous bodies and contrasting paler legs.

Microsculpture. Vertex shiny, covered with very shallow microlines in isodiametric pattern, constricted neck with more evident transverse sculpticells; pronotal disc shiny with very shallow microlines in transverse mesh, laterobasal depressions with very shallow microlines in isodiametric pattern in deepest portions, transverse sculpticells along edges adjacent to disc; elytral intervals without discernible microlines, though micropunctures the diameter of single sculpticells are present; elytral striae lined with isodiametric sculpticells.

Male genitalia. The single known specimen is a female.

Female reproductive tract. Gonocoxa basally broad, triangular gonocoxite 2 with acuminate apex (Fig. 279A); gonocoxite 1 with apical fringe of 11-12 setae, mesal 4-5 setae near medioapical angle in double series; gonocoxite 2 with 3 lateral ensiform setae and 1 dorsal ensiform seta; apical nematiform setae moderate, 0.32× length of gonocoxite 2; bursa copulatrix symmetrical, 1.33× length of common oviduct, with a rounded dorsal pouch with lateral extensions of lightly sclerotized membrane, and a medial band of spike-like microtrichia (Fig. 279B); spermatheca elongate, 1.3× length of spermathecal duct, without basal lobe.

Holotype ♀ labeled “HI Maui Haleakala NW slope Waikamoi Pres. trans. 3 el. 1820-1850 m 7-V-1991 J.K. Liebherr // scraping exfoliating bark of koa” (CUIC); specimen with pin hole in right side, now pointed (Fig. 278A).

Etymology. The species epithet fulgida refers to the very shiny body surface of this beetle.

Distribution. The type locality is within The Nature Conservancy of Hawaii Waikamoi Preserve (Fig. 277).

Habits. The unique specimen of this species was collected with 62 B. erro under exfoliating bark flaps of large Acacia koa during daytime.

Phylogenetic relationships. This species is the adelphotaxon of the species triplet B. insociabilis (B. fraudator + B. filipes) (Fig. 9). The type locality of Blackburnia fulgida falls within the geographical confines of localities from which B. insociabilis has been collected (Fig. 277); however the lone locality for the former is approximately 400 m higher in elevation than any known locality of the latter.
Fig. 280. *B. (Metromenus) insociabilis*. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view. D. Female bursa copulatrix, ventral view, showing rounded dorsal pouch with lateral extensions, medial band of spikelike bursal microtrichia, and spermatheca.

*Blackburnia (Metromenus) insociabilis* (Blackburn), new combination
(Figs. 277, 278B, 280)

*Anchomenus insociabilis* Blackburn, 1878a: 121.

*Metromenus insociabilis*: Blackburn & Sharp, 1885: 211.

*Atelothrus insociabilis*: Sharp, 1903: 220.

*Atelothrus stenopus* Sharp, 1903: 218 (new synonymy).

DIAGNOSIS. Very similar to *B. kauwa* (Figs. 273B, 278B), with basally setose pronotum with narrow lateral marginal depressions and slightly sinuate basolateral pronotal margins,
dark shiny piceous body contrasted with brunneous legs and antennae, and emarginate metatarsomere 4. But, diagnosed by: 1, vertex shiny, isodiametric microsculpture reduced; 2, pronotal disc with transverse mesh microsculpture obscured by shininess of cuticular surface; 3, elytral intervals shiny, transversely stretched sculpticells visible only close to elytral striae, middle of intervals shiny, with few micropunctures the diameter of sculpticells; and 4, pronotal laterobasal bead complete, traceable medially. Standardized body length 7.2-7.5 mm.

Pterothorax. Metepisternum short, broad, lateral margin 1.3× length of anterior margin.

Male genitalia. Aedeagal median lobe gracile, straight to slightly curved medioventrally, ventral excavation extended to short apex with rounded tip extended 1.2× thickness of apex at opening of internal sac (Fig. 280A); basal sagittal crest short, narrow; median lobe of even width in basal ⅔, slightly constricted on right side, tapered to a finely rounded tip (Fig. 280B).

Female reproductive tract. Gonocoxa basally broad, triangular gonocoxite 2 with acuminate apex (Fig. 280C); gonocoxite 1 with apical fringe of 11-12 setae, mesal 4-6 setae near medioapical angle in double series; gonocoxite 2 with 3 lateral ensiform setae and 1 dorsal ensiform seta; apical nematiform setae short, 0.29× length of gonocoxite 2; bursa copulatrix symmetrical, subequal to length of common oviduct, with a rounded dorsal pouch with lateral extensions of lightly sclerotized membrane (Fig. 280D), and a medial band of spikelike microtrichia; spermatheca elongate, 1.1× length of spermathecal duct, without basal lobe.

Variation. Of three specimens examined for pronotal setae, two possessed both basal pronotal setae, and the third specimen had one basal seta present unilaterally.

Lectotypes. For Anchomenus insociabilis, lectotype ♂ on card with 3 parallel lines, the top thickest, and perpendicular inked slash—Blackburn’s Maui code (Zimmerman 1957)—and “insociabilis” handwritten on reverse (BMNH) hereby designated. For Atelothrus stenopus, lectotype ♂ labeled “♂ Atelothrus stenopus Type D.S. Haleakala 4000 ft. V.1895. Perkins.” (BMNH) hereby designated.

Distribution. This species has been rarely collected from isolated localities across the windward forest of Haleakala, East Maui (Fig. 277).

Localities. Collected only by Blackburn, Perkins, and Gagné. The nineteenth-century collections were near Olinda and Waikamoi Gulch; 900 to 1200-m elevation. W.C. Gagné collected one specimen at Charlie Camp, 1425 m elevation, in Kipahulu Valley (BPBM).

Habits. The Kipahulu specimen was collected from a mossy tree trunk at night.

Phylogenetic relationships. This species is the adelphotaxon of the species pair B. fraudator of Molokai and B. filipes of Lanai (Fig. 9).
Fig. 281. *B. (Metromenus) fraudator*. A. Male aedeagal median lobe, right lateral view. B. Male aedeagal median lobe, euventral view. C. Left female gonocoxa, ventral view. D. Female bursa copulatrix, ventral view, showing rounded dorsal pouch, medial band of spikelike bursal microtrichia, and spermatheca.

Piceous dorsal and ventral body surfaces. Tarsomere 4 is emarginate as in *B. hakeakapa*, the preceding 3 species, and *B. filipes* of Lanai, with outer lobe of fourth metatarsomere 0.4× median basal tarsomere length. Tarsomeres 1-3 have broad, deep inner and outer dorsolateral sulci, the median portion of tarsomere distinctly defined by sulci. Standardized body length 5.9-7.3 mm.
**Pterothorax.** Metepisternum short, broad, lateral margin 1.2 to 1.6× length of anterior margin.

**Male genitalia.** Aedeagal median lobe gracile, with broad medioventral expansion, ventral excavation extended to short, straight apex with rounded tip extended 1.0× thickness of apex at opening of internal sac (Fig. 281A); basal sagittal crest short, narrow to absent; median lobe basally broad, slightly constricted on right side, tapered to a finely rounded tip (Fig. 281B).

**Female reproductive tract.** Gonocoxa basally broad, triangular gonocoxite 2 with acuminate apex (Fig. 281C); gonocoxite 1 with apical fringe of 11 setae, mesal 4 setae near medioapical angle in double series; gonocoxite 2 with 3-4 lateral ensiform setae and 1 dorsal ensiform seta; apical nematiform setae short, 0.26× length of gonocoxite 2; bursa copulatrix symmetrical, subequal to length of common oviduct, with a rounded dorsal pouch lined with sclerotized membrane, and with irregular extensions of lightly sclerotized membrane (Fig. 281D); bursa with medial band of spikelike microtrichia; spermatheca ovoid, 0.6× length of spermathecal duct, without basal lobe.

**Variation.** The basal pronotal setae are absent from most specimens of this species. Of 85 specimens inspected for these setae, including specimens from the 1890s to the 1990s, 77 have glabrous pronota, 5 have both basal setae present, and 3 have one unilateral seta.

**Lectotype♀ labeled “Molokai Mts. 4000 ft. Perkins. VI.1896.” (BMNH) hereby designated.**

**Distribution.** This species is known only from the mountains of Molokai west of Kamakou (Fig. 282).

**Localities.** Apparently broadly distributed on Kamakou volcano, Molokai, including Waikolu Valley, Wailau Valley, Waiaakuilani Gulch, and TNCH Kamakou Preserve. Within the Preserve it has been found at Hanalilolilo, Pepeopae Bog including Puu Alii Bog trailhead at Pelekunu overlook, West and East Forks of Kawela Gulch, and Puu Kolekole.

**Habits.** This species seems equally at home in arboreal or terrestrial situations. Adults climb at night on *Cibotium, Pipturus*, ohia, and low ferns. They have been seen running on trails, boardwalks, or open stream banks, in the company of *B. consticta* or *B. vagans*.

**Phylogenetic relationships.** This species is geographically isolated from its adelphotaxon, *B. filipes* of Lanai (Fig. 9).
Blackburnia (Metromenus) filipes (Sharp), new combination
(Figs. 278D, 283, 284)

Atelothrus filipes Sharp, 1903: 218.

DIAGNOSIS. Shiniest of the four shiny, picaceous species; B. kauwa, B. insociabilis, and B. fraudator have some visible microsculpture on vertex, but this species lacks any microsculpture on the vertex, only micropunctures the size of sculpticells visible. This species is also diagnosed by the small, narrow pronotum (Fig. 278D), maximum width 1.2× head width across eyes (other species have ratios ranging from 1.25 to 1.30); infuscated legs, not greatly contrasted with picaceous venter (as in B. insociabilis); and generally smaller size: standardized body length 6.1-6.8 mm.

Pterothorax. Metepisternum short, broad, trapezoidal, lateral margin 1.4 to 1.5× length of anterior margin.

Male genitalia. Aedeagal median lobe gracile, with broad medioventral expansion, ventral excavation extended to short, evenly downturned apex with rounded tip extended 1.33× thickness of apex at opening of internal sac (Fig. 283A); basal sagittal crest various, long and broad to short and narrow; median lobe moderately broad basally, slightly constricted at midlength, tapered to a finely rounded tip (Fig. 283B).

Female reproductive tract. Gonocoxa basally broad, triangular gonocoxite 2 with acuminated apex (Fig. 283C); gonocoxite 1 with apical fringe of 9-11 setae, mesal 4 setae near medioapical angle in double series; gonocoxite 2 with 3 lateral ensiform setae and 1 dorsal ensiform seta; apical nematiform setae short, 0.29× length of gonocoxite 2; bursa
copulatrix symmetrical, subequal to length of common oviduct, with a rounded dorsal pouch, with detached lateral extensions of lightly sclerotized membrane; bursa with medial band of spikelike microtrichia; spermatheca elongate, $1.0 \times$ length of spermathecal duct, without basal lobe.

**Lectotype** $\sigma$ labeled "$\sigma$ Atelothrus filipes. Type D.S. Lanai, 2000 ft. Perkins. I.1894." (BMNH) hereby designated.

**Distribution.** This species is restricted to Lanaihale on the island of Lanai (Fig. 284).

**Localities.** Distributed throughout the higher elevations of Lanai, including Lanaihale, Haalepaakai, and Waiakeakua. Recorded localities span 600 to 1020 m elevation.

**Habits.** All collection records involve arboreal habitats, with adult beetles from native vegetation, e.g., *Metrosideros* (ohia lehua), or in one case, *Araucaria* (Norfolk Island Pine).

**Phylogenetic relationships.** This species is the adelphotaxon of *B. fraudator* of Molokai (Fig. 9).

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My heart’s in the highlands at the break of day,
over the hills and far away.
There’s a way to get there,
and I’ll figure it out somehow.
But, I’m already there in my mind,
and that’s good enough for now . . . (Dylan 1997)
ADVENTIVE SPECIES

As of this writing there have been adventive introductions of three exotic platynine carabid species to the Hawaiian Islands. We present a local diagnosis to distinguish these species from the native Hawaiian Platynini, as well as a general diagnosis that permits identification of these species in the context of their natural relatives. It is our hope that further introductions of exotic insects do not occur; however, the eventualty of such invasions seems unavoidable given the pace of world commerce. As such, the local diagnosis should be used as a first level of identification, and the general diagnosis used to ascertain that the specimen in question actually represents one of the known invaders. Should a specimen not match the general diagnosis, the references cited for species-level synonymy should be consulted for positive species identification. Of course, other platynine genera may become established, so regional works dealing with possible source areas should ultimately be examined until ambiguity is removed from the identification (e.g., Darlington [1952] for New Guinea and adjacent islands, Lindroth [1966] for North America, Habu [1978] for Japan).

Tribe Platynini
Subtribe Sphodrina

Laemostenus (Laemostenus) complanatus (Dejean)
(Figs. 15A, D, 285A, 286)
For synonymy see Casale (1988).

LOCAL DIAGNOSIS. A large, shiny, piceous beetle with slight metallic blue reflection on the medially flattened elytra (Fig. 285A), the elytral intervals covered with isodiametric sculpticells arranged in irregular longitudinal rows; pronotum with both lateral and basolateral setae; flight wings fully developed; tarsomeres with dorsal pelage of fine, long setae; each tarsal claw with 3-4 fine serrate teeth on internal margin. Standardized body length 12.5-16.0 mm.

GENERAL DIAGNOSIS. The subgenus Laemostenus is diagnosed by: 1, eyes convex; 2, elytra subtruncate, basal elytral carina not markedly curved; 3, flight wings fully developed; 4, abdominal sternites smooth or slightly wrinkled, without accessory setae; 5, metatibia sparsely setose mesally, with patch of fine setae near apex; 6, mesotibia straight; 7, metatarsomeres smooth dorsally, though with pelage of setae; 8, tarsal claws serrate; and 9, body coloration dark, piceous, with bluish reflection on elytra. Within the subgenus, L. complanatus is the only macropterous species with medially flattened elytra and indistinctly punctate elytral striae.

Colonization history. Zimmerman (1972) reported the first Hawaiian specimen of this species to be one collected by Thomsen on Hawaii Island during 1950. Comprehensive surveys of museum holdings show that this specimen is indeed the oldest Hawaiian record, suggesting that L. complanatus probably was introduced to Hawaii Island sometime during the 1940s. The initial record was from Kipuka Puaulu, or Bird Park, a kipuka along the Mauna Loa Road at 1500 m elevation. In 1956 Gressitt found it along the Saddle Road (BPBM). A 1959 record adds Kilauea Military Camp (BPBM), and by 1961 it was found
Fig. 285. Adventive species habitus, dorsal view. A. *Laemostenus (Laemostenus) complanatus*. B. *Calathus ruficollis ruficollis*. C. *Metacolpodes buchanani*.
in Kilauea to the west at 1200 m elevation (BPBM). By 1964 it had reached Waimea, north near the Kohala Mountains (BPBM). Subsequent records to the present day implicate localities within the confines of the above points. It has occupied habitats from 1150 to 2000 m elevation. It has not yet been recorded from Hualalai volcano, though habitats there can reasonably be expected to support this species.

**Distribution.** Currently found on Kilauea, eastern Mauna Loa, Mauna Kea, and the southward slopes of the Kohala Mountains (Fig. 286). The single recorded collection from another island is from Aiea Ridge, Oahu, August 1959 (Slifer, BPBM).
**Habits.** Specimens of this species are most often encountered under loose bark of upright
trees or snags, or under downed logs or rocks. Associated tree species include *Acacia koa,*
*Metrosideros polymorpha* (ohia lehua), and *Sapindus saponaria* L. (Soapberry). Ground-
level records include capture in pitfall traps, under basal rosettes of mullein, *Verbascum thapsus* L.,
or under rocks. It thrives in non-native forests or disturbed situations along forest edges. Of the native platynine fauna, its habitat preference is most similar to that of
*B. incendiaria,* as that species has also been found under rocks in the saddle region of
Hawaii, as well as in association with mullein plants. A study of the competitive
interactions between these two species seems in order. In addition, *L. complanatus* has been
found in closed-canopy tropical ash—*Fraxinus uhdei* (Wenzig)—forest adjacent to native
koa-ohia (*Acacia-Metrosideros*) forest in Laupahoehoe Natural Area Reserve. The ability
of this species to colonize and procreate in native forest needs to be examined.

*Calathus (Neocalathus) ruficollis ruficollis* Dejean
(Figs. 15B, E, 285B)

For synonymy see Ball & Negre (1972).

**LOCAL DIAGNOSIS.** Pronotum quadrate with broad base, depressed anterolateral angles,
both lateral and basolateral setae present; prosternal process with distinct carina encircling
posteroventral margin (Fig. 285B); tarsal claws with 5 distinct pectins along internal
margin; body coloration flavous to brunneous, dorsal body surface, including vertex of
head, pronotum, and elytra, covered with granulate isodiametric microsculpture.
Standardized body length 8.2-9.5 mm in Oahu specimens.

**GENERAL DIAGNOSIS.** Among members of the Nearctic subgenus *Neocalathus* Ball &
Negre, *C. ruficollis* is characterized by: 1, prosternal process margined (Fig. 15B); 2, 3
mesofemoral anteroventral setae; and 3, 3 dorsal elytral setae associated with the third
eytral interval (Ball & Negre 1972). Among the World *Calathus* fauna, species of
subgenus *Neocalathus* are characterized by: 1, bifid mentum tooth; 2, presence of scutellar
setae; 3, presence of dorsal elytral setae; 4, margined prosternal process; and 5, protarsal
dorsally smooth in both sexes, with protarsomeres 1-3 dilated in the male (Lindroth 1956).

**Colonization history.** The earliest labeled specimen from Hawaii for this species is from
Waikiki, 1928 (NMNH). Undated Honolulu specimens (NMNH) were also collected by
J.C. Bridwell, most likely between 1914 and 1919, the years of his collections of other
Hawaiian Platynini. The only subsequent record—1982, UV light trap, Hickam Field
(Preston, BPBM)—suggests that this species has not appreciably expanded its range outside
the drier lee coastal habitats of Oahu.

The attributes of the Oahu specimens suggest that this species was introduced from
southern California. Ball & Negre (1972) quantified the variation among populations of this
species across its native range. The species occurs along the North American Pacific Coast
from Puget Sound south to Baja California Norte and Guadalupe Island, exhibiting
substantial morphological variation associated with geography. Based on the presence of
3 mesofemoral setae, broad and flat laterobasal portions of the pronotum, granulate pronotal
microsculpture, rufous body color, apically hooked right paramere, and body length (7.4-
8.6 mm, using the conventions of Ball & Negre), the Oahu specimens are most similar to
those from the San Diego, and Maneandero, Mexico, population samples that were assigned
to the subspecies *ruficollis*. Areas of the native range excluded as likely source areas include the Bay Area and North Coast of California and areas to the north, as well as the Channel Islands of California.

The occurrence of fully developed flight wings in the Hawaiian specimen collected at UV light also points to San Diego as the source of the population. Individuals of *C. ruficollis* are nearly all brachypterous, with only 1% of the total specimens possessing fully developed flight wings. Many population samples are composed strictly of brachypterous specimens. Conversely, El Segundo and San Diego samples each contained 3 macropterous individuals among the 60 specimens from each locality. Of the seven Hawaiian specimens, only the one trapped at Hickam Field is macropterous, suggesting that the originating population source of the Hawaiian invasion should include the recessive gene for macroptery (Aukema 1995).

**Distribution.** Apparently restricted to Pearl Harbor and Honolulu.

**Habits.** The single Hawaiian specimen with ecological data was collected by D. Preston in an ultraviolet light trap. On the North American mainland, this species is common in oak woodlands, but has also been recorded from near the seashore among *Artemesia* and other xerophytic vegetation (Lindroth 1966). *Calathus* species are known to overwinter as larvae, not adults as per usual in most carabids.

**Subtribe Platynina**

*Metacolpodes buchanani* (Hope)

(Figs. 12A-B, 285C)

For synonymy see Habu (1978).


**LOCAL DIAGNOSIS.** Among the Hawaiian fauna, this macropterous species with the brilliant metallic green elytra, shiny rufous, quadrisetose pronotum, and rufous head with protruded compound eyes cannot be easily mistaken (Fig. 285C). Also, unlike native Platynini, this species exhibits denticulate sutural apices on the elytra. Standardized body length 11.0-13.2 mm.

**GENERAL DIAGNOSIS.** *Metacolpodes* Jeannel is a generic entity within the large, inadequately understood complex of tropical Platynini allied to *Platynus* Bonelli. Jeannel (1948) distinguished it by: 1, denticulate elytral sutural apex; 2, meso- and metatarsomere 1 with dorsolateral sulci; 3, tarsomere 5 appearing glabrous ventrally; and 4, prosternal process not bordered posteroventrally. Habu (1978) distinguishes it from other congeners by the metallic green elytra, and dark femoral apices (i.e., “knees”) contrasted with the rufous basal 9/10 of the segment.

**Colonization history.** This species was first observed in the Hawaiian Islands by F.G. Howarth, who collected it in Kalihi Valley, Oahu, in April 1991 (BPBM). By 1992, it had been collected in Oahu’s Halawa Valley (Preston, BPBM), and at Lihue, Kauai (HDAC). By 1993 it had expanded its range on Kauai upward to 1100 m elevation at Puu ka Pele (Jamieson 1999), and in 1995, JKL encountered it on the summit of Puu Kaua, Waianae Mountains, Oahu, and on Kauai’s Mt. Kahili and Waialae Cabin, the latter site well into the mountains to the east of Waimea Canyon (CUIC). In 1997 it was found on Molokai.
(Waikolu Valley near the seashore; Englund, CUIC) and Hawaii Island (forest at 800 m elevation above Kailua-Kona; Polhemus, CUIC). A single specimen was found in 1999 at 1150 m elevation on Kaumakani, East Maui (Polhemus, NMNH), a peak on the south rim of Waihoi Valley above Hana. So, in little more than eight years this species has colonized all of the high Hawaiian Islands. The means to do this may have been passive transport as air cargo rather than active flight. First records on Kauai (Lihue, UV light), Molokai (Waikolu Valley, 0 m elevation), East Maui (Kaumakani), and Hawaii Island (Kaloko Drive, 800 m) are situated 2.5, 6.5, 11, and 10 km, respectively, from an interisland airport. Introduction of this species by commercial air traffic would best explain this pattern of first occurrences.

**Distribution.** The current distribution includes the high islands of Kauai, Oahu, Molokai, Maui, and Hawaii. It has been found between sea level and 1180 m elevation, the upper elevational limit at Waialae Cabin, Kauai.

**Habits.** Four of the 11 collections of this species in Hawaii have been at lights or in light traps. Individuals have been beaten from a variety of vegetation during day or night, including ohia lehua (*Metrosideros polymorpha*), *Cibotium* tree fern, and low ferns. One individual was even found under the groundcloth of JKL’s tent perched on a knifelike ridge of Mt. Kahili, Kauai, at 900 m elevation.

In Sulawesi, *M. buchanani* was also collected mostly by light trapping and beating vegetation (Paarmann & Bolte 1990). Subsequent laboratory studies showed that adult beetles preferred to hide on foliage off the ground, especially when they were teneral or not reproducing. Female beetles produced an average of 660 eggs over an average lifespan of 204 days. During the reproductive period of these beetles, females were found, on average, closer to the ground, suggesting their preference for terrestrial oviposition (Paarmann & Paarmann 1997). All this points to the potential for this species to seriously compete with the native Hawaiian platynines. During rearing of larvae for 25 different species of the native fauna (Liebherr, in press), no species has approached the levels of fecundity shown by *M. buchanani*. If this exotic tramp can live and reproduce in arboreal situations, as do many of the native species, *M. buchanani* larvae could coexist, and potentially prey upon native carabid larvae, especially if the invaders grow larger either faster or earlier than syntopic native species. However, should *M. buchanani* larvae be restricted to ground-level microhabitats, they might be subject to the same mortality factors that have reduced other ground-restricted species—e.g., *B. insignis* and *B. b sleptoides* of Oahu—to extremely low population densities or extinction.

**Nomenclatural note.** This species was described by Hope (1831) in MacLeay’s genus *Colpodes*. It remained associated with this name until Jeannel (1948) made it the type species of his *Metacolpodes*, noting affinity to *Loxocrepis* Eschscholtz. However, in the same work Jeannel misidentified the type species of *Colpodes*—*C. brunneus* MacLeay—considering it little different from Holarctic *Agonum* Bonelli (Liebherr 1998). Thirty years later, Habu (1978) compounded this mistake by recombining *Metacolpodes* as a subgenus of *Agonum*. In fact, *Metacolpodes* is not closely related to *Agonum*. Based on presence of a dorsal depression on the head, cordate pronotum, and female spermatheca with short, narrow duct, members of *Metacolpodes*—see Habu (1978)—are more closely related to species of the widespread genus *Platynus* (Liebherr 1998). However, we are not prepared to state to what lineage within the widespread *Platynus* complex *M. buchanani* bears greatest affinity. Therefore, we have made the conservative decision to use Jeannel’s
combination, as his type designation for *Metacolpodes* forever ties together the two names in combination at some taxonomic level. Thus the issue of *M. buchanani*’s relationships, and how to codify those nomenclaturally are left to future study.

Habu (1978) interpreted the original species spelling, *buchannani*, as a *lapsus calami*, interpreting the unjustified emendation *buchanani* first introduced by Chaudoir (1859) as a corrected spelling. Under the former code of zoological nomenclature (I.C.Z.N. 1985, articles 32d, 33b), such an action would have been rejected, with the original spelling retained (e.g., Liebherr & Zimmerman 1998), as Hope (1831) used only the former spelling, and did not correct it in a corrigendum following the main body of the article. The current code (I.C.Z.N. 1999, article 33.3.1) allows “prevailing usage” to overturn criteria of original spelling and unjustified emendation. This shift to preserve stability of names over priority requires us to reverse our position and use the unjustified emendation of Chaudoir (1859), subsequently justified by consistently incorrect usage.
ACKNOWLEDGMENTS

This revision has had a long history, starting with the junior author’s studies several years before the senior author was born (Zimmerman 1948). The junior author’s early activities benefited greatly from the support of the Hawaiian Sugar Planters’ Association and the Bernice P. Bishop Museum, the courtesy of the British Museum of Natural History (now The Natural History Museum, London), and advice and information from R.C.L. Perkins. The senior author began participation in this project during a sabbatic leave from Cornell University spent in Hawaii, spring 1991. Beginning then, museum studies supported by Bishop Museum were coupled with a concerted field survey of these beetles. At that time the junior author passed along his working manuscript and specimens, thereby furthering development of the project. As final species decisions were made by the senior author, the junior author has insisted that species authorship be restricted, though in any case, species circumscriptions have required concerted and sequential study of type specimens.

The senior author thanks G. Allan Samuelson, Scott E. Miller, Gordon M. Nishida, Dan A. Polhemus, and Neal L. Evenhuis for access to the Bishop Museum collections, library, and archives, and for sustained life support while in Honolulu. Modern field survey of Hawaiian carabids would not have been possible without the assistance and permission of numerous individuals, institutions, and agencies. These include, in alphabetical order, Castle and Cooke Co., Cherry Helicopters, East Maui Irrigation, Ltd., Haleakala National Park, Hawaii Natural Areas Reserve Commission, Hawaii Volcanoes National Park, Interisland Helicopters, Kahua Ranch, Kokee Natural History Museum, McBryde Sugar Co., Pacific Helicopter Tours, Palani Ranch, Puu Kukui Watershed and West Maui Land and Pineapple Co., State of Hawaii Department of Land and Natural Resources, The Nature Conservancy of Hawaii, TNCH Kamakou Preserve, TNCH Waikamoi Preserve, United States Army, U.S. Fish and Wildlife Service, Windward Aviation. We thank those who were willing to work hard in the field to find carabid beetles in both rain and shine, night and day: Adam Asquith, Curtis Ewing, Rosie Gillespie, Dan Gruner, Betsy Harrison-Gagné, Sabina Jessel, Dave Kavanaugh, Art Medeiros, Dan Polhemus, Raina Takumi, and Catherine and Maurice Tauber. Dan Otte kindly provided his stipple maps of the Hawaiian Islands as the template for the distribution maps. Essential laboratory assistance was provided by Zachary H. Falin, Chris J. Marshall, Michael J. McDonald, José L. Santisteban, Teresa Wells, and Kipling W. Will. We thank Dr. Will for sharing his taxonomic knowledge of *Abaris* spp. and *Notonomus peronii*, proving there is indeed nothing new under the sun. Curtis P. Ewing drew genitalia and pronota, and P. V. York took the photographs of the British Museum types. The manuscript benefited greatly from the critical editorial reviews of George E. Ball, Dan Polhemus, and an anonymous referee.

Field surveys during the 1990s were graciously supported by The National Geographic Society. The National Science Foundation is gratefully acknowledged for its continuing funding of this project (DEB-9208269, DEB-9806349). The American Philosophical Society provided travel funds for museum research at The Natural History Museum, London, and The Hope Museum, Oxford University. The Grace Griswold Fund of the Department of Entomology, Cornell University, provided funds to support publication costs. Nonetheless, this publication would not have been completed without the financial support of Hildegard E. Liebherr.

Contribution No. 2000-004 to the Hawaii Biological Survey.
BIBLIOGRAPHY

Anonymous

Armstrong, R. W. (ed.)

Asquith, A.

Aukema, B.

Ball, G. E., & G. J. Hilchie

Ball, G. E., & J. Negre

Basilewsky, P.

Blackburn, T.


1878b Characters of new genera and descriptions of new species of Geodephaga from the Hawaiian Islands. II. Entomol. Mon. Mag. 15: 156-158.


Blackburn, T., & D. Sharp
Bridwell, J. C.  

Britton, E. B.  

Carson, H. L., & D. A. Clague  

Casale, A.  

Chauoir, M. l. b. d.  

Clague, D. A.  

Clague, D. A., & G. B. Dalrymple  

Coultier, J. W.  

Cuddihy, L. W., & C. P. Stone  

Darlington, P. J., Jr.  

Davis, C. J., & G. D. Butler, Jr.  

Deuve, T.  

Dylan, B.

Emden, F. I. van

Erichson, W.

Farris, J. S.

Fullaway, D. T.

Gagné, W. C.
1979 Canopy-associated arthropods in Acacia koa and Metrosideros tree communities along an altitudinal transect on Hawaii Island. Pac. Ins. 21: 56-82.


Gagné, W. C., & L. W. Cuddihy

Gidaspow, T.

Goloboff, P. A.

Habu, A.

Hobdy, R.

Hope, F. W.

Howarth, F. G.


I. C. Z. N.

Jamieson, D. W.

Jeannel, R.

Karsch, F.

Kennedy, M. J., O. A. Chadwick, P. M. Vitousek, L. A. Derry, & D. M. Hendricks

Kirch, P. V.

Knudsen, V.

Langenheim, V. A. M., & D. A. Clague

Lea, A. M.

Liebherr, J. K.
in press The unity of characters: ecological and morphological specialization in larvae of Hawaiian platynine Carabidae (Coleoptera). Invertebr. Taxon.


Liebherr, J. K., & D. A. Polhemus 1997b Comparisons to the century before: the legacy of R. C. L. Perkins and Fauna Hawaiensis as the basis for a long-term ecological monitoring program. Pac. Sci. 51: 490-504.


Lorenz, W. 1998a Systematic list of the extant ground beetles of the world (Insecta, Coleoptera "Geadephaga": Trachypachidae and Carabidae incl. Paussinae, Cicindelinae, Rhysodinae). Published by the author, Tutzing, Germany.

1998b Nomina Carabidarum, a directory of the scientific names of ground beetles (Insecta, Coleoptera "Geadephaga": Trachypachidae and Carabidae incl. Paussinae, Cicindelinae, Rhysodinae). Published by the author, Tutzing, Germany.
Manning, A.  

Merwin, W. S.  

Meyen, F. J. F.  

Moore, J. G.  


Munro, G. C.  

Nixon, K. C.  

Paarmann, W., & H. Bolte  

Paarmann, W., & D. Paarmann  

Page, R. D. M.  
Pemberton, C. E.

Perkins, R. C. L.
1892 Notes on collecting, Oahu, 1892, p. 13. Bishop Museum archives, Ms. SC Perkins, Box 1.
1894a Diary . . . first visit to Maui [Foreword + 6 Mar to 12 May], p. 20. Bishop Museum archives, Ms. SC Perkins, Box 1.
1894b Kauai, 1894, p. 3. Bishop Museum archives, Ms. SC Perkins, Box 1.2.
1895a Kauai 1895, p. 5. Bishop Museum archives, Ms. SC Perkins, Box 1.2.
1896a *Waianae Mountains*, Oahu.—February 1896, p. 1. Bishop Museum archives, Ms. SC Perkins, Box 1.11.
1896b *West Maui and Haleakala in V 96*, p. 2. Bishop Museum archives Ms. SC Perkins, Box 1.11.
1896c Molokai—June 1896. Bishop Museum archives, Ms. SC Perkins, Box 1.11.
1896d Kauai—July & August 1896., p. 2. Bishop Museum archives, Ms. SC Perkins, Box 1.11.
1896e Kau & Puna VIII & IX-96 (partly in each month). Bishop Museum archives, Ms. SC Perkins, Box 1.11.
1897 January 1897 & February '97. Bishop Museum archives, Ms. SC Perkins, Box 1.11.

Pratt, L. W., & S. M. Gon III

Price, S.
Pukui, M. K., S. H. Elbert, & E. T. Mookini

Ratzeburg, J. T. C.

Samuelson, G. A., J. K. Liebherr, & K. W. Will

Scott, H.

Semenov, A.

Sharp, D.
1885 Topographical table of Hawaiian Coleoptera, with summary, generalizations, and comments, pp. 263-300. In: Memoirs on the Coleoptera of the Hawaiian Islands (see Blackburn & Sharp 1885).
1892a Letter to Mr. Perkins, Hills Road, Cambridge, July 15th, Bishop Museum archives, Ms. Grp. 141, Box 2.
1900 Letter to Mr. Perkins, University Museum of Zoology, Cambridge, Novr. 5th. Bishop Museum archives, Ms. Grp. 141, Box 2.

Sloane, T. G.

Southwood, T. R. E.

Stearns, H. T.

Stork, N. E.
Swezey, O. H.

Swezey, O. H., & D. T. Fullaway

Taiti, S., & F. G. Howarth

Thompson, R. G.

Timberlake, P. H.

Twain, M. (S. L. Clemens)

Usinger, R. L., & E. C. Zimmerman

Vitousek, P. M., O. A. Chadwick, T. E. Crews, J. H. Fownes, D. M. Hendricks, & D. Herbert

Wagner, W. L., D. R. Herbst, & S. H. Sohmer

Walker, J. J.

Weber, P. W.

Whitehead, D. R.
1973 Annotated key to Platynus, including Mexasphodrus and most "Colpodes," so far described from North America including Mexico (Coleoptera: Carabidae: Agonini). Quaest. Entomol. 9: 173-217.

Williams, F. X.
Wilson, E. O.

Zimmerman, E. C.
Data used as the basis for this revision are available in CD-R format from the senior author (JKL5@Cornell.edu). Six files are included, two comprising specimen-based information, three of cladistic character data, and a sixth text file that presents synonymical information for all generic and specific names now placed in *Blackburnia* Sharp, 1878.

**Specimen-based information.** Throughout the development of this revision, specimen data were recorded in a Paradox file with a flat structure: filename hawaplat.db. The flat file format was deemed the most conservative means to associate data as it was developed and incorporated, though more efficient structures can be developed from it for specialized searches and uses. We present the original data file with the intention of having all data in one file, permitting users to modify copies of the file for their own uses. As such, these data can be downloaded from the disk and used with the same etiquette as other published data in the scientific literature. We take no responsibility for any modifications to these data that might occur after an end-user copies them to another format. We also provide this information in dBase IV format: hawaplat.dbf.

Data fields included were intended to assist the authors in specific tasks, and their structure may not be optimal for other uses. These fields include:

- **Taxon name.** Four fields define the taxon names in the same configuration as is presented in this revision: genus, subgenus, species epithet, and author. The author field includes multiple describers if appropriate, as well as parenthesized names if the current combination differs from the original combination. Within this set of species, species epithets uniquely identify biological entities, so we use the species epithet field as a common field linking a taxon database to a geographic database comprising the fields below.

- **R. C. L. Perkins Lot No.** Lot numbers were initially recorded for specimens we could attribute to Perkins’ collecting efforts, and for which lot numbers were written on the undersurface of the mounting cards (Anonymous n.d., Liebherr & Polhemus 1997a). We then sorted specimens based on label information, and in consultation with Perkins’ diaries (Manning 1986), coalesced specimens into series consistent with published information. This added information allows Perkins’ specimens to be sorted by locality or date. Nonetheless, we did not add lot numbers to the entries for these specimens, as these numbers were not on the labels. Specimens with lot numbers in the database thus are those in the various collections that actually bear these numbers on the undersides of the cards.

- **Collector.** Only last names of collectors are included, unless two with the same name occur—e.g., J. T. Polhemus and D. A. Polhemus—and then the less commonly occurring name includes initials. For multiple collector lots, names were concatenated using “/”.

- **Specimen number.** This database is **NOT** a specimen-based instrument. We feel such detail is redundant, as each specimen we examined bears a determination label with dates of determination ranging from 1996 to 1999. Moreover, decisions made by us on species membership are not enhanced by having each specimen individually identifiable in a database. Should future taxonomists disagree with our species assignments, they may affix their determination label to the specimen in question, publish the corrections, and change this database to reflect those corrections. Therefore, we use the series as the individual unit in this database. Specimen number reflects the number of specimens in each series deposited within individual institutions. This structure retains the ability to view species abundance
data in the context of other variables, or to assemble the data for original series by ignoring
the information on institution deposition.

*Island and Volcano.* These two fields are distinguished, because most of the islands
contain uplands that comprise the flanks of distinct volcanoes—Waianae versus Koolau, Puu
Kukui versus Haleakala, and the four mature volcanoes of Hawaii—and we wished to be
able to sort species and specimens by these major orographic units.

*Localities.* Geographic locality information was coded in a hierarchical fashion, with
Primary Locality being the most general descriptor, Secondary Locality a specification of
the primary descriptor, Tertiary Locality a specification of the secondary level, and Distance
used as a field to relate distance and direction between a particular collecting locality and
some known point. All three levels were not required for all records, and so lower levels
may be blank. Localities are coded in regard to the historical context of collecting. For
example, specimens collected on Haleakala summit in the 1890s are simply listed as
“Haleakala,” whereas specimens collected there in recent times are listed as “Haleakala N.
P.” The purposes of the locality descriptors were: 1, to present label data for paratypes; and
2, to permit unambiguous assignment of latitude/longitude coordinates to localities. In many
records, lat/long values for differently coded localities may be identical, as these values do
not rely on historical context. If broadly defined Perkins’ localities—e.g., Haleakala, or
Molokai mountains, or Koholualamano—can be more specifically described based on date
information in conjunction with his diaries, the proposed more specific locality is indicated
in the Tertiary Locality field by preceding the name with the equals (=) sign.

*Latitude and Longitude.* We used latitude and longitude for two purposes: 1, mapping
geographic distributions of species or localities; and 2, presenting distributionally based
patterns of abundance, species richness, or collecting history. The first use requires that
localities be specific to the second, if possible. The second use requires that localities be
sortable at larger scales, such as on grid maps scaled to the minute or more. To
accommodate both uses we adopted a convention whereby latitude/longitude was recorded
as a continuous string, including degrees and minutes as metric units, and seconds as
decimal minutes. This convention permits truncation of the data field to allow sorting data
by minutes, as in grid cell analysis, or use of the entire string to place distributional points
on maps. Because we wanted to use the stipple maps provided by Dr. Dan Otte, as they
marvelously convey the topographic complexity of the islands in a way useful to
systematists, we wanted to relate the collection points to those maps in an easy fashion. This
can be most easily done by scaling grids onto scanned images of the maps, and positioning
locality symbols to the decimal minute. This has distinct advantages over mapping
programs, as high concentrations of locality points can be represented through judicious
hand plotting.

*Elevation.* Four fields—high and low elevation in feet and meters—are used to present
information on the elevation of collecting localities. We retained English feet as units, as
those were used by Perkins, and have useful connotations to field biologists who generally
speak of different montane life zones as 3000 ft., 4000 ft., 5000 ft., or timberline at about
6000 ft., etc. Moreover, English units are used on most U.S.G.S. topographic maps.
Elevations were bracketed by high and low values when lots were collected along an
elevational transect.

*Date.* Date, month, and year were recorded in separate fields, with ranges of days or
months accommodated by appropriately setting the field width.
Collection. The repository of specimens examined is included for future use by identifiers. Codes are presented in Table 5.

JKL Lot No. A unique number was assigned to each of the lots collected by the senior author. These lots identify each series using a number derived from the year, month, and date, plus a decimal lot number ranging from .01 to .99. In later years of the 1990s surveys, these unique numbers were placed on all specimen date-locality labels, permitting association of all specimens for all taxa collected in the same situation.

Perkins' material was also assigned lot numbers when the material could be associated by known lot numbers (Anonymous n.d.). For specimen labels reporting the month but not the date, the date field was reported as “00.” In a few instances where Perkins reported the lot from a particular year only, both month and date fields were coded “00.” Post-Perkins' material was also assigned lot numbers based on the date of collection and any further more specific information available such as collector, host, or elevation, but, as no other field notes were available to determine in what particular circumstances specimens were collected, these “lots” must be used with some caution.

We also include a Paradox database file—Perkins.db—that includes all the information included in Anonymous (n.d.). The fields were defined to reflect the format on the “Key to Numbers + Localities of Mr. Perkins’ Hawaiian Insects.” This information is also provided in dBase IV format: Perkins.dbf.

Cladistic character data. We include three files in Hennig86 format, directly usable for Nona (Goloboff 1995). Each file includes character data for the 129 species and 130 terminals analyzed cladistically (Fig. 9). Character numbers are presented in Liebherr & Zimmerman (1998). The first data file represents the observed cladistic data for all species included in this revision: filename hawaiian.ss. The shortest trees found using these data total 1081 steps. The second file includes Farris optimized values for missing male and female data for 11 of the 12 species lacking such data, assuming the preferred topology for the $B. aae + B. curtipes$ clade (see text): noblanks.ss. This file produces trees of 1083 steps. The third file is identical to noblanks.ss, but has a geographic distribution character added as character 207 (i.e., Kauai = 0, Oahu = 1, Maui Nui = 2, Hawaii = 3): file name noblgeog.ss. This character was not used in any tree-finding operations, but was used to evaluate the optimality of various of the multiple equally parsimonious cladograms with regard to assumptions of dispersal.

Synonymic checklist. This simple text file (synonymy.doc) includes the concatenated synonymies for all generic and species-level names applicable to *Blackburnia*. Species names follow the sequence in this treatment.
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Bold face indicates valid taxa revised in this volume and the inclusive pages for their taxonomic treatments.

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