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Author(s): James K. Liebherr
Source: Annals of Carnegie Museum, 77(1):31-78.
Published By: Carnegie Museum of Natural History
DOI: http://dx.doi.org/10.2992/0097-4463-77.1.31
URL: http://www.bioone.org/doi/full/10.2992/0097-4463-77.1.31

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ANNALS OF CARNEGIE MUSEUM

Vol. 77, Number 1, Pp. 31–78 20 July 2008

TAXONOMIC REVISION OF HAWAIIAN *BEMBIDION* LATREILLE (COLEOPTERA: CARABIDAE: BEMBIDIINI) WITH A DISCUSSION OF THEIR REDUCTIVE AND DERIVATIVE EVOLUTIONARY SPECIALIZATIONS

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ABSTRACT

The *Bembidion* fauna (Coleoptera: Carabidae: Bembidiini) of the Hawaiian Islands is taxonomically revised, entailing the recognition of 23 native, precinctive species, and one adventively introduced Old World species, *Bembidion niloticum* Dejean. Two species previously placed in *Gnatholymnaeum* Sharp—*G. blackburni* Sharp, 1903, and *G. spurcum* (Blackburn, 1881)—are formally placed as member taxa within *Bembidion* Latreille, with *Gnatholymnaeum* recognized at subgenus rank. This taxonomic placement establishes ***Bembidion blackburni* Csiki, 1928, as a junior secondary homonym,** and ***Bembidion ateradustum*, new name,** is proposed as a replacement. Twenty-one species are recognized as member taxa of *Bembidion* subgenus *Nesocidium* Sharp, five of which are newly described: ***Bembidion waialeale*, new species,** from Kauai; ***Bembidion paratomarium*, new species,** and ***Bembidion gagneorum*, new species,** from Oahu; ***Bembidion kamakou*, new species,** from Molokai; and ***Bembidion haleakalae*, new species,** from East Maui. ***Bembidion molokaiense* Sharp (new synonymy)** is treated as a junior synonym of *Bembidion ignicola* Blackburn, and ***Metrocidium brevicolle* Sharp (new synonymy)** is placed as a junior synonym of *Bembidion munroi* (Sharp). Taxonomic treatment includes a key to species, diagnoses and descriptions of the male genitalia and female reproductive tract for all species, and complete descriptions of external characters for newly described species. Length of the male aedeagal flagellum in subgenus *Nesocidium* species was found to be subequal in length, to 60-75% longer than the female spermathecal duct, consistent with previous reports that list emplacement of the male spermatophore within the female spermathecal duct as a primary function of the male flagellum. Geographical distribution varies in concert with dispersal ability. All species including at least some individuals with fully developed flight wings are distributed on multiple oceanic islands. Representative taxa within putative clades of vestigially winged species occupy adjacent oceanic islands, implying overwater dispersal by wingless ancestors of present-day species followed by speciation. Ecological preference conforms to the taxon cycle at the archipelago level, with the ancestor of Hawaiian *Bembidion* hypothesized to have inhabited coastal habitats. Present-day ecological specialists include a deep-soil inhabitant, and numerous species found predominantly in arboreal microhabitats such as mossy vertical tree trunks and horizontal nurse logs. Geographic distributions of the species define areas of endemism appropriate for conservation that are geographically congruent with areas defined by other carabid beetle taxa in *Blackburnia* Sharp and *Mecyclothorax* Sharp, as well as by taxa in other insect groups.

Key Words: biogeography, genitalic evolution, revisionary systematics, sexual selection

INTRODUCTION

The Hawaiian Islands support a carabid beetle fauna composed of three major radiations of native species, classified as members of the more cosmopolitan genera *Bembidion* Latreille (Bembidiini) and *Mecyclothorax* Sharp (Psydrini), as well as constituting all species in the Hawaiian precinctive genus *Blackburnia* Sharp (Platynini). Recent field work has focused on a comprehensive survey of Hawaiian natural areas in order to characterize the present state of many components of the resident insect fauna (Liebherr 2004), and also to taxonomically revise the native carabid beetles (Liebherr and Zimmerman 2000; Liebherr 2001, 2003, 2005, 2006a, 2007; Liebherr and Short 2006). The highly restricted geographic distributions of many Hawaiian carabid beetle species demonstrate that they can serve to identify natural areas of endemism (Nelson and Platnick 1981; Liebherr 2005). Established hypotheses of areas of endemism are extremely testable, as additional groups inhabiting the areas can be studied to determine whether their distributions are congruent. Congruent distributions of many taxa identify areas that support distinct biotas, and predict areas within which as yet unstudied or poorly studied precinctive taxa might reside.

This paper represents an updated taxonomic treatment of native Hawaiian *Bembidion* species, and is based on a substantially increased foundation of field-collected material. Previous treatments include Dr. David Sharp's (1903) major revision that constituted part of the *Fauna Hawaiiensis*. Sharp's revision was based on earlier specimens and taxonomic work conducted and fostered by the Rev. Canon Thomas Blackburn (Blackburn and Sharp 1885; Lea 1912), as well as a substantial amount of newly collected material from Dr. R. C. L. Perkins (Scott 1956; Manning 1986). Dr. E. B. Britton (1948) reexamined the Blackburn and Perkins material held in the Natural History Museum, London, and produced the first comprehensive key to species, including the first photographs published of the species. This work has served as an excellent means to identify Hawaiian *Bembidion* species—and Hawaiian species of several other genera—but recent surveys have uncovered several undescribed species, and also have expanded our knowledge of the geographic and ecological distributions of many previously described species. Thus it became clear that an updated taxonomic treatment was required that would better illustrate the biogeographic patterns and species-level diversity of this group. During this exercise, it was discovered that *Bembidion* (*Nesocidium*) species male and female adults exhibit an apparent evolutionary interdependence of sclerotized structures in their internal genitalia. The male flagellum, an elongate cuticular whip that extends from the central sclerite complex at the apex of the male aedeagal internal sac, and the female spermathecal duct are shown to be similar in length among conspecific beetles, though these structures covary greatly among the species. Evolutionary reduction, conversely, has been long recognized as a phenomenon characterizing Hawaiian *Bembidion* (Sharp 1903), as the vast majority of Hawaiian species exhibit vestigial metathoracic flight wings. Wing loss is evolutionarily associated with other reductive characters of the eyes, cuticular pigmentation, and setation. The associations between these reductive characters and biogeographic relictualism are also investigated for these beetle species. Finally, the conservation status of Hawaiian *Bembidion* is discussed in light of their relictualism and habitat preference. The possible extinction of species is directly related to these factors, connecting these minute insects to the technological forces of our civilization that adversely impact native biodiversity.

MATERIAL AND METHODS

Biological Material and Collecting Methods.—This revision was based on 1240 specimens; 572 borrowed from institutional collections and 668 collected from the field by the author or associated field-based colleagues. Institutions that lent specimens, with the coden used below and their curators noted, include: American Museum of Natural History (**AMNH**; Lee Herman), the Natural History Museum, London (**BMNH**; Roger Booth), Bernice P. Bishop Museum (**BPBM**; Al Samuelson, Shepherd Myers), Cornell University Insect Collection (**CUIC**), Field Museum of Natural History (**FMNH**; Alfred Newton, Margaret Thayer), Haleakala National Park (**HALE**; Raina Takumi Kaholoa`a), Hawaii Volcanoes National Park (**HAVO**; David Foote), Museum für Naturkunde, Humboldt Universität (**MNHU**; Bernd Jäger), National Museum of Natural History, Smithsonian Institution (**NMNH**; Terry Erwin), Santa Barbara Museum of Natural History (**SBNH**; Michael Caterino), University of California-Riverside (**UCRC**; Doug Yanega), University of Hawaii-Manoa (**UHEM**; Daniel Rubinoff), and University of Vermont (**UVMC**; Ross Bell). Specimens were also borrowed from Curtis Ewing (**CPEC**).

Specimens were field-collected during comprehensive surveys of Hawaiian insects. Terrestrial microhabitats were investigated by sifting leaf and ground litter and subsequent examination of the siftate, Berlese extraction, submersion of the siftate in still ponds of small creeks, and through use of a double-boiler. This latter method (Frank Howarth, pers. comm.) involves placement of siftate into a large pot which is placed in contact with boiling water in order to warm and dry the siftate. *Bembidion* beetles and larvae, as well as smaller soil inhabitants such as Acari, other insect larvae and adults are driven to the surface of the litter by the drying and warming, where they can be aspirated and preserved. Beetles were also collected by grubbing, a technique or dodge employed by R.C.L. Perkins, wherein a meter or so diameter circle of soil surface is scraped clear of leaves and litter, with the ensuing arena then examined for running beetles. *Bembidion* individuals were also collected from streamside riparian situations under rocks and in moss. More arboreal situations, such as mossmats adhering to tree trunks and branches, were sampled by beating over a sheet during both day and nighttime, and also by application of synthetic pyrethrin insecticide after placement of a sheet below the mossmat. Sheets were kept in place a minimum of 0.5 hr and up to 2 hr to catch insects exiting the moss. Specimens were variously collected into 70% ethanol, or preferably into ethyl acetate killing vials for storage of 12-24 hr, with subsequent preservation for transport in 70% ethanol. This latter sequence allows effective setting of legs and antennae for microscopic examination of ventral structures, and for photography.

Taxonomic Techniques.—Specimens were pointed or platen-mounted from alcohol, and labeled with associated locality data including latitude and longitude as degrees and decimal minutes. Habitus photographs were made on a transmissible light stage with auxiliary fiber optics lighting using a Microptics® photographic setup. Dissections of males and females were conducted after relaxing the specimens in near boiling water including a drop of Kodak Photo-Flo® wetting agent, dissection using minuten nadeln, and clearing overnight in cold 10% KOH. All dissections were neutralized in dilute acetic acid, and female reproductive tracts were stained in Kodak Chlorazol Black® stain dissolved in methyl cellosolve. All dissections were mounted temporarily in glycerin on microscope slides for examination and photography.

Beetle size was quantified using a standardized body length consisting of the sum of distances from: 1, the medioapical margin of the labrum to the cervical ridge of the head capsule posteriorly bordering the vertex; 2, the median length of the pronotum; and 3, the distance from the base of the scutellum to the apex of the left elytron. In practice, the body articulation of most species in the subgenus *Nesocidium* is tight enough so that a single measure from the median apex of the pronotum to elytral apex sufficed to quantify the latter two parameters. Eye development was quantified as the horizontal length of the compound eye measured in mm, and by the ocular ratio, being the ratio of the maximum width across the outer eye surface to the minimum distance between the eyes across the frons. All measurements were made with the aid of a calibrated ocular grid.

General terminology of the male aedeagus follows

Lindroth (1957), with Maddison (1993) followed for most structures of the internal sac. Other terms, such as ostium flag, were taken from Erwin and Kavanaugh (1981). The configuration of the brush sclerite and its associated sclerites conforms best to species in Lindroth's (1976) study of the New Zealand *Bembidion* fauna, especially the Australian *B. errans* Blackburn. Male dissections were described and measured in glycerin on a 0.5 mm scale ocular reticle that was bordered by a berm of dental wax to hold in the glycerin, that assembly mounted in small plastic Petri dish. The dish and reticle could be examined under both dissecting and compound microscopes, at up to 400× if necessary. The male flagellum length was estimated by "rolling" the aedeagus along the reticle grid, much like a stick and hoop, thereby allowing the measurement of length to be made along the natural curvature of the flagellar complex,

The female reproductive tract of the included species conformed in general to results for Bembidiini in Liebherr and Will (1998). Species of subgenus *Gnatholymnaeum* exhibit a broadly sclerotized collar at the base of the spermathecal duct (Figs. 5A, B), topologically congruent with the annulus recepticulus (Lindroth 1985). Gonocoxal setal terminology was based on Shpeley et al. (1985) and Shpeley and Ball (1993). The spermatheca of Hawaiian *Bembidion* species is either broadly ovoid, with a shallow median constriction, or biovate, with a more distinct median constriction. The basal expanded area, where the spermathecal and spermathecal gland ducts enter, represents a fusion of the nodulus and the ramus (Maddison 1993), the latter of which is not well-developed in Hawaiian *Bembidion*. The apical cornu (Maddison 1993) is also less well-defined in the Hawaiian species, and so spermathecal shape is described using only colloquial terms. The spermathecal gland complex is bipartite in Bembidiini, with a sclerotized basal tubule supported by taenidia-like coiled cuticle, herein called the spermathecal gland atrium, and a flocculent distal area composed of diffuse secretory cells connected to a central collecting tube via very small ductules, herein called the spermathecal gland secretory complex. These two areas correspond respectively to the gland conduit, and the glandular follicle of Schuler (1960). The length of the female spermathecal duct was estimated through use of a calibrated ocular grid, with the specimen moved on the compound microscope stage to accommodate the natural curves and loops of the duct. The number of male and female dissections is noted in order to place observed variation in both types of genitalic structures within a context of sampling opportunity and effort.

Elytral setal positions are numbered using the system in Erwin and Kavanaugh (1981), with modifications noted in Maddison (1993). Microsculpture terminology generally follows Lindroth (1974). Many of these species are characterized by reduced microsculpture, the sculpticells of which were better observed by viewing the specimen in a diffuser tube, or by placing the head of the specimen mounting pin directly in the line of view over the specimen. When focused on the specimen in this latter orientation, scattered side light dominates the brighter, directly reflected light, enhancing illumination of sculpticell margins.

All specimen data are available from the author as an electronic database (Liebherr 2000) updated from that described in Liebherr and Zimmerman (2000). Lectotypes are designated for all type series where a unique holotype was not cited in the description, due to potential ambiguities of specimen attribution caused by the initial division of specimens from the *Fauna Hawaiiensis* (Sharp 1903, 1913) between the Natural History Museum, London, and the Bishop Museum, Honolulu (Manning 1986). Character information was recorded using the Lucid Builder© program (C.P.I.T.T. 2001), with the associated Lucid Player© used to assist in constructing the dichotomous key, and in writing the species diagnoses and descriptions.

SYSTEMATIC ZOOLOGY

Order Coleoptera Linnaeus, 1758
Family Carabidae Latreille, 1802
Tribe Bembidiini Stephens, 1827

Bembidion Latreille, 1802

Bembidion Latreille, 1802:82 (type species *Cicindela quadrimaculata* Linnaeus, 1761, by Andrewes, 1935:17) [generic-level taxa relevant to Hawaiian species listed below].
Bembidium Gyllenhal, 1810:12 (unjustified emendation).
Gnatholymnaeum Sharp, 1903:276 (junior synonym of *Amerizus* Chaudoir, 1868, Lindroth 1980; type species *Gnatholymnaeum blackburni* Sharp by original monotypy).
Nesolymnaeum Sharp, 1903:277 (junior synonym of *Gnatholymnaeum,* Britton 1948; subgenus of *Bembidion,* Lindroth 1980; type species *Bembidion spurcum* Blackburn by original monotypy).
Nesocidium Sharp, 1903:280 (synonymy, Britton 1948; type species *Nesocidium smaragdinum* Sharp, 1903, by Lorenz 1998a).
Atelidium Sharp, 1903:284 (synonymy, Britton 1948; type species *Atelidium munroi* by original monotypy).
Metrocidium Sharp, 1903:285 (synonymy, Britton 1948; type species *Metrocidium brevicolle* Sharp by Lorenz 1998a).
Nesomicrops Sharp, 1903:286 (subgenus of *Bembidion,* Britton 1948; type species *Nesomicrops kauaiensis* Sharp by original monotypy).
Macranillus Sharp, 1903:287 (junior synonym of *Nesomicrops* Sharp, Britton 1948; type species *Macranillus coecus* Sharp by original monotypy).

Hawaiian ***Bembidion*** Fauna

The native Hawaiian *Bembidion* fauna consists of two lineages; the subgenus *Gnatholymnaeum* composed of two species, and 21 species that constitute the subgenus *Nesocidium*. The classificatory position of *Gnatholymnaeum* has varied over taxonomic history. Sharp (1903) considered the taxon plus the related *Nesolymnaeum* to be near *Lymnaeum* Stephens 1828, "at the beginning of the Bembidiides (p. 276)." Britton (1948) retained *Gnatholymnaeum* as distinct, but synonymized *Nesolymaeum* with it. He supported Sharp's contention that the taxon was related to *Lymnaeum* and also to *Amerizus* Chaudoir 1868, an Asian-American taxon characterized by

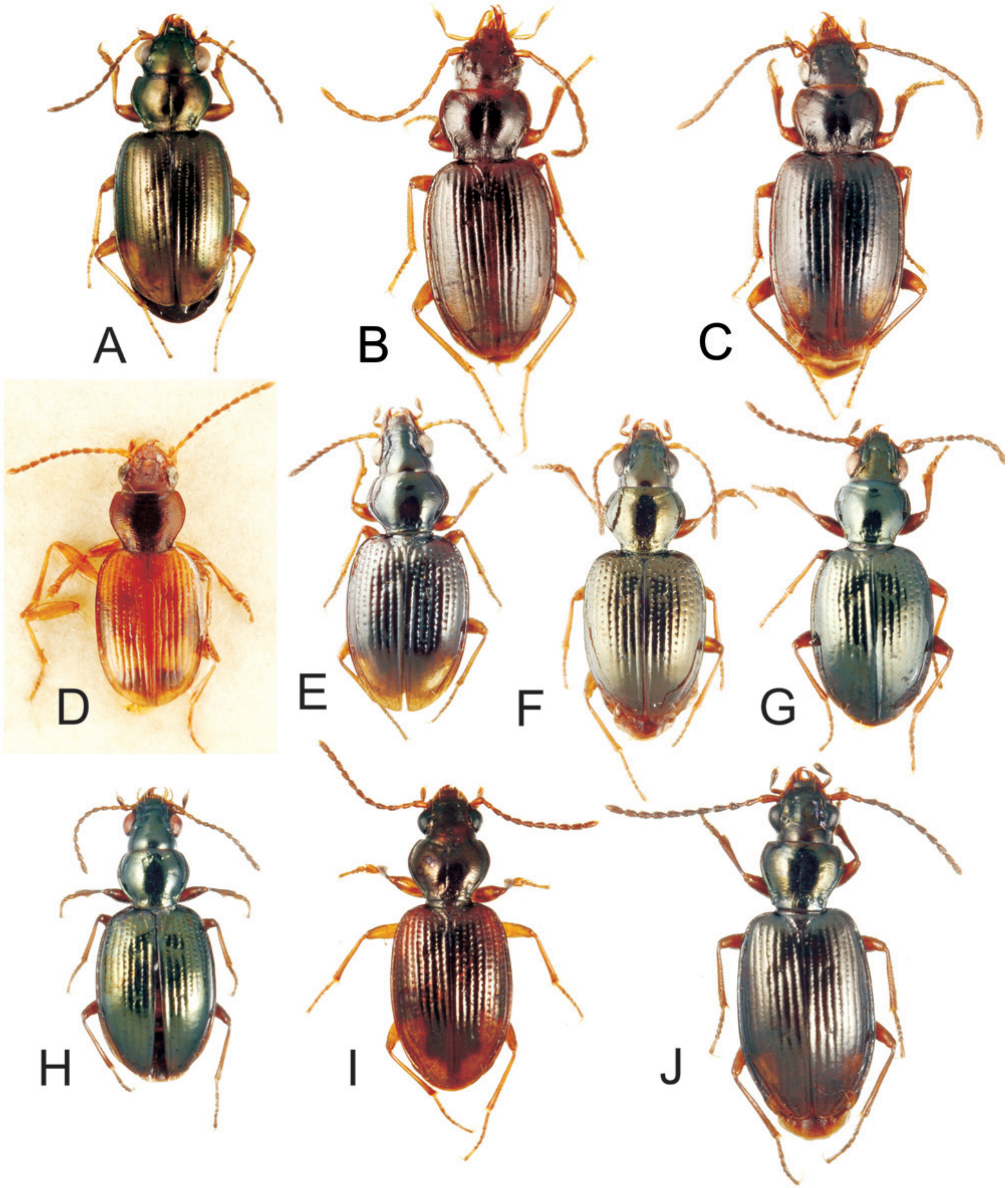


Fig. 1.—Dorsal habitus of *Bembidion* spp. **A**, *B. niloticum*; **B**, *B. blackburni*; **C**, *B. spurcum*; **D**, *B. advena*; **E**, *B. ignicola* (Kauai); **F**, *B. ignicola* (Oahu); **G**, *B. ignicola* (East Maui); **H**, *B. ignicola* (Hawaii I.); **I**, *B. pacificum*; **J**, *B. teres*.

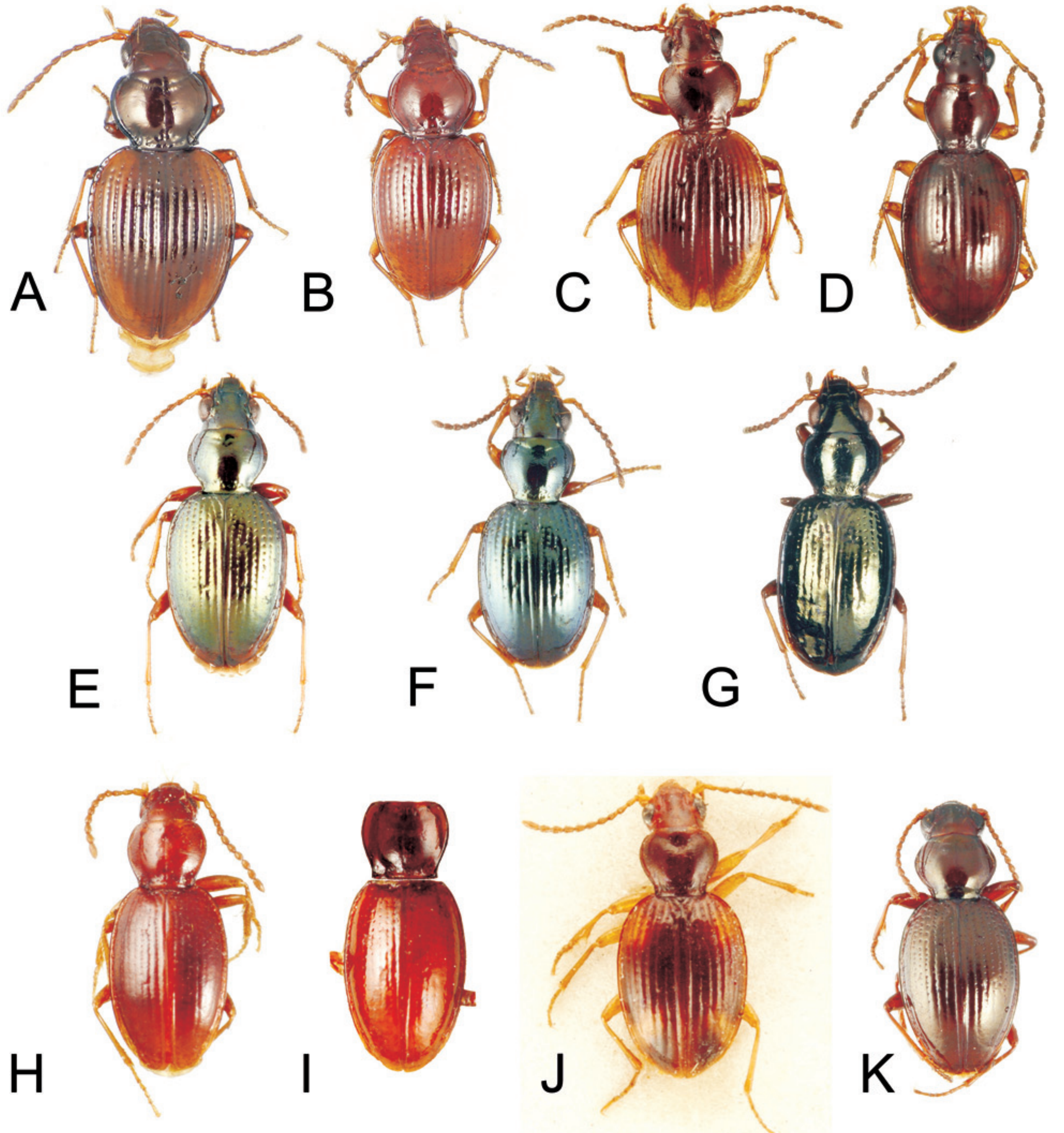


Fig. 2.—Dorsal habitus of *Bembidion* spp. **A**, *B. admirandum*; **B**, *B. munroi*; **C**, *B. rude*; **D**, *B. waialeale*; **E**, *B. smaragdinum*; **F**, *B. fulgens* ; **G**, *B. auratum*; **H**, *B. kauaiense*; **I**, disassociated pronotum and elytra of *B. coecum* at slightly larger proportionate scale; **J**, *B. perkinsi*; **K**, *B. koebelei*.

elongate mandibles. Lindroth (1980) focused on characters that differentiated *Gnatholymnaeum* and *Nesolymnaeum*, considering the former to be a synonym of *Amerizus*, treated as a subgenus of *Bembidion*, and the latter as a distinct subgenus of *Bembidion*, though he did so provisionally as he did not have sufficient high-quality taxonomic specimens to be able to homologize the internal sac sclerites of *Nesolymnaeum spurcum* Sharp with those of other *Bembidion*. Perrault (1981) supported a relationship between *Gnatholymnaeum* (in the sense of Britton 1948) and *Amerizus*, but placed *Lymnaeum* as a separate subgenus within *Bembidion* based its globular spermathecal configuration typical of *Bembidion*. He hypothesized that *Gnatholymnaeum* had an elongate, fusiform spermatheca much like *Amerizus* and *Tiruka* Andrewes 1935, though he could not test this hypothesis due to lack of specimens.

Examination of male and female genitalic and reproductive tract structures in both *Gnatholymnaeum blackburni* Sharp and *G. spurcum* has revealed characters supporting monophyly of the two species and their placement in *Bembidion*. The male aedeagal internal sac armature includes several synapomorphies shared by *Bembidion* species, including a central sclerite complex (csc, Maddison 1993), with the right and left sides of the csc connected to a brush sclerite (Figs. 3H-J). The left lobe of the csc is associated with a short flagellum, and a short dorsal plate (Figs. 3H, J) and ostium flag (of Erwin and Kavanaugh 1981) are also present. The female spermatheca is heavily sclerotized and globular (Figs. 5A, B), much like those in many other *Bembidion* (e.g., *Bembidion ignicola* Blackburn, Fig. 5C), and unlike the fusiform spermatheca of *Amerizus* and *Tiruka* (Perrault 1981). The two *Gnatholymneum* taxa exhibit a synapomorphous annulus recepticulus of the spermathecal duct, i.e., a thickened, heavily sclerotized duct base at its junction with the bursa copulatrix (Lindroth 1985).

The Hawaiian *Gnatholymnaeum* also exhibit the plesiomorphically subdivided maxillary galea observed in most Bembidiini taxa. In *G. spurcum*, there is an oblique line of flexion near the basal 2/5 of the galea length, whereas in *G. blackburni*, which exhibits more elongate mouthparts, this line of flexion is near mid-length. Conversely, *Amerizus* is characterized by derived fusion of these two segments, with the elongate galea functioning as a unified, spinose, grasping blade (see Maddison 1993). Based on the above combination of synapomorphies and symplesiomorphies, and the possession of the bembidiine tribal-level synapomorphies of subulate apical palpomeres, the two Hawaiian species are herein united in the subgenus *Gnatholymnaeum* treated as a subgenus of *Bembidion*.

The second lineage, *Nesocidium* Sharp, is defined, among other characters, by a hypertrophied flagellar complex of the male aedeagal internal sac. In all species the basal assemblage of brush sclerite and central sclerite complex extends to or beyond the base of the aedeagal median lobe, in the most extreme forms circling upon itself outside the aedeagus so that parts of it lie near the base of the abdomen (Figs. 4A-C). Lindroth (1976) noted a similar configuration in the Australian *B. errans*, the type species of subgenus *Ananotaphus* Netolitzky 1931 (Toledano 2005). The Hawaiian *Nesocidium* species share a very similar flagellar configuration with *B. errans* (Fig. 4A), including structures Lindroth called the brush sclerite, hook sclerite (= flagellar base articulation with the left lobe of the central sclerite complex [Maddison 1993]), and simple basal sclerite (= central sclerite complex [Maddison 1993]). In both groups the male protarsomeres 1 and 2 are strongly dilated with acuminate apices. They also share a ground-plan including two free dorsal elytral setae situated in the third elytral interval, and a pronotal configuration in which the laterobasal depression is extended to the basolateral margin, not bordered laterally by a carina. In addition, the basal pronotal seta is situated anterad the hind angle. This pronotal configuration is also observed in the monophyletic New Zealand radiation described as *Zecillenus* (Lindroth 1980). *Zecillenus* species exhibit an elongate aedeagal flagellum with an associated basal sclerite possibly homologous with the brush sclerite (Lindroth 1980:fig. 2). However the flagellum is not so long as to extend beyond the base of the median lobe. The South American species described in *Antiperyphanes* Jeannel (1962) also exhibit a greatly hypertrophied flagellum, however in these beetles the dorsal elytral setae are positioned in the third stria, not free as in *Ananotaphus* and *Nesocidium*. At present, monophyly of the Hawaiian *Nesocidium* relative to the Australian *Ananotaphus* is not well established. Nomenclaturally, unification of these taxa would necessitate synonymy of *Ananotaphus* under the older name *Nesocidium.* I do not take such an action in order to maximize taxonomic stability, as a thorough study of *Ananotaphus*, *Zecillenus*, *Nesocidium*, as well as more distant relatives in South America (Toledano 2005), should be undertaken to provide a more global hypothesis of relationships that would support a definitive classification.

KEY TO THE ADULTS OF *BEMBIDION* SPECIES KNOWN TO OCCUR IN THE HAWAIIAN ISLANDS

1. Frontal grooves subparallel, broadly depressed on frons, less well defined on clypeus and not reaching clypeal anterior margin (Figs. 1C, J) . . 2

1'. Frontal grooves deeply incised, rectilinearly approaching each other anteriorly and continuously extended from frons to clypeal anterior margin (subgenus *Notaphocampa* Netolitzky) (Fig. 1A) .... *B. niloticum* Dejean

2(1). Mouthparts very elongate, distance from mandibular articulation to labral anterior margin less than distance along mandible from labral margin to mandibular apex, basal and penultimate maxillary palpomeres elongate (Figs. 1B, C);

anterior tibiae longitudinally grooved on lateral face; pronotal laterobasal depression margined externally by carina that extends anterad from hind angle (subgenus *Gnatholymnaeum* Sharp) 3

2'. Mouthparts not elongate, length of mandibular extension beyond labral anterior margin less than distance from mandibular articulation to labral margin, maxillary palpomeres shorter, length of penultimate maxillary palpomere subequal to antennal scape (Figs. 1D-J, 2, 3A-F); anterior tibiae not grooved on lateral face; pronotal laterobasal depression not separated from basolateral margin by a carina (subgenus *Nesocidium* Sharp) 4

3(2). Eyes convex, ocular ratio 1.44-1.47; pronotum more transverse, basolateral margin more sinuate anterad acute to right hind angle (Fig. 1C); elytral striae distinctly punctate basally, the punctures expanding width of stria; metathoracic flight wings macropterous .... *B. spurcum* Blackburn

3'. Eyes reduced, outer surface only slightly extended beyond curve of ocular lobe, ocular ratio 1.38-1.39; pronotum more elongate, basolateral margin straight anterad right hind angle (Fig. 1B); elytral striae indistinctly punctate, the punctures causing stria to waver without increasing width; metathoracic flight wings vestigial, micropterous flaps .... *B. blackburni* (Sharp)

4(2'). Elytral humeri broad basally, the elytral lateral margins subparallel at midlength (Fig. 1D-J); eyes well developed, convex laterally, length > 0.20 mm 5

4'. Elytral humeri narrower basally, the elytra narrowly to broadly rounded laterally and elytral lateral margins convex throughout length (Figs. 2, 3A-F); eyes variously developed, from convex laterally and large—length > 0.20 mm—to extremely small and flat 8

5(4). Elytra piceous mediobasally, though apex may be paler (Figs. 1E-J) 6

5'. Elytra flavous except for two piceous lateral triangles and a transverse subapical piceous cloud (Fig. 1D) .... *B. advena* Sharp

6(5). Body size larger, standardized body length 3.7-5.0 mm; pronotal disc with evident isodiametric to transverse-mesh microsculpture 7

6'. Body size smaller, standardized body length 2.7-3.1 mm; pronotal disc shiny, without evident microsculpture .... *B. ignicola* Blackburn

7(6). Elytra with both subapical and apical pale spots (Fig. 1I), in some individuals humeri diffusely paler also; pronotal disc covered with distinct isodiametric microsculpture; pronotal basolateral margin abruptly curved outward just anterad hind angle; standardized body length 3.7-4.1 mm .... *B. pacificum* Blackburn

7'. Elytra with only subapical pale spot (Fig. 1J); pronotal disc covered with indistinct transverse sculpticells; pronotal basolateral margin less abruptly curved outward anterad hind angle; standardized body length 4.3-5.0 mm .... *B. teres* Blackburn

8(4'). Pronotum without lateral seta, basal seta near hind angle present or absent 9

8'. Pronotum bisetose each side, with lateral and basal setae present 10

9(8). Pronotal lateral margin very broad throughout length (Fig. 2A), reflexed margin distinctly upraised, depression surface irregular, especially in basal half; male aedeagal flagellar complex greatly extended from base of median lobe (Fig. 4C); female spermathecal duct greatly swollen at base (Fig. 6A); standardized body length 2.9-3.5 mm .... *B. admirandum* (Sharp)

9'. Pronotal lateral margin narrow (Fig. 2B), extended laterally from disc but outer edge not upraised, extended margin too narrow to show surface irregularities; male aedeagal flagellar complex not extended beyond base of median lobe (Fig. 4D); female spermathecal duct little swollen at base (Fig. 6B); standardized body length 2.6-3.1 mm .... *B. munroi* (Sharp)

10(8'). Two dorsal elytral setae evident on each elytron, the anterior near one-third of elytral length, the posterior near midlength 11

10'. Only a single dorsal elytral seta present in basal half of third elytral interval 20

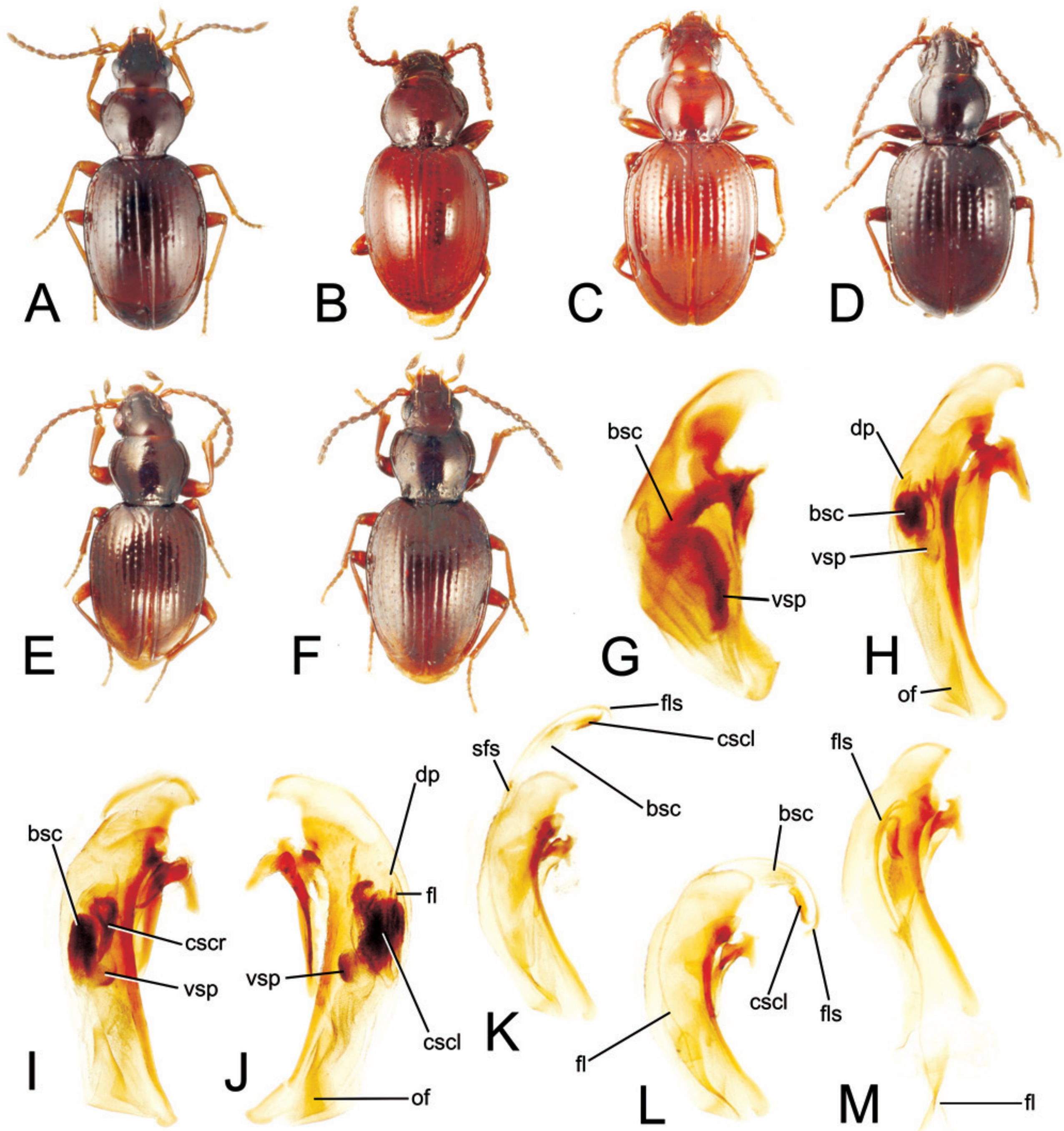
11(10). Dorsal elytral setae in depressions that extend across third elytral interval (Figs. 2C-G) 12

11'. Dorsal elytral setae in articulatory sockets that do not extend across third elytral interval (Figs. 2H-K, 3A) 16

12(11). Elytral humerus and apex concolorous with elytral disc (Figs. 2D-G) 13

12'. Elytral humerus, apex, and sutural interval flavobrunneous, concolorous with pronotal disc, and much paler than piceous medial portion of each elytron (Fig. 2C) .... *B. rude* (Sharp)

13(12). Dorsal body surface piceous with metallic sheen (Figs. 2E-G); elytral striae 1-7 punctate in basal half of elytral length, the elytral intervals convex 14



Figs. 3A-F.—Dorsal habitus of *Bembidion* spp. **A**, *B. corticarium*; **B**, *B. gagneorum*; **C**, *B. paratomarium*; **D**, *B. atomarium*; **E**, *B. kamakou*; **F**, *B. haleakalae*. Figs. 3G-M.—Male aedeagal median lobe, *Bembidion* spp. **G**, *B. niloticum*, right lateral view; **H**, *B. spurcum*, right lateral view; **I**, *B. blackburni*, right lateral view; **J**, *B. blackburni*, left lateral view; **K**, *B. ignicola* (Kauai), right lateral view; **L**, *B. ignicola* (Oahu), right lateral view; **M**, *B. ignicola* (East Maui), right lateral view, flagellum partially everted. Figure codens: **bsc**, brush sclerite; **cscl**, central sclerite complex left lobe; **cscr**, central sclerite complex right lobe; **dp**, dorsal plate; **fl**, flagellum; **fls**, flagellar sheath; **of**, ostium flag; **sfs**, secondary flagellar sclerite; **vsp**, ventral setal patch.

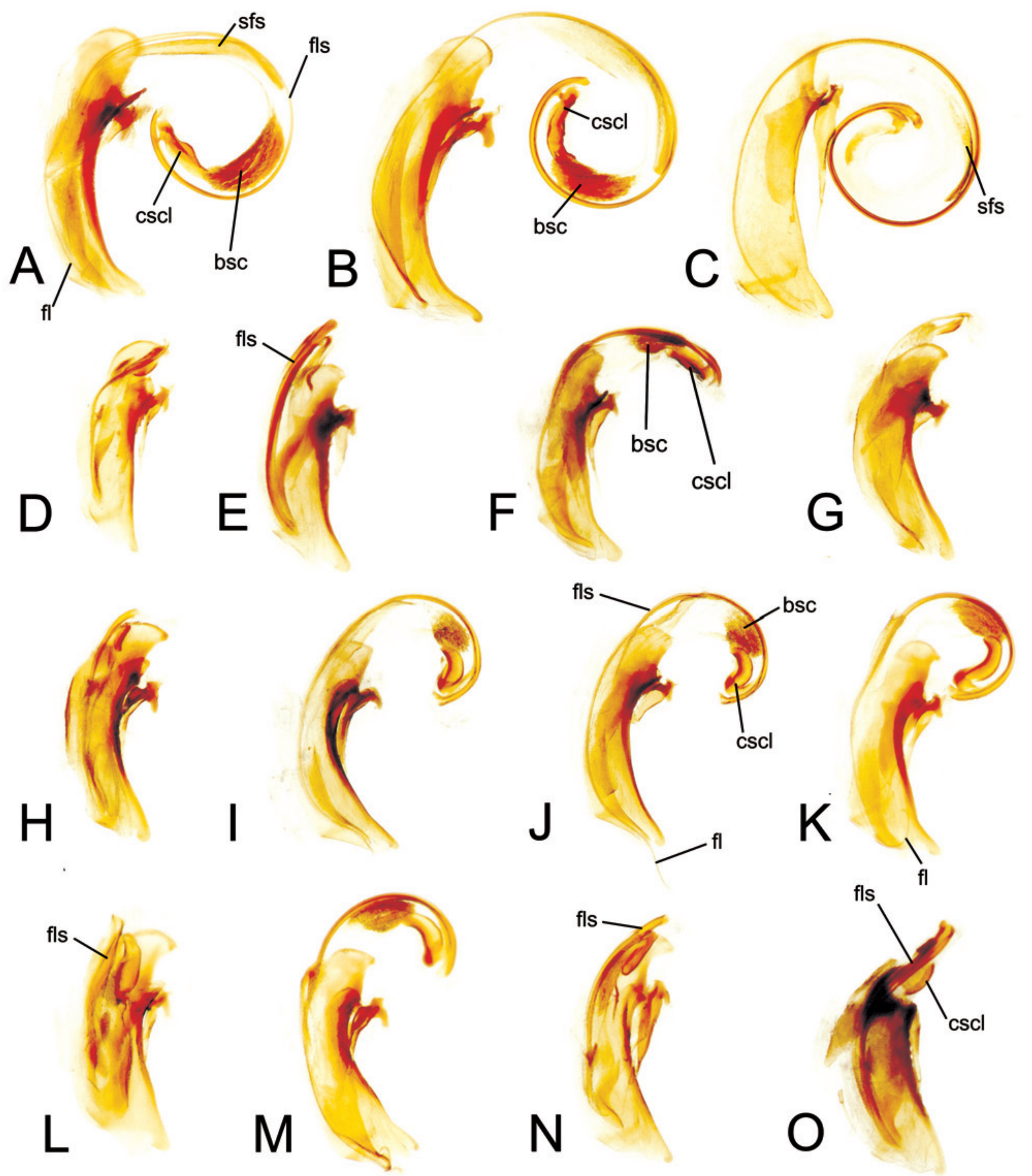


Fig. 4.—Male aedeagal median lobe of *Bembidion* spp, right lateral view. **A,** *B. pacificum*; **B,** *B. teres*; **C,** *B. admirandum* (teneral specimen); **D,** *B. munroi*; **E,** *B. rude*; **F,** *B. waialeale*; **G,** *B. smaragdinum*; **H,** *B. fulgens*; **I,** *B. corticarium*; **J,** *B. corticarium*, flagellum partially everted; **K,** *B. gagneorum*; **L,** *B. paratomarium*; **M,** *B. atomarium*; **N,** *B. kamakou*; **O,** *B. haleakalae*. Figure codens: **bsc,** brush sclerite; **cscl,** central sclerite complex left lobe; **fl,** flagellum; **fls,** flagellar sheath; **sfs,** secondary flagellar sclerite.

13’. Dorsal body surface brunneous (Fig. 2D); elytral sutural stria much deeper than outer striae, with indistinct punctures basally, smooth apically, the lateral elytral intervals only slightly convex .... *B. waialeale*, new species

14(13). Forebody with evident microsculpture, vertex with transverse mesh, most evident on mesal surfaces of frontal grooves, pronotal disc with indistinct transverse lines irregularly joined in loose mesh; pronotum broader, ratio of maximum pronotal width/median pronotal length > 1.24 15

14’. Forebody shinier, vertex and pronotal disc shiny without evident sculpticells; pronotum narrower, ratio of maximum pronotal width/median pronotal length < 1.22 .... *B. smaragdinum* (Sharp)

15(14). Elytral intervals convex, striae deeply incised, five to six punctures along length of parascutellar stria, striae 1-6 distinctly punctate basally (Fig. 2F); bluish-green metallic sheen on elytra and pronotal disc .... *B. fulgens* (Sharp)

15’. Elytral intervals nearly flat, sutural and parascutellar striae and stria 6 shallow, impunctate basally and on disc, only striae 2-5 punctate in basal half to one-third of length (Fig. 2G); elytra with golden-green metallic sheen, pronotal disc less metallic, with indistinct green metallic reflection .... *B. auratum* (Perkins)

16(11’). Compound eyes not projected from ocular lobe, outer surface flattened, horizontal eye diameter 0.055-0.12 mm (Fig. 2H) 17

16’. Compound eyes with convex outer surface that projects from ocular lobe, horizontal eye diameter > 0.13 mm (Figs. 2J, K, 3A) 18

17(16). Pronotal hind angle setose, basolateral margin indistinctly sinuate anterad hind angle; approximately five distinct ommatidia along horizontal diameter of compound eye; indistinctly convex elytral intervals covered with isodiametric mesh microsculpture; standardized body length 2.8 mm .... *B. kauaiense* (Sharp)

17’. Pronotal hind angle glabrous, basolateral margin with long distinct sinuation anterad hind angle; compound eye with indistinct ommatidia, two to three across horizontal diameter that is about 0.55 mm long; nearly flat elytral intervals without visible microsculpture (60×), surface shiny; standardized body length 2.3 mm .... *B. coecum* (Sharp)

18(16’). Elytral surface concolorous (Figs. 2K, 3A); elytral intervals flat to slightly convex, discal striae shallow, impunctate or shallowly punctate 19

18’. Elytra with transverse humeral and subapical fasciae (Fig. 2J); elytral intervals convex, discal striae deeply impressed and distinctly punctate .... *B. perkinsi* (Sharp)

19(18). Eyes convex, extended across most of ocular lobe, ocular ratio 1.75; elytral striae 1-5 continuous and distinctly punctate in basal half of elytra (Fig. 2K), striae 6-7 represented by series of 11-14 isolated punctures .... *B. koebelei* (Sharp)

19’. Eyes smaller, less convex, ocular ratio 1.48-1.51; elytral striae 1-5 shallow and punctate in basal half of elytra (Fig. 3A), striae 6-7 indicated basally by four to six minute, isolated punctures .... *B. corticarium* (Sharp)

20(10’). Elytral striae 1-7 evident, mesal three to five striae punctate and impressed in basal half of length, more lateral striae either continuous, punctate basally, or basally consisting of series of isolated punctures (Figs. 3C-F) 21

20’. Sutural elytral stria distinctly deeper than second stria on basal half of disc, third stria indicated by approximately six shallow punctures anterad midpoint of length, lateral striae obsolete (Fig. 3B) .... *B. gagneorum*, new species

21(20). Frons between frontal grooves shiny, without distinct microsculpture (60× magnification), vertex of head with very shallow, indistinct transverse-mesh microsculpture posterad posterior supraorbital seta; elytral apex diffusely paler than disc (Figs. 3C, D) 22

21’. Frons between frontal grooves with evident transverse-mesh microsculpture, the meshes more distinct and isodiametric towards posterior margin of head capsule; elytra with distinct pale apical macula that extends along margin from middle of posterior group of lateral elytral setae to elytral apex (Figs. 3E, F) 23

22(21). Elytral intervals convex on disc, striae 1-6 punctate and continuous for at least a portion of their length; pronotal lateral margin broader, paler depressed area along disc as wide as darker explanate margin (Fig. 3C) .... *B. paratomarium*, new species

22’. Elytral intervals flat on disc, striae 1-3 continuous, striae 4-7 indicated by series of isolated punctures; pronotal lateral margin narrow throughout length, the margin carinate without paler area adjacent to disc (Fig. 3D) .... *B. atomarium* (Sharp)

23(21'). Elytral humeri projected forward relative to elytral base just posterad pronotal hind angles, elytral lateral marginal depression extended from this anteriorly angulate margin; sinuation of pronotal basolateral margin short, more abrupt (Fig. 3E) .... *B. kamakou*, new species

23'. Elytral humeri not projected forward of elytral base, elytral margin evenly curved posterad base of lateral marginal depression; sinuation of pronotal basolateral margin more elongate, curvature less abrupt (Fig. 3F) ... *B. haleakalae*, new species

Bembidion, subgenus ***Notaphocampa*** Netolizky, 1914 (non-native)

Bembidion **(*Notaphocampa*)** ***niloticum*** Dejean, 1831 (Figs. 1A, 3G, 8, 9, 10, 12)

Bembidium niloticum Dejean, 1831:73.
Notaphus batesi Putzeys, 1875:lii (other synonyms inapplicable to Hawaii not listed; see Lorenz 1998b).
Bembidium batesi (*niloticus* Bates): Harold, 1877:342 (junior synonym of *Bembidium opulentum* Nietner, 1858).
Bembidium (*Notaphus*) *batesi*: Bates, 1883:269 (synonymy).
Bembidion (*Notaphocampa*) *niloticum* var. *batesi*: Netolitzky, 1914:167.
Bembidion niloticum batesi: Britton, 1948:246.

Diagnosis.—This common introduced species of lowland riparian habitats in Hawaii can be readily diagnosed by the rectilinear frontal grooves that anteriorly approach one another on the frons and clypeus, and by the deep pronotal laterobasal depressions lined medially with minute punctures, and bordered laterally by a short carina extended to the setose hind pronotal angle (Fig. 1A); basal pronotal margin concave just mesad hind angles so that medial portion extends posterad; frons, vertex and pronotum with well-developed, almost granulate isodiametric microsculpture; elytral base with distinctly punctate striae, the intervals flat with isodiametric mesh microsculpture; elytral apex with broad, pale macula extended anterad along suture and moreso along lateral margin, the elytral striae reduced to shallow isolated punctures, especially laterally; standardized body length 3.5-4.0 mm.

Male Genitalia.—(n=2). Male aedeagal median lobe robust, the apex broadly truncate with a minute projection on ventroapical margin (Fig. 3G); parameres 3-setose; internal sac of median lobe with large sinuous brush sclerite, ventral setal patch (vsp) visible in dextral view; several longitudinal folds of internal sac evident near eudorsal surface of lobe.

Female Reproductive Tract.—(n=1). Bursa copulatrix a broadly ovoid, membranous sac, length from spermathecal duct to gonocoxite bases about 1.15× bursal breadth when compressed on microslide; annulus receptaculus sclerite adjoining right side of spermathecal duct at entry to bursa; spermathecal duct with two opposing 135° turns and a single complete loop before junction with spermatheca (as in Schuler's [1960] drawing of *Bembidion* (*Princidium*) *punctulatum* Drapiez); spermatheca with broad base, constricted to more narrowly rounded apex, gland duct entering just distad position of broadest circumference; spermathecal gland duct short before atrium composed of about 35 taenidial coils, the atrium divided into a narrow basal half and broader apical half joined by a narrow constriction; spermathecal gland secretory complex linear, whip-like, about 2-3× length of spermatheca. Basal gonocoxites with two setae along lateroapical margin; apical gonocoxites with tightly rounded tip, two lateral ensiform setae lying ventrad a falcate lateral margin, a single smaller dorsal ensiform seta, and two apical nematiform setae about 0.25× as long as apical gonocoxite 2.

Nomenclatural Note.—Putzeys (1875:lii) described a *Bembidion* from Japan, starting the description with the section heading "57. **Notaphus Batesi** (*niloticus* Bates).", and below stating: "Cet insecte est certainement tres-voisin du *B. niloticum* Dej., mais je le considère comme en étant distinct…" It does not appear that Putzeys meant this form to represent a new species, as he did not insert the abbreviation "n. sp." after the taxon as he did for all other new species descriptions in this paper. In addition, no other new species had a parenthetical older name following his new name. However, his unusual presentation format left doubt regarding his meaning. Harold (1877) mimicked Putzeys' unusual name formation, citing "*B. batesi* Putz. (*niloticum* Bates)", synonymizing it with *B. opulentum* Nietner—currently a junior synonym of *B. foveolatum* Dejean (Toledano 2005). His ambiguous parody of Putzeys' unusual format does not allow any clear conclusion beyond his interpretation that the name was a junior synonym at some specific or infraspecific rank. Bates (1883) subsequently synonymized *B. batesi* Putzeys with *B. niloticum* Dejean. He therefore was the first reviser to unambiguously cite the Putzeys name, making it a valid species-level epithet while simultaneously synonymizing it. Subequently Netolitzky (1914) interpreted Putzeys' name as an infraspecific variety of Dejean' *B. niloticum*, placing both in his newly described subgenus *Notaphocampa*. Finally and differently than all workers before him, Csiki (1928) misinterpreted *Notaphus batesi* as a replacement name, no doubt thrown off by Putzey's incorrect, parenthetic trailing epithet-author combination "*niloticus* Bates." Thus he also listed "B. niloticum Bates" as junior homonym of *B. niloticum* Dejean. Bates never claimed authorship for a species with this name, and in both instances cited by Csiki (Bates 1873, 1883) correctly ascribed the name to Dejean. Thus "B. niloticum Bates" (Csiki 1928:70) is not an available name (Lorenz 1998b).

Distribution.—Kauai (Fig. 8): Huleia Stream, 0 m el.; Keahua Arboretum, Wailau Homesteads, 150 m el.; Polihale Beach S.P., 0 m el.; Waiahuakua Str., at Kalalau Tr., 120 m el.; Waimea R. mouth, 0 m el. Oahu (Fig. 9): Ewa Plantation; Hickam Field; Hauula; Honolulu, Diamond Head, Kaimuki, Manoa Vy., Moanalua Gardens, Palolo; Konahuanui; Kunia; Punaluu; Waipahu; Waipio. Molokai (Fig. 10): Kaunakakai, 0 m el. Hawaii (Fig. 12): Kohala Watershed, Upper Hamakua Ditch, Kawainui Str., 1210 m el.

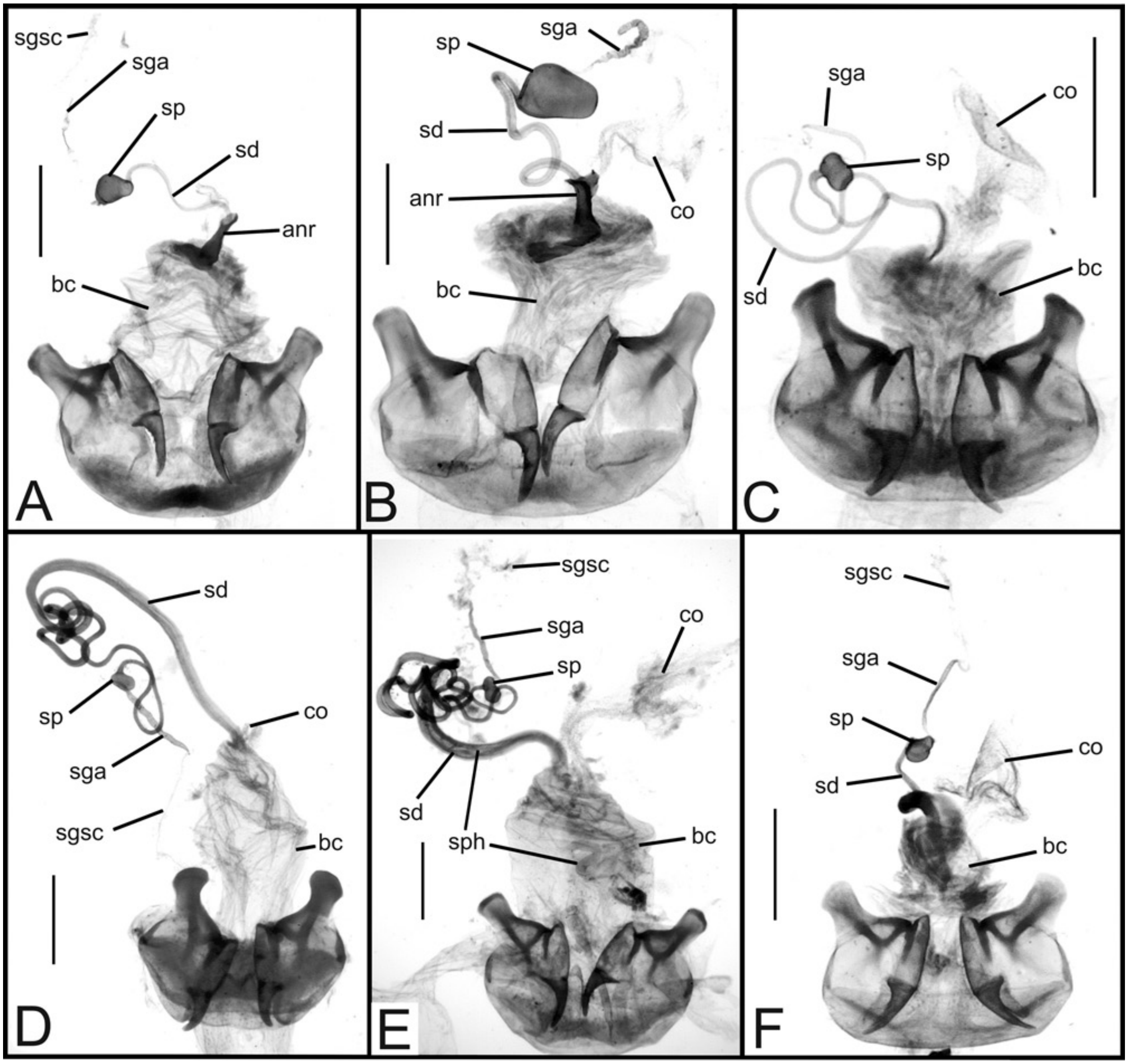


Fig. 5.—Female reproductive tract of *Bembidion* spp, ventral view. **A,** *B. spurcum*; **B,** *B. blackburni*; **C,** *B. ignicola* (Oahu); **D,** *B. pacificum*; **E,** *B. teres*; **F,** *B. rude*. Figure codens: **anr,** annulus recepticulus; **bc,** bursa copulatrix; **co,** common oviduct; **sd,** spermathecal duct; **sga,** spermathecal gland atrium; **sgsc,** spermathecal gland secretory complex; **sp,** spermatheca; **sph,** spermatophore. Scale bars = 0.25 mm.

Introduction History. This Old World species was first collected in Oahu in 1910 at Palolo (Kuhns, UCRC) and Diamond Head (Swezey, BPBM). It had reached Hauula on the north shore by 1914 (BPBM). Timberlake subsequently collected it on Konahuanui and in the Moanalua Gardens neighborhood in 1916 (UCRC). The species was first collected on Kauai in 1919 at Waimea and later in 1928 along Huleia Stream above Nawiliwili Harbor, Lihue (Swezey, BPBM). It was first collected on Hawaii Island at Upper Hamakua Ditch in 1921 (Swezey, BPBM). The lone record from Molokai is based on a collection from the shore at Kaunakakai in 1943 (Krauss, BPBM).

Habits.—This species has been collected flying to lights at night, and in waterside habitats. These include muddy borders of freshwater ponds backing the sea beach at Polihale, Kauai, among grasses and sedges along the pond margins at Keahua Arboretum, Kauai, and under jetsam along the Waimea River, Kauai.

Bembidion, subgenus ***Gnatholymnaeum*** Sharp, 1903, **new rank**

Gnatholymnaeum Sharp, 1903:276; Britton, 1948.
Bembidion (subgenus *Amerizus* Chaudoir, 1868) (junior subgeneric synonym, Lindroth 1980).
Nesolymnaeum Sharp, 1903:277 (junior synonym of *Gnatholymnaeum,* Britton 1948).
Bembidion (subgenus *Nesolymnaeum)* (Lindroth 1980).

Diagnosis.—Both of these species are instantly recognizable by: 1, the elongate mandibles, maxillae and maxillary palps (Fig. 1B, C), the mandibles extended beyond labral anterior margin more than distance from dorsal mandibular articulation to labral margin; 2, eyes small, slightly convex, the posterior supraorbital seta posterad hind margin of eye; 3, pronotum with broad lateral marginal depressions bordered laterally by an elongate lateral carina extended onto pronotal disc about 0.5× distance to lateral pronotal seta; 4, metasternal process marginal bead of equal width on sides and at apex, metasternum setose medially; 5, anterior tibia carinate dorsally, the carina bordered basally by distinct longitudinal grooves; 6, ventroapical setae of tarsomeres elongate, those on tarsomere 3 longer than tarsomere 4, those on fourth extended 0.80× length of tarsomere 5. Elytral setation is characteristic of other *Bembidion* subgroups (Erwin and Kavanaugh 1981), including: 1, parascutellar seta ed1 on interval between base of parascutellar stria and sutural stria 1; 2, two dorsal elytral setae (ed3, 5) positioned at the middle or slightly toward the outer half of interval 3, both setae in shallow depressions that span the interval; 3, two ed7 setae mesad deeply excavated portion of stria 7; 4, seta ed8 at apex of stria 7; 5, nine lateral elytral setae, eo1-8 plus an extra medial seta (Maddison 1993).

Bembidion (Gnatholymnaeum) spurcum Blackburn, 1881
(Figs. 1C, 3H, 5A, 7A, 8, 9, 10, 11)

Bembidion (*Notaphus*) *spurcum* Blackburn, 1881:228.
Nesolymnaeum spurcum: Sharp, 1903:277.
Gnatholymnaeum spurcum: Britton, 1948:242.
Bembidion (*Nesolymnaeum*) *spurcum*: Lindroth, 1980:204.

Diagnosis.—Smaller than *B. blackburni*, standardized body length 4.0-4.4 mm. Also diagnosable by: 1, eyes moderately convex, ocular ratio 1.44-1.50 (Fig. 1C); 2, pronotal hind angles setose; 3, pronotal base broad, ratio of maximum pronotal width to basal width 1.26-1.32; and 4, mandibles slightly less elongate, total mandibular length measured from ventral condyle to apex 0.59-0.66× median pronotal length. Frons with distinct granulate isodiametric microsculpture, pronotal disc with elongate transverse microsculpture, width of sculpticells about 4× longitudinal length, elytral disc covered with fine transverse lines, not forming a mesh and causing faint iridescence. Metathoracic flight wings fully developed.

Male Genitalia.—(n=2). Aedeagal median lobe gracile, elongate, with evenly rounded apex (Fig. 3H); left paramere about twice as long as right, 3-setose, right paramere 2-setose; median lobe internal sac with right and left lobes of central sclerite complex (csc) connected to brush sclerite that is covered with upraised, transverse sculpticells; short narrow, parallel-sided flagellum extended from apex of left lobe of csc, length of flagellum about equal to length of left lobe; dorsal plate present immediately eudorsad csc left lobe, ventral sclerite patch (vsp) present euventrad brush sclerite.

Female Reproductive Tract.—(n=1). Bursa copulatrix thinly membranous, slightly longer than broad when compressed on microslide; vagina between gonocoxites lined laterally by papillate cuticle that is covered with granulate microsculpture and bears 8-10 setae, bordered ventrally by folds of cuticle bearing overlapping, scalloped hemispherical sculpticells; annulus recepticulus "L"-shaped (Fig. 5A), with sclerotized basal arm extended toward right side of bursa, and spermathecal duct passing through middle of tubular upright arm; spermathecal duct curved, 2-3× length of upright annulus arm; spermatheca iregularly ovoid, with side opposite spermathecal gland duct straighter; gland duct adjoining spermatheca just distad its point of broadest circumference; gland atrium composed of approximately 35 taenidial-like coils, coils constricted near apical one-third; spermathecal gland secretory complex with short duct-like base, and very irregularly flocculent apex, complex about 1.5× length of gland atrium; gonocoxa narrow (Fig. 7A), basal gonocoxite 1 with one or without a lateroapical seta; apical gonoxite 2 narrowly triangular, with tightly rounded tip, two moderately sized lateral ensiform setae and a smaller dorsal ensiform seta; apical nematiform setae short, 0.12× length of apical gonocoxite 2.

Variation.—Specimens in the series from Mt. Kaala, Oahu, lack the subapical, lateral macula on the elytra (Fig. 1C), however specimens agree with regard to all other characters, and so this absence is considered to represent intraspecific variation.

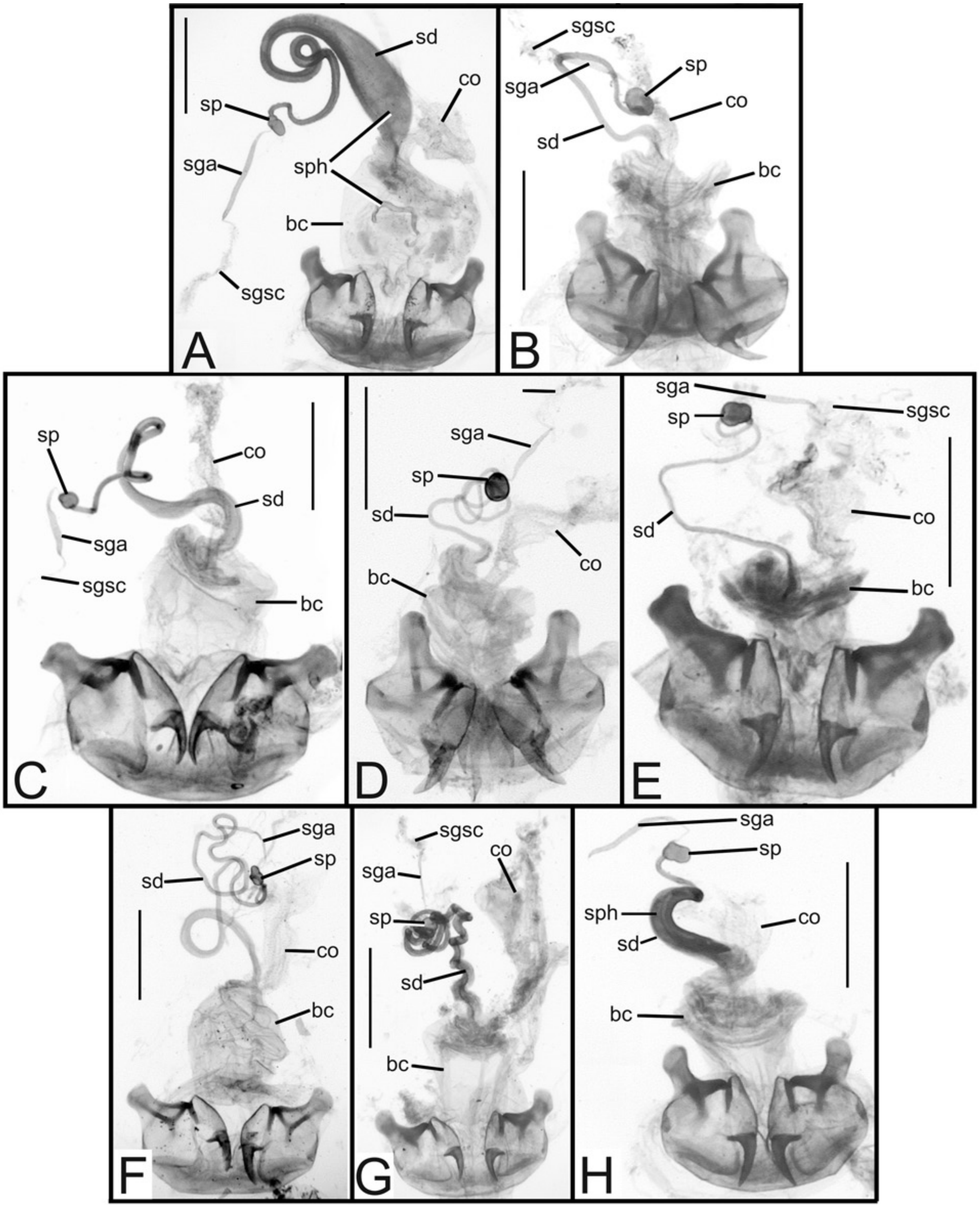


Fig. 6.—Female reproductive tract of *Bembidion* spp, ventral view. **A,** *B. admirandum*; **B,** *B. munroi*; **C,** *B. waialeale*; **D,** *B. smaragdinum*; **E,** *B. fulgens*; **F,** *B. corticarium*; **G,** *B. gagneorum*; **H,** *B. haleakalae*. Figure codens: **bc,** bursa copulatrix; **co,** common oviduct; **sd,** spermathecal duct; **sga,** spermathecal gland atrium; **sgsc,** spermathecal gland secretory complex; **sp,** spermatheca; **sph,** male spermatophore. Scale bars = 0.25 mm.

Type.—Lectotype female (BMNH), platen-mounted with "Blackburn Maui code" (Zimmerman 1957) on obverse, 'Bemb spurcum' on reverse" hereby designated. The type locality of "Haleakala…4000 feet (Blackburn 1881)" corresponds to the vicinity of Waikamoi Gulch, a water source developed for irrigation by the time Blackburn visited the forest there (Blackburn 1885). Blackburn (1881) did not mention the number of specimens in his type series, so even though Blackburn and Sharp (1885) subsequently noted the species to be represented by a "Unique" specimen, that specimen must be considered a syntype (I.C.Z.N. 1999:Article 72.1.1), necessitating the above lectotype designation.

Distribution.—Kauai (Fig. 8): Kokee S.P., Halemanu. Oahu (Fig. 9): Mt. Kaala summit bog, head of W Makaha Str., 1160 m el.; Poamoho Tr., 750 m el. Molokai (Fig. 10): T.N.C.H. Kamakou Preserve, Makakupaia, Kaunakakai Gulch, R.C.L.P. lot 345 (Anonymous N. D.), ~850 m el., Puu Kolekole, Kolekole Cabin, 1207 m el., West Kawela Gulch at water tunnel, 1100 m el. Maui (Fig. 11): Haleakala, 1210 m el., Hanawi N.A.R., Kuhiwa Str. E Poouli Cabin, 1615 m el.; Koolau For. Res., Kula Pipeline Rd., 1265 m el.

Habits.—This species has been collected predominantly under rocks or among jetsam along stream margins. Three specimens were sifted from ground litter along the Poamoho Trail, Oahu. Blackburn (1881) described this species from a specimen collected "in decaying leaves, at an elevation of about 4000 feet" during May (Blackburn and Sharp 1885).

Bembidion (Gnatholymnaeum) blackburni
(Sharp, 1903)
(Figs. 1B, 3I-J, 5B, 7B, 8, 9, 10)

Gnatholymnaeum blackburni Sharp, 1903:276.
Bembidion (*Amerizus*) *blackburni*: Lindroth, 1980:203.

Diagnosis.—Individuals of this species are larger than those of *B. spurcum*, standardized body length 4.5-4.8 mm. In addition, this species is diagnosable by: 1, eyes small and little convex, not extended over posterior portion of ocular lobe, ocular ratio 1.19-1.37 (Fig. 1B); 2, pronotal hind angles glabrous; 3, pronotal base narrower, ratio of pronotal maximum width to basal width 1.43-1.49; and 4, mandibles more elongate, total mandibular length measured from ventral condyle to apex 0.64-0.71× median pronotal length. Frons with slightly transversely stretched microsculpture, pronotal disc covered with fine transverse lines connected to form a very elongate mesh, transverse lines on elytral disc very fine and indistinct, resulting in a purplish iridescence. Metathoracic flight wings reduced to vestigial flaps.

Male Genitalia.—(n=2). Aedeagal median lobe elongate, slightly more robust than in *B. spurcum*, apex with tip slightly downturned and apical face of apex broadly convex (Figs. 3I, J); parameres of equal length, left broad nearly to narrowly projected apical lobe, right narrow, both 3-setose apically with median seta longest; median lobe internal sac with right and left lobes of central sclerite complex (csc) connected to a sinuous brush sclerite with rugose surface formed by a combination of upraised papillate sculpticells and extremely transverse sculpticells; short flagellum present that lies appressed to left side of csc left lobe, with base extended basally, and apex an acuminate tip that extends to apical margin of csc left lobe; dorsal plate present immediately basodorsally csc left lobe, and ventral setal patch (vsp) present ventrad csc in uneverted sac (Fig. 3J).

Female Reproductive Tract.—(n=1). Bursa copulatrix thinly membranous, basally narrower, apically expanded in circumference (Fig. 5B); "L"-shaped annulus receptaculus present with basal arm longer than observed in *B. spurcum*; spermathecal duct passing through upright arm of annulus, configured with a complete coil and two abrupt turns, about 4-5× length of upright arm of annulus; spermatheca broad basally, side opposite spermathecal gland duct straight, apex broadly rounded and covered with annular constrictions; gland atrium composed of about 80 coils, constriction just beyond midlength; spermathecal gland secretory complex with tubular base about as long as atrium, and irregularly flocculent apical secretory region; gonocoxa narrow (Fig. 7B); basal gonocoxite 1 with one or two lateroapical setae; gonocoxite 2 narrowly triangular, with tightly rounded tip, two moderately-sized lateral ensiform setae and a small dorsal ensiform seta; apical nematiform setae short, 0.20× length of apical gonocoxite 2.

Type.—Lectotype male (BMNH) labeled "Gnatholymnaeum blackburni Type D.S. Kauai Perkins" hereby designated.

Nomenclatural Note.—Recognizing that *Gnatholymnaeum blackburni* Sharp 1903 is properly placed within *Bembidion* (Lindroth 1980) establishes *Bembidion blackburni* Csiki 1928 of Australia as a junior homonym. This latter species name was proposed to replace *Bembidion dubium* Blackburn 1888 due to its status as junior homonym of *Bembidion dubium* Heer 1837. *Bembidion ateradustum*, **new name**, is proposed as the second replacement name for *B. dubium* Blackburn, the epithet being a compound construction of the Latin words for black or piceous, and burn.

Distribution.—Kauai (Fig. 8): High Plateau [Kaholuamano vicinity], R.C.L.P. lot 682, 1210 m el.; Makaweli [Kalaluapuu], R.C.L.P. lot 640, 1210 m el. Oahu (Fig. 9): Kahana [above Waiahole Ditch]; Mt. Kaala summit, 1220 m el.; Poamoho Tr., 750 m el. Molokai (Fig. 10): T.N.C.H. Kamakou Pres., Puu Kolekole, Kolekole Cabin, 1180 m el., West Kawela Gulch, 1040-1100 m el.

Habits.—This species occurs in terrestrial, riparian microhabitats, including rocky, shaded streambeds, and cobble-covered shores of small, low-order streams. Such habitats are not generally associated with taxa exhibiting vestigial flight wings (Darlington 1936), though the brachypterous *Nabis gagneorum* Polhemus (1999), and the vestigially winged *Blackburnia munroi* (Sharp) and *Mecyclothorax palustris* (Sharp) (Liebherr and Zimmerman 2000, Liebherr 2007) occur syntopically in Molokai. Thus the banks of the low-order streams where *B. blackburni* has been collected afford ecological stability sufficient to maintain populations of several flightless species. It is also possible that *B. blackburni*'s ecological preferenda include mossy rock faces

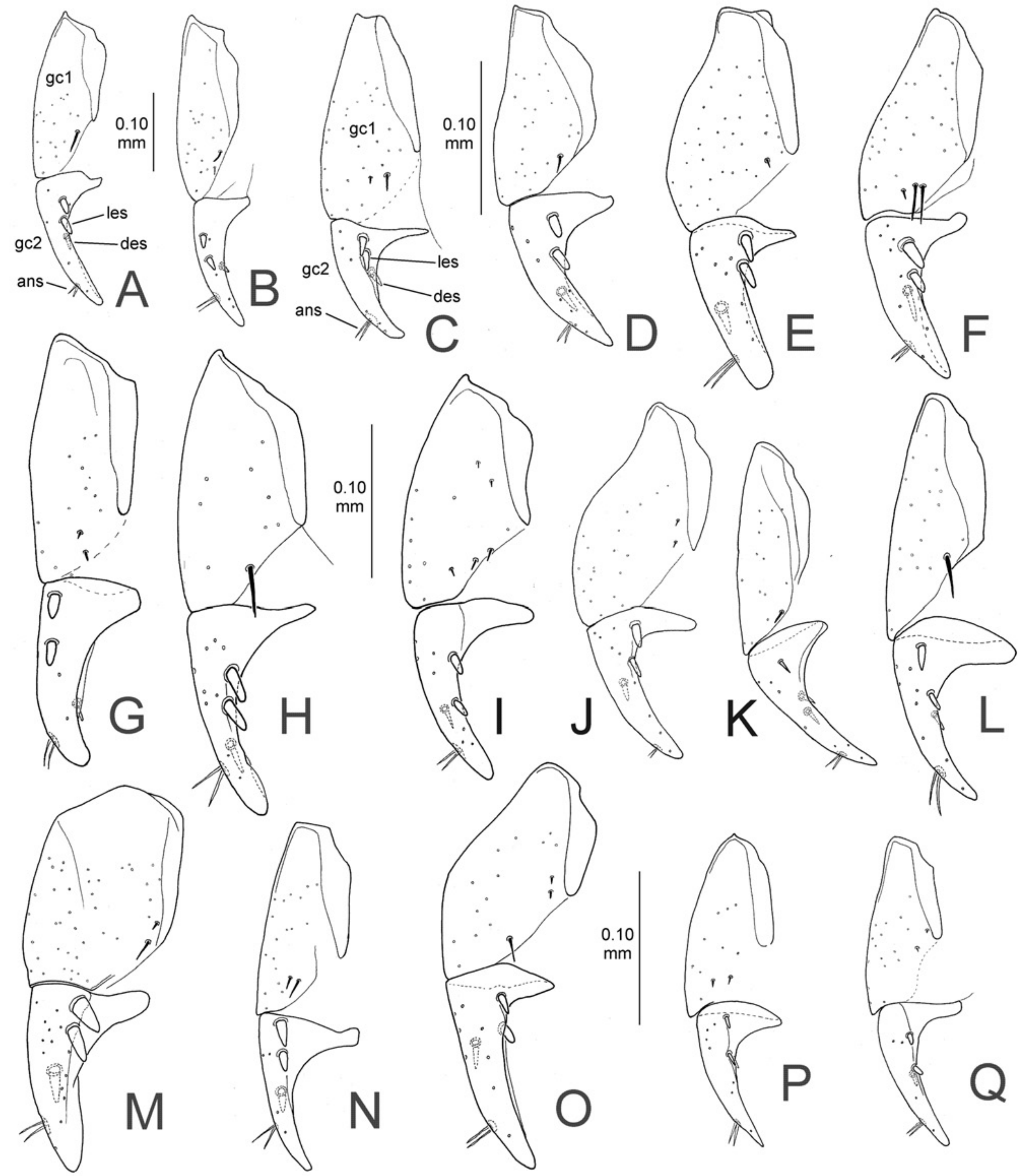


Fig. 7.—Left gonocoxa of *Bembidion* spp, ventral view. **A,** *B. spurcum*; **B,** *B. blackburni*; **C,** *B. ignicola* (Kauai); **D,** *B. ignicola* (Oahu); **E,** *B. ignicola* (East Maui); **F,** *B. ignicola* (Hawaii I.); **G,** *B. pacificum*; **H,** *B. teres*; **I,** *B. admirandum*; **J,** *B. munroi*; **K,** *B. rude*; **L,** *B. waialeale*; **M,** *B. smaragdinum*; **N,** *B. fulgens*; **O,** *B. corticarium*; **P,** *B. gagneorum*; **Q,** *B. haleakalae*. Figure codens: **ans,** apical nematiform setae; **des,** dorsal ensiform setae; **gc1,** basal gonocoxite 1; **gc2,** apical gonocoxite 2; **les,** lateral ensiform setae. Scale bar for 7A, B between drawings; scale bars for 7C-Q among drawings in each row.

or adjacent forest floor habitats, as in Darlington's (1936) examples of eastern North American vestigially winged *Bembidion*—*B. praticola* Lindroth and *B. semicinctum* Notman (Lindroth 1963)—that are distributed both along streams but also in damp microhabitats away from the water's edge.

Bembidion, subgenus ***Nesocidium*** Sharp, 1903, **new rank**

Nesocidium Sharp, 1903:280 (junior synonym of *Bembidion*, Britton 1948).
Atelidium Sharp, 1903:284 (junior synonym of *Bembidion*, Britton 1948; **New Synonymy,** junior synonym of *Nesocidium* Sharp).
Metrocidium Sharp, 1903:285 (junior synonym of *Bembidion,* Britton 1948; **New Synonymy,** junior synonym of *Nesocidium* Sharp).
Nesomicrops Sharp, 1903:286.
Bembidion (subgenus *Nesomicrops*), Britton 1948 (**New Synonymy,** junior synonym of *Nesocidium* Sharp).
Macranillus Sharp, 1903:287 (junior synonym of *Nesomicrops* Sharp, Britton 1948).

Diagnosis.—The various Hawaiian species of this subgenus vary considerably in overall habitus (Figs. 1D-J, 2, 3A-F), but share the following; 1, frontal grooves distinct to shallow and more ill-defined, subparallel on anterior portion of frons and not extended continuously from frons onto clypeus; 2, pronotal lateral marginal depression narrow along sinuate basolateral margin; 3, laterobasal pronotal depression shallow, continuous with lateral marginal depression anterad hind angle, laterobasal carina absent; 4, posterior pronotal seta, when present, situated anterad hind angle; 5, one or two dorsal elytral setae (if only one, the posterior seta ed5 is absent) free of the third elytral stria; 6, eight or nine lateral elytral setae, eo1-8 always present, median extra seta (Maddison 1993) present (*B. teres*) or absent; 7, metasternal process margined, margin at apex subequal to somewhat broader than margins at sides (e.g. Lindroth 1963, Fig. 148a, d, e) triangular apex may be elevated relative to more basal portion of process, and set off by medial arcuate continuation of lateromarginal beads; 7, male aedeagal median lobe with hypertrophied flagellar complex (Figs. 3K-M, 4), the flagellar base extended outside base of median lobe; 8, female spermathecal duct -bursa copulatrix junction without a distinct, sclerotized annulus receptaculus (Figs. 5C-F, 6); 9, female spermatheca heavily sclerotized and pigmented, appearing castaneous in cleared specimens, distinctly darker in color than translucent to transparent spermathecal duct.

Bembidion (Nesocidium) advena Sharp, 1903
(Figs. 1D, 18)

Bembidium (*Synechostictus*?) *advena* Sharp, 1903:278.
Bembidion advena: Britton, 1948:246.

Diagnosis.—Uniquely exhibiting elytra that have lateral margins subparallel at midlength, and a distinctly bicolored body (Fig. 1D), head capsule and prothorax dark brunneous with an aeneous luster, contrasted with flavous elytra that bear triangular lateral maculae and an ovoid median subapical macula; standardized body length 3.4 mm. Pronotal lateral marginal depression narrow throughout length, only slightly broader near lateral seta; dorsal elytral setae situated in depressions that span third interval and adjoining portions of adjacent intervals; elytral striae 1-7 continuous and punctate basally, shallower and impunctate apically but still traceable. Frons with distinct, reticulate isodiametric microsculpture; microsculpture on pronotal disc equally well-developed, but slightly transversely stretched; elytral disc with slightly transversely stretched isodiametric sculpticells, their lateral breadth up to twice their length. Metathoracic flight wing configuration not examined; metepisternum short, with lengths of anterior and lateral margins subequal. As all other Hawaiian *Bembidion* species that exhibit a short metepisternum have vestigial flight wings, it is hypothesized that individuals of *B. advena* are also vestigially winged.

Male Genitalia.—The unique male holotype has left protarsomeres 3-5 missing and left meso- and metalegs broken off and glued to the platen, and so the specimen was not dissected. The male aedeagus is partially everted from the specimen, and from what can be seen, the median lobe appears robust, as in *B. ignicola* (e.g. Figs. 3K-M), with the tip set off by slight constrictions relative to the more medial portion of the shaft, as in *B. admirandum* (e.g. Fig. 4C).

Type.—Holotype male (BMNH) platen-mounted on large card and labeled "Bembidion advena Type D.S. Haleakala Perkins 251."

Distribution.—Maui (Fig. 18): Haleakala [nr. Ukulele Camp] R.C.L.P. lot 251, 1524 m el.

Habits.—No ecological data are associated with the lone holotype specimen, though Perkins collected it in his lot 251, which includes the note "One unique carabid with light elytra black spotted taken by grubbing on 8.IV.`94 (Anonymous N.D.)." Thus it can be concluded that at least one individual of this species resided on the forest floor of *Acacia koa* A. Gray-*Metrosideros polymorpha* Gaud. mixed forest, an ecotope currently present just east of the Ukulele Camp site, Haleakala. Future collecting by grubbing and by Berlese extraction of leaf letter are likely the best means to rediscover this insect. Uncommonly collected species of *Mecyclothorax* Sharp—*M. sobrinus* Sharp and *M. multipunctatus* (Blackburn) (Britton 1948)—have been discovered using the former technique at this locality (Liebherr 2000).

Bembidion (Nesocidium) ignicola Blackburn, 1879
(Figs. 1E-H, 3K-M, 5C, 7C-F, 8, 9, 10, 11, 12)

Bembidion (*Lopha*) *ignicola* Blackburn, 1879:109.
Bembidium (*Emphanes*) *ignicola:* Sharp, 1903:279.
Bembidium (*Emphanes*) *molokaiense* Sharp, 1903:279 (**New Synonymy**).

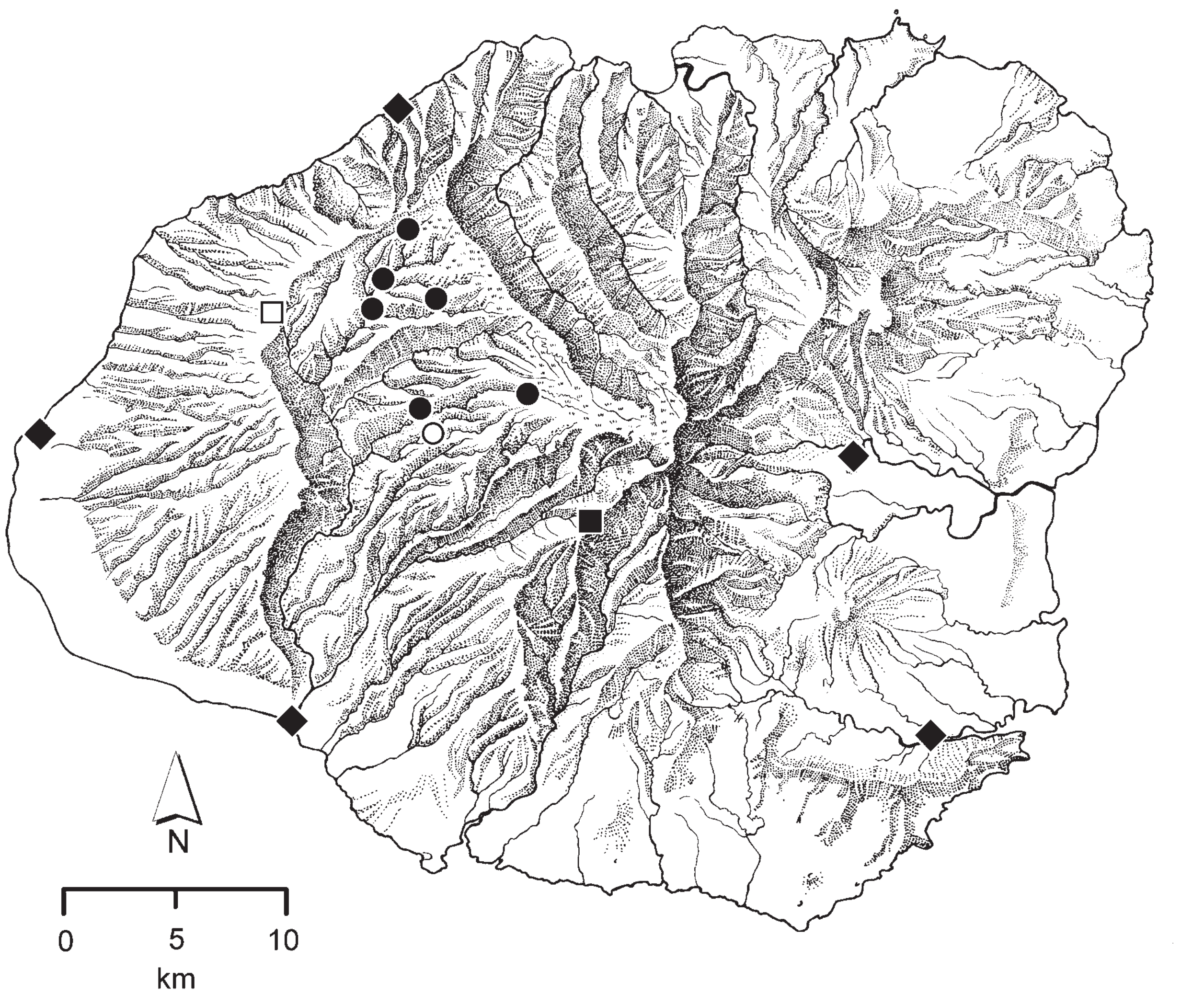


Fig. 8.—Distributional records in Kauai for: *B. niloticum* (◆); *B. blackburni* (■); *B. ignicola* (●); *B. spurcum* + *B. ignicola* (□); *B. blackburni* + *B. ignicola* (○).

Nesocidium laeticulum Sharp, 1903:280 (synonymy Britton 1948).
Nesocidium lahainense Sharp, 1903:281 (synonymy Britton 1948).
Bembidion molokaiense: Britton, 1948:248.

Diagnosis.—Smaller beetles, standardized body length 2.7-3.1 mm; dorsal body surface piceous with aeneous to caeruleus reflection; frons smooth, shiny between distinctly incised frontal grooves, at most with indistinct sculpticells near clypeal margin; pronotal disc without evident microsculpture, indistinct transverse lines visible over portions of the surface; humeri variably developed, from quadrate and broad (Fig. 1E, F) to slightly more rounded (Figs. 1 G, H), but lateral elytral margins always more parallel at midlength than the most similar metallic species (*B. koebelei* of Oahu, *B. smaragdinum* of Molokai, *B. fulgens* of Maui, and *B. auratum* of Hawaii I.; Figs. 2E-G, K); elytral striae 1-4 continuous and punctate in basal half, striae 5-7 progressively less impressed, stria 7 a series of isolated punctures in some individuals; anterior dorsal elytral seta situated in depression that spans interval 3, posterior seta in depression in some individuals, situated in a coplanar portion of interval 3 in others; margin of metasternal process 2-3× as broad at apex than on sides of process, tip coplanar to slightly elevated relative to base.

Male Genitalia.—(n=14). Aedeagal median lobe broad, apex with evenly rounded tip that is not downturned (Figs. 3K-M); parameres of equal length, 3-setose, broader left paramere gradually narrowed to a narrowly rounded tip; central sclerite complex (csc) arcuately extended beyond base of median lobe; brush sclerite covered with longitudinally elongate, raised scales, csc left and right lobes apparently fused, the portion connected to elongate flagellum determined by homology encoded in the system of Maddison (1993) to be the left lobe; flagellar length estimated

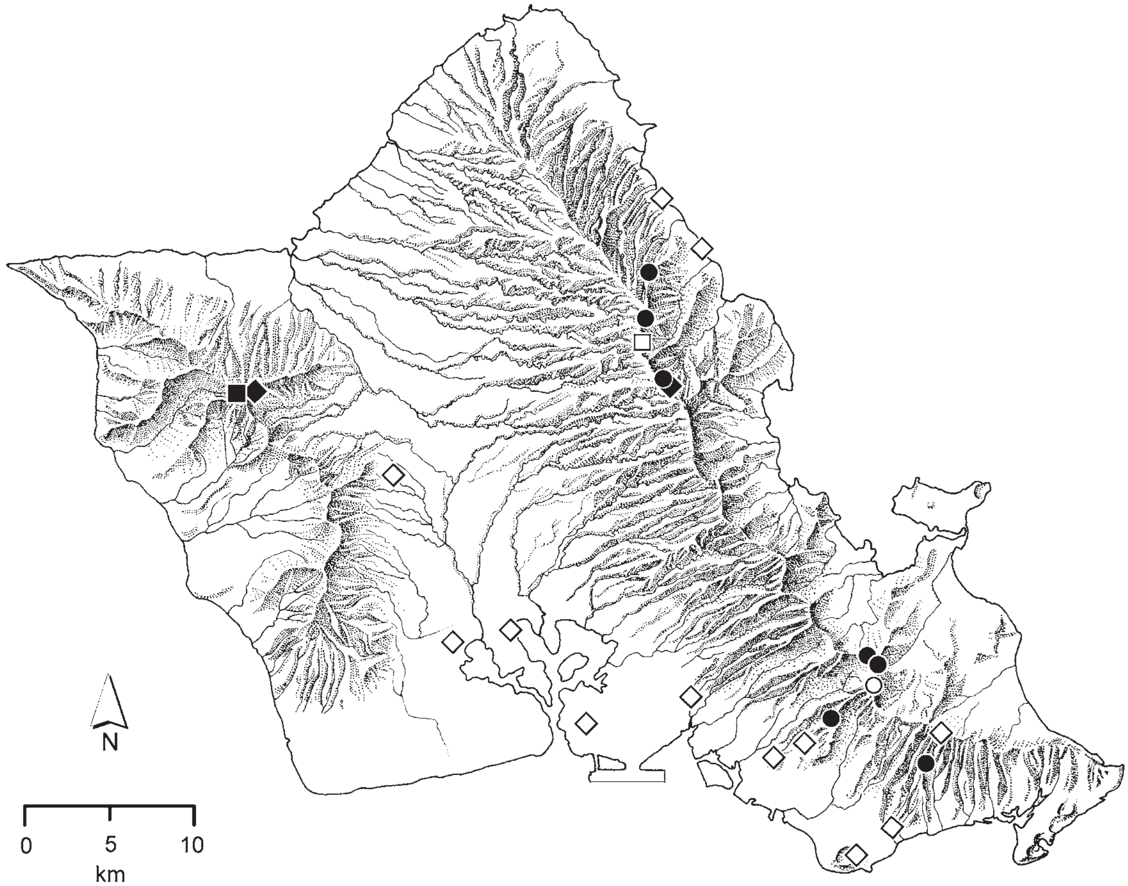


Fig. 9.—Distributional records in Oahu for: *B. niloticum* (◇); *B. spurcum* (■); *B. spurcum* + *B. blackburni* (□); *B. ignicola* (●); *B. blackburni* + *B. ignicola* (◆); *B. ignicola* + *B. koebelei* (○).

to be 1.0 mm (compared to 0.7 mm straight-line length of median lobe measured from base of basal bulb to rounded tip); flagellum held within an elongate flagellar sheath—presumably with U-shaped transverse profile—the sclerotized sheath base extended to point basad the csc left lobe, and connected to a membranous sheath that surrounds the entire brush sclerite + csc left lobe + flagellum complex.

Female Reproductive Tract.—(n=6). Bursa copulatrix thinly membranous, apically expanded with lobe to left of junction with common oviduct (Fig. 5C); spermathecal duct flexible, transparent overall, but with crescent of darker, granulate cuticle on one side of duct near entry to bursa, elongate, about 1.1 mm long; spermatheca broadly ovoid but with shallow medial constriction, spermathecal gland duct entering just basad constriction on side opposite spermathecal duct; spermathecal gland atrium composed of about 25 taenidia-like coils; gland secretory complex about 1.5× length of atrium; gonocoxa moderately broad (Figs. 7C-F); basal gonocoxite 1 with one to three lateroapical setae, count often differing bilaterally by one; apical gonocoxite 2 with two lateral ensiform setae, the apical seta at the base of the lateral cutting margin, apex acuminate in dorsoventral aspect (Figs. 7C, D, F), broadly rounded in lateral aspect (Fig. 7E); two moderately elongate apical nematiform setae.

In one specimen from Oahu, the base of the spermathecal duct is plugged by an elongate, opaque, tubular structure that is interpreted as the remnants of a male spermatophore. The structure is approximately 0.10 mm long, and about one-tenth that in diameter.

Variation.—This species is found on all islands, and displays both ontogenetic and geographic variation. Metathoracic flight wing polymorphism is among the most obvious forms of variation. Individuals may be: 1, macropterous, with fully developed flight wings including a reflexed apex when folded under the elytra; or 2, brachypterous, with flight wings anywhere from 0.4 mm to 1.2 mm long (Sharp 1903:281). In all individuals, whether macropterous or brachypterous, the metepisternum is elongate, with the lateral margin longer than the anterior margin.

The elytra may display a testaceous subapical macula laterad stria 4 and just posterad the posterior dorsal elytral seta (Fig. 1E). This pale window appears to be

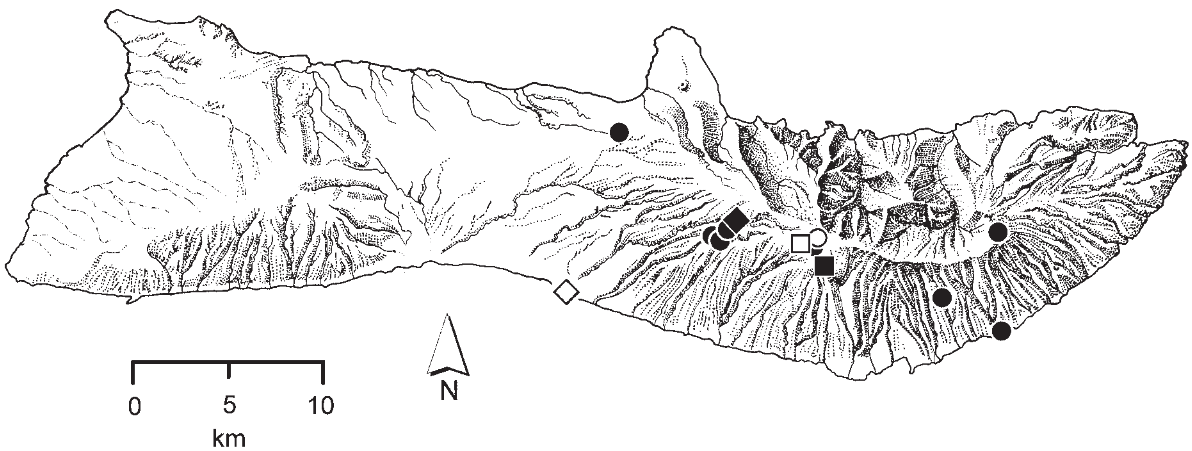


Fig. 10.—Distributional records in Molokai for: *B. niloticum* (◇); *B. spurcum* (◆); *B. ignicola* (●); *B. spurcum* + *B. blackburni* + *B. ignicola* (■); *B. spurcum* + *B. blackburni* + *B. ignicola* + *B. teres* (□); *B. ignicola* + *B. teres* (○).

developmentally variable, as most teneral individuals exhibit it, and more fully sclerotized and melanized individuals may or may not exhibit it. This suggests that this portion of the elytron may melanize later in adult life than the rest of the body. As it is not possible to ascertain the actual age of individuals by their melanization, there may also be genetic variation in this trait, with some individuals retaining the pale macula throughout life. Finally, there is a geographic component to this trait, as more otherwise fully melanized beetles from Kauai tend to exhibit this macula, though there are also Kauai beetles that have completely piceous elytra. Conversely, beetles from Oahu, Molokai, Maui and Hawaii I. more prevalently display completely piceous elytra without the macula.

Pronotal shape also varies in this species, and this trait appears to have a geographic basis. Beetles from Kauai, Oahu, and Molokai (e.g. Figs. 1E, F) have a more transverse pronotum, with the ratio of maximum width to median pronotal length > 1.24. Beetles from East Maui and Hawaii I. have a narrower prothorax (Figs. 1G, H), with the ratio of pronotal width to length < 1.22. Beetles from West Maui are more variable in this trait, with individuals falling into either category.

The multiple patterns of variation, based both on adult maturity, genetic variability, and geography suggest a widespread species that has colonized the various islands infrequently, leaving the various island populations isolated from each other. Overlain on this large-scale pattern is the ecologically associated trait of wing polymorphism, with individuals selected for wing configuration based on the stability, persistence and isolation of their habitats (Southwood 1977).

Types.—For *Bembidion ignicola* Blackburn, male holotype (BMNH), platen-mounted with "Blackburn Hawaii I. code (Zimmerman 1957) on obverse, 'Kalaiaeha ignicola' on reverse." The type locality is apparently Kilauea—not Kalaieha, a locality near Puu Oo on Mauna Kea—based on Blackburn's statement "Unique, found in a hot steam crack, beside the crater Kilauea on Mauna Loa, at an elevation of about 4000 feet, in February (Blackburn and Sharp 1885:217)." For *Bembidium molokaiense* Sharp, female lectotype (BMNH) labeled "Type D.S. Molokai Perkins 177." For *Nesocidium laeticulum* Sharp, female lectotype (BMNH) labeled "Nesocidium laeticulum Type D.S. Kauai Perkins 256 (left specimen on card)" hereby designated. For *Nesocidium lahainense* Sharp, female lectotype (BMNH) labeled "Nesocidium lahainense Type D.S. Lahaina Koebele" hereby designated.

Distribution.—Kauai (Fig. 8): Alakai Swamp Tr., Kawaikoi Str., 1125 m el.; High Plateau [Kaholuamano vicinity], R.C.L.P. lots 256, 273, 509, 528, 563, 631, 682 (Anonymous N.D.), 1210 m el.; NaPali Kona For. Res., Mohihi Rdg.; Mohihi-Waialae Tr., 1030 m el., Pihea Tr., 1000 m el., Waiakoali Str., Camp 10 Rd., 1030 m el.; Waialae Cabin, Waialae R., 1090-1210 m el. Oahu (Fig. 9): Castle Tr., Kaluanui, 700 m el.; Kahana, above Waiahole Ditch; Konahuanui, 790 m el.; Mt. Kaala, 1207 m el.; Nuuanu Pali, Lulumahu Str., 665 m el.; Punaluu [Helemano], 820 m el.; Schofield-Waikane Tr., 760 m el.; Tantalus summit; Waialae Iki. Molokai (Fig. 10): Halawa Tr.; Kalae, R.C.L.P. lot 172; T.N.C.H. Kamakou Pres., East Kawela Gulch, 1097-1170 m el., West Kawela Gulch 1040-1100 m el., Puu Kolekole vicinity, 1097-1207 m el.; Kamiloloa, 915 m el.; Makalihua, above, 745 m el.; Manawainui Vy.; Mapulehu; Molokai Mts. [Makakupaia], R.C.L.P. lot 174, 915 m el., [Onini Gulch], 175 m el., [West Kawela Gulch], R.C.L.P. lot 595, 1210 m el., [about 2000 ft.], R.C.L.P. lot 177, 605 m el.; Puu Ohelo. Lanai: Haalelepaakai to Waiakeakua Saddle trail on NE ridge, 985 m el. Maui (Fig. 11): Haleakala: Haipuaena, 455 m el.; Haleakala N.P., Haleakala Crater, Paliku, Puu Koolau vicinity, 2195-2255 m el, Kipahulu Vy., 940-2100 m el., Kuiki, 2130-2285 m el., Leleiwi overlook, 2010 m el., NW upper slope, Halemauu Tr., 2285 m el., Northeast Rift, New Greensword Bog, 1850 m el.; Hana For. Res., Heleleikeoha Str. fence camp, 1615 m el., Waihoi Vy., 600-1372 m el.; Hanawi N.A.R., 1680 m el., Kuhiwa Str. E Poouli Cabin, 1615 m el., Kuhiwa Vy., 1585 m el.; Honomanu; Keanae; North Slope, 455 m el.; Waikamoi Flume, Waikamoi Gulch to Haipuaena Gulch, 1310 m el.; T.N.C.H. Waikamoi Pres., Ukulele Pipeline, 1524 m el. West Maui Mountains: Hanaula reservoirs, 1210 m el.; Lahaina; Lihau N.A.R., 1060-1235 m el.; Mt. Eke N.A.R., 1330-1335 m el. Hawaii I. (Fig. 12): Hilo, Saddle Rd., trail N of road, 1240 m el.; Kau For. Res., 1160 m el., Mountain House Rd., 915 m el.; Kilauea, 1210 m el.; Kilauea-Hilo Rd., 29 miles; Kilauea, Volcano House; Kilauea For. Res.; Kohala Watershed, Upper Hamakua Ditch, Kawainui Str., 1210 m el.; Waikaloa Str. above Waimea; Laupahoehoe N.A.R., Blair Rd., 1230 m el.; Volcano, Kilauea S.R.A., 1160 m el.

Habits.—Individuals of *B. ignicola* have been encountered most often in riparian microhabitats, where they can be found in fine sand and gravel under stones, or in moss or on wet rock faces. The species also occurs in forest

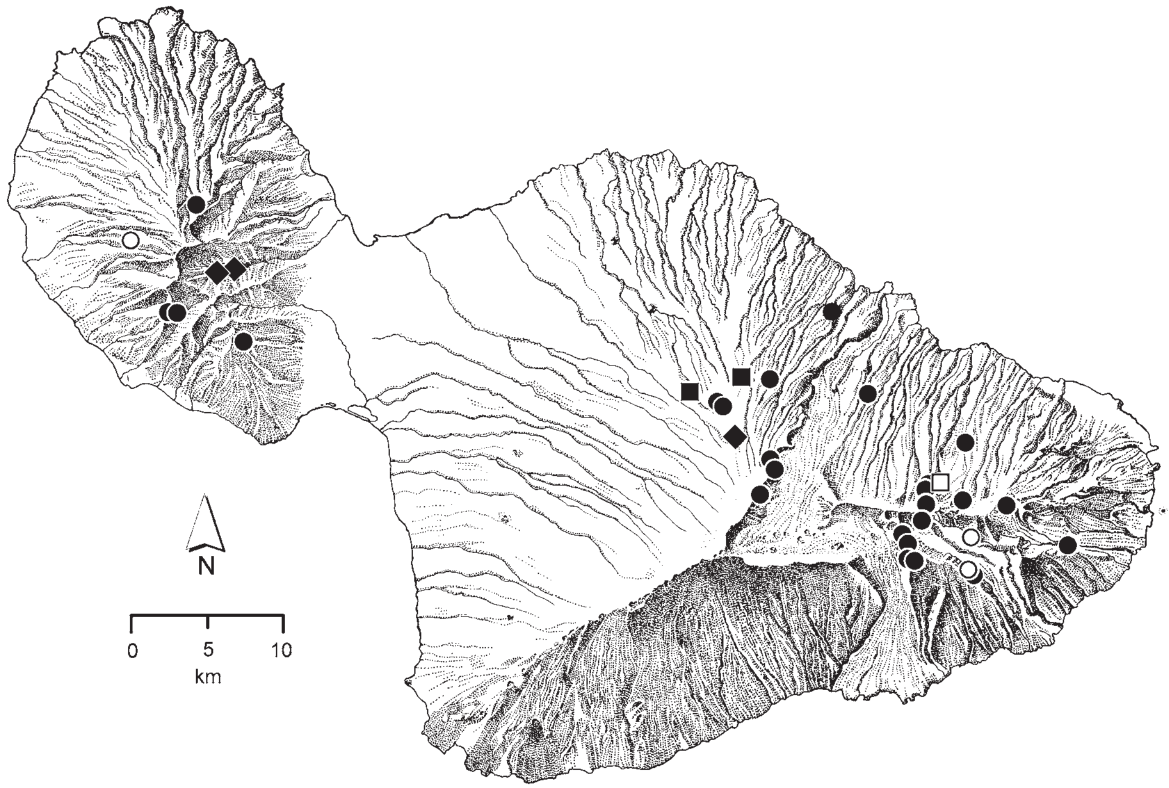


Fig. 11.—Distributional records in Maui for: *B. spurcum* (■); B. teres (◆); *B. ignicola* (●); *B. spurcum* + *B. teres* + *B. ignicola* (□); *B. teres* + *B. ignicola* (○).

habitats, and individuals have been recovered from sifted litter from *Metrosideros* forest floor, and from near *Cibotium* tree ferns. This author's first series was collected by pouring water onto moss-covered *Cibotium* ferns living in a mowed lawn at the Kilauea State Recreation Area house. The holotype was collected by Blackburn "in a steam crack beside the crater Kilauea, Hawaii, where I almost burned my fingers securing it (1879:109)." The initial presentation of this extreme habitat may have facilitated the later synonymic species descriptions of Sharp (1903), as the specimens Sharp examined and described were from more typical streamside and forest floor habitats. Blackburn himself was not fooled, as he determined a specimen from Maui as *B. ignicola* (BMNH).

Bembidion (Nesocidium) pacificum Blackburn, 1878 (Figs. 1I, 4A, 5D, 7G, 13, 15)

Bembidium (*Lopha*) *pacificum* Blackburn, 1878:157.
Bembidium (*Emphanes*) *pacificum:* Sharp, 1903:279.
Bembidion pacificum: Britton, 1948:247.

Diagnosis.—This species is most similar to *B. teres* (Figs. 1I, J), but: 1, individuals consistently smaller, standardized body length 3.7-4.1 mm; 2, frontoclypeal suture distinctly depressed between frontal grooves; 3, pronotum with short sinuation anterad setose hind angles, the basolateral margins divergent from just anterad setal articulatory socket; and 4, elytral humeri more rounded. Frons with transversely stretched isodiametric mesh between frontal grooves, the grooves with distinct lateral margin defined by broad ridge mesad anterior supraorbital seta; pronotal disc with mixture of isodiametric microsculpture in laterobasal depressions and more transverse sculpticells on convex portions of disc; elytral striae 1-7 broadly depressed in basal 0.75 of elytral length, distinctly punctate in basal half of length, punctures expanded onto adjoining intervals; elytral intervals convex basally with granulate, slightly transversely stretched sculpticells, the intervals flat and sculpticells less elevated near apex; prosternal process with triangular, elevated apex, marginal bead on sides continuous with arcuate bead that defines basal border of elevated apical triangle. Metathoracic flight wings fully developed, wing fold defining reflexed apex visible beneath anteromedial edge of pale apical elytral macula.

Male Genitalia.—(n=2). Aedeagal median lobe elongate, evenly arcuate to rounded, non-protruded apex (Fig. 4A); left paramere 1.5× as long as right, apex a blunt rectangular projection extended one-half its width beyond broader parameral base, right paramere narrow with apex tightly rounded, both 3-setose; flagellar complex extremely hypertrophied, with csc and flagellum extended beyond margin of basal bulb 1.5× length of flagellar path within median lobe; surface of brush sclerite shagreened, covered with

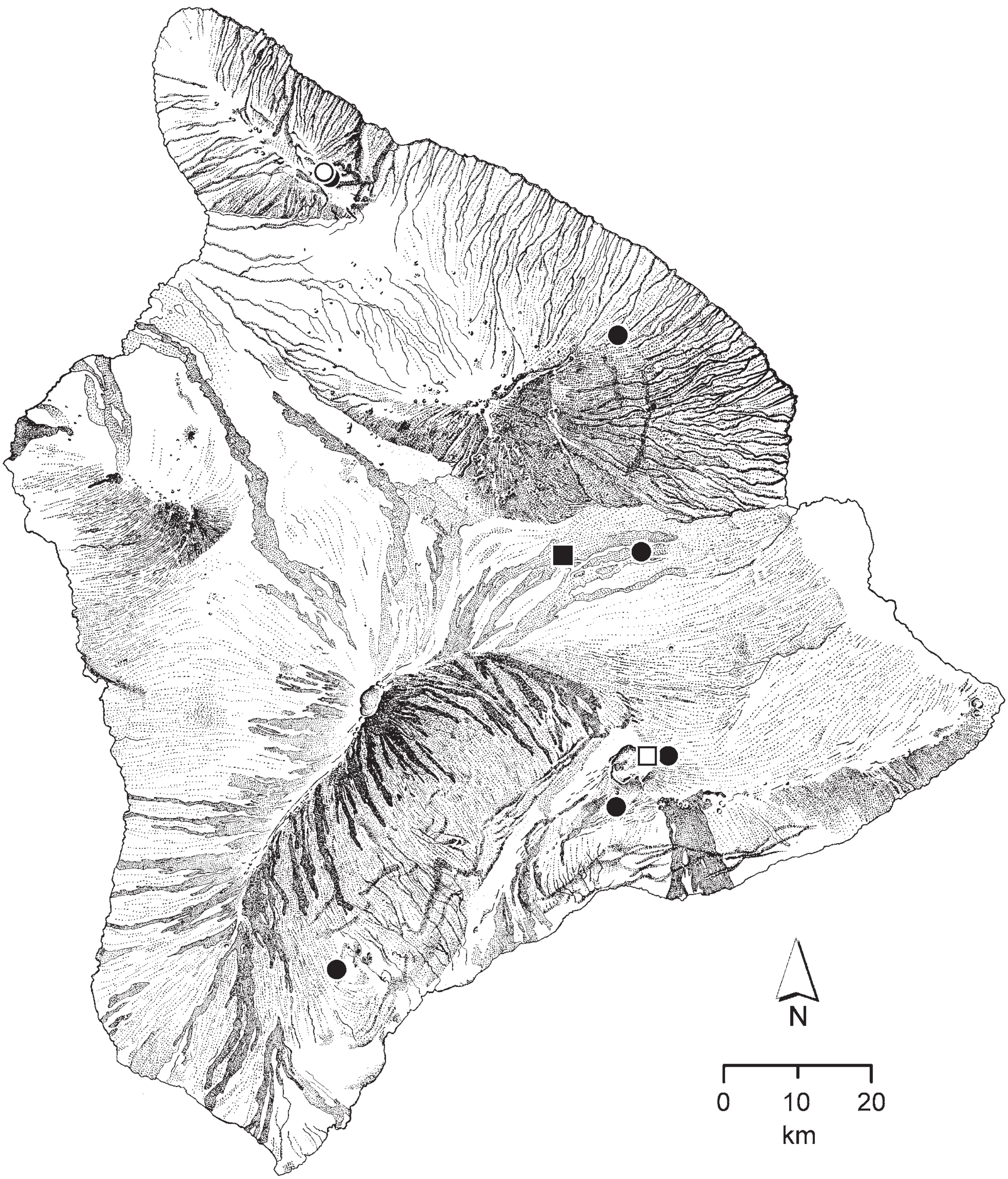


Fig. 12.—Distributional records in Hawaii Island for: *B. ignicola* (●); *B. auratum* (■); *B. ignicola* + *B. auratum* (□); *B. ignicola* + *B. niloticum* (○).

densely packed elongate scales that are distinctly keeled; central sclerite complex connected basally to flagellum that is held within flagellar sheath, the articulation homologously determined to be with the csc left lobe, though left and right lobes appear fused; flagellum and flagellar sheath supported near base of median lobe by an elongate sclerite covered with strigose sculpticells arranged in a longitudinally undulated pattern, herein coined the secondary flagellar sclerite (sfs, Fig. 4A); flagellum estimated to be 3.0 mm long, compared to straight-line measure of 1.2 mm from base of median lobe basal bulb to median lobe apex.

Female Reproductive Tract.—(n=1). Bursa copulatrix thinly membranous, columnar, gradually narrowed to insertion of spermathecal duct (Fig. 5D); spermathecal duct quite sclerotized and inflexible, with intensely coiled region near midpoint, estimated length 2.8 mm; spermatheca ovoid, spermathecal gland entering on side opposite duct; gland atrium composed of approximately 80 taenidia-like coils; gland secretory complex about 1.5× length of atrium; gonocoxa of moderate width, basal gonocoxite 1 with two short lateroapical setae (Fig. 7G); apical gonocoxite 2 with two lateral ensiform setae positioned near mesal edge of coxite base, one small dorsal ensiform seta near apical limit of lateral cutting margin, and two moderately short apical nematiform setae.

Type.—Lectotype male (BMNH), platen-mounted with "Blackburn Waianae Mts., Oahu label (Zimmerman 1957) on obverse, 'pacificum' on reverse" hereby designated.

Distribution.—Kauai (Fig. 15): Mts. above Waimea [Kaholuamono], R.C.L.P. lots 256, 273, 1210 m el. Oahu (Fig. 13): Waianae Mountains (locality unknown); Honolulu; Pauoa Vy.; Tantalus, R.C.L.P. lot 545; behind Tantalus.

Habits.—All collections of this species have been in ground-level habitats (e.g. Blackburn and Sharp 1885:217), including among dead *Elaeocarpus bifidus* Hooker & Arnott (Elaeocarpaceae) leaves, and in a small wet gulch. *Elaeocarpus* trees occur in mesic to wet forest, and along margins of bogs in Kauai and Oahu (Wagner et al. 1990). One additional specimen was found by grubbing. Blackburn (1878) noted that the species was "Rare, but widely distributed, from the sea level to an elevation of about 3000 feet" on Oahu. The most recent Oahu specimens of this species were collected in 1920, and the only Kauai collections were made by R.C.L. Perkins in 1894 (Liebherr 2004).

Bembidion (Nesocidium) teres Blackburn, 1881
(Figs. 1J, 4B, 5E, 7H, 10, 11, 13)

Bembidium (*Lopha*) *teres* Blackburn, 1881:229.
Bembidium (*Synechostictus*) *teres:* Sharp, 1903:278.
Bembidion teres: Britton, 1948:246.

Diagnosis.—Beetles of this species look like an elongated version of *B. pacificum*, with longer overall body length, standardized body length 4.3-5.0 mm; pronotal basolateral sinuation more elongate, the lateral margins subparallel for a short distance anterad basal seta; and elytral humeri broad, quadrate, the lateral elytral margins straighter posterad humeri (Fig. 1J). Sharp (1903) noted the diagnostic frontoclypeal sutural configurations in these two species, with *B. teres* exhibiting a suture that is little depressed medially relative to the medial surfaces of the frons and clypeus. Frontal grooves broadly depressed, deepest mesad broad ridge mesad anterior supraorbital seta; frons with granulate isodiametric microsculpture, the sculpticells more transverse on dorsum of neck; pronotal disc with evident transverse-mesh microsculpture; elytral striae shallow but continuous in basal 0.75 of elytral length, punctate, the punctures little expanded onto adjoining intervals; elytral intervals nearly flat, covered with isodiametric sculpticells; extra seta (Maddison 1993) medially augments lateral setae eo1-8; apex of pro-sternal process broadly angulate, basal sides angled relative to apical faces, marginal bead of subequal width throughout. Metathoracic flight wings fully developed, wing fold defining reflexed apex visible beneath anteromedial portion of pale apical elytral macula.

Male Genitalia.—(n=3**).** Aedeagal median lobe elongate, evenly arcuate on shaft, the tightly rounded, slightly protruded apex more downturned (Fig. 4B); left paramere 1.67× as long as right, apex a narrow, tubular, parallel-sided projection twice as long as broad, the apical projection distinct from broader basal portion of paramere, both parameres 3-setose; flagellar complex identical to that of *B. pacificum* above, even to identical estimate of 3.0 mm flagellar length and 1.2 mm median lobe length.

Female Reproductive Tract.—(n=2). Bursa copulatrix thinly membranous, columnar, gradually narrowed to insertion of spermathecal duct (Fig. 5E); spermathecal duct quite sclerotized and inflexible, with broader basal region, and apical intensely coiled region extended to spermatheca, estimated length 2.8 mm; spermathecal duct walls composed of polygonally tiled cuticle, the tiled sculpticells irregularly four- or five-sided; duct cuticle distorted into serial ridges on insides of curves; spermatheca ovoid with a medial constriction, spermathecal gland duct entering just basad constriction on side opposite spermathecal duct; gland atrium composed of approximately 85 taenidia-like coils; gland secretory complex about 1.5× length of atrium.

The female specimen successfully dissected with its spermatheca and gland assembly intact (Fig. 5E) has a long asciform sclerotized structure lodged in the base of the spermathecal duct, and a second more irregularly folded tubular structure loose in the bursa copulatrix. The lodged asciform structure is 0.60 mm long and has two more heavily staining regions (Chlorazol Black) near the apical end. Both are interpreted as remnants of one or more male spermatophores.

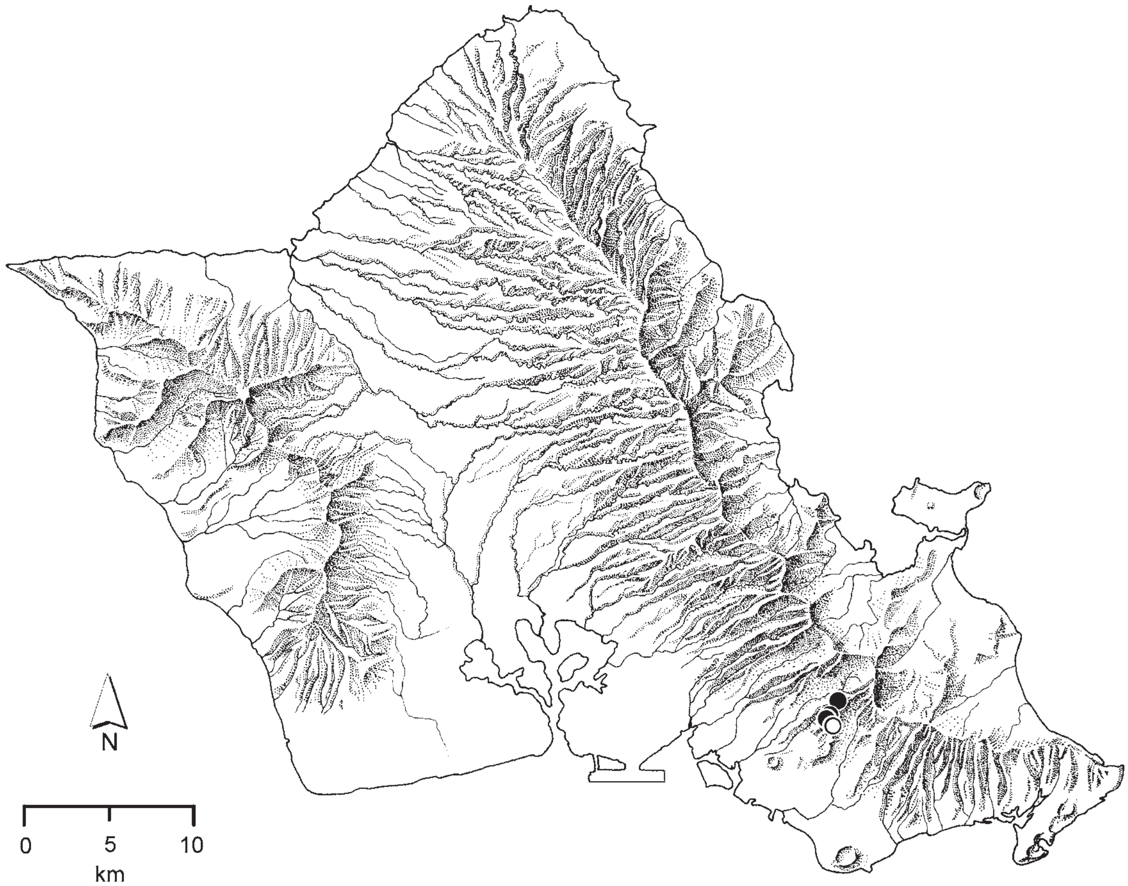


Fig. 13.—Distributional records in Oahu for: *B. pacificum* (●); *B. pacificum* + *B. teres* (○).

Type.—Lectotype male (BMNH) labeled "Blackburn Maui label (Zimmerman 1957) on obverse, 'teres' on reverse" hereby designated. The type locality of "Haleakala…4000 feet (Blackburn 1881)" corresponds to the vicinity of Waikamoi Gulch.

Distribution.—Kauai: [island record only]. Oahu (Fig. 13): Tantalus 605 m el.; Waialae Mts. [Waialua Mts? = Mt. Kaala]. Molokai (Fig. 10): T.N.C.H. Kamakou Pres., East Kawela Gulch, 1097 m el., West Kawela Gulch at water tunnel, 1100 m el.; Molokai Mts. [West Kawela Gulch], R.C.L.P. lot 595, 1210 m el. Maui (Fig. 11): Haleakala, 1210 m el., R.C.L.P. lot 845, 915 m el.; Haleakala N.P., Kipahulu Vy., Kaukauai Str., 915-1433 m el., Palikea Str., 1060 m el; Hana For. Res., Heleleikeoha Str., 1615 m el.; Hanawi N.A.R., 1830 m el., Kuhiwa Str., 1615 m el.; T.N.C.H. Waikamoi Pres., Honomanu drainage, upper arm, 1950 m el. West Maui Mountains: above Lahaina, R.C.L.P. lot 709, 915 m el.; Iao Valley, R.C.L.P. lots 118, 689.

Habits.—Nearly all specimens of this species have been found along streams, either under rocks, streamside vegetation or in moss. One specimen was labeled in association with *Melicope* (Rutaceae), known in Hawaiian as alani. Blackburn (1881) described the species from a series of two specimens collected "in decaying leaves, at an elevation of about 4000 feet" on Haleakala, during the month of May (Blackburn and Sharp 1885).

Bembidion (Nesocidium) admirandum (Sharp, 1903)
(Figs. 2A, 4C, 6A, 7I, 14)

Metrocidium admirandum Sharp, 1903:286.
Bembidion admirandum: Britton, 1948:252.

Diagnosis.—Among all Hawaiian *Bembidion*, beetles of this species are uniquely distinguishable by the very broadly explanate, glabrous pronotal lateral margins (Fig. 2A); as in some individuals of *B. munroi*, the elytra bear pale humeral and lateroapical maculae, but individuals of *B. admirandum* are generally larger, standardized body length 2.9-3.5 mm. Among species with well-developed elytral striae, *B. admirandum* lacks a separate parascutellar stria, the base of sutural stria 1 continous with punctures laterad scutellum. This character is also exhibited by some individuals of *B. munroi*. Males of *B. admirandum* can be instantly determined based on the above plus the configuration of the male aedeagus wherein the flagellar complex is greatly extended from the base of the median lobe (Fig. 4C). Alternatively, females can be unambiguously determined by the greatly swollen base of the spermathecal duct (Fig. 6A). Frontal grooves deeply incised, bordered laterally by upraised, parallel-sided callosity that itself is separated from position of anterior supraorbital seta and posterior portion of eye margin by a second parallel groove, posterior supraorbital seta on mesal edge of callosity; pronotal hind angles acute, basal pronotal setae positioned anterad angle, basolateral margins parallel for twice distance from basal setae to basal margin; pronotal laterobasal depressions broad, linearly delimited mesally and surface bearing approximately 10 broad punctures; discal elytral striae deep and broad, lined with deep punctures separated by 1-3× their diameter, elytral intervals convex, broadly rounded; elytral apex with only sutural and eighth stria present; frontal grooves lined with distinct transverse sculpticells, frons shinier, with transverse sculpticells irregularly occurring in shallow, irregular depressions; pronotal disc shiny, covered with shallow transverse-mesh microsculpture; elytral intervals very shiny, microsculpture obsolete. Metepisternum very short, anterior margin longer than lateral margin; metathoracic flight wings vestigial, reduced to very short flaps of cuticle without any evidence of veins, apex extended only to adjacent posterior margin of metanotum; metasternal process with elevated apical triangle, lateromarginal bead continuous and slightly broadened medially where it defines basal border of upraised apical triangle.

Variation.—A single male specimen assigned herein to *B. admirandum* was collected on Mt. Kahili, the highest crest of the southern spur radiating from Mt. Waialeale (Fig. 14). This specimen has a standardized body length of 2.9 mm, discontinuously smaller than the 3.1-3.5 mm length range for all other specimens. The specimen is quite piceous and shiny, and the elytral intervals are flatter than in other *B. admirandum* specimens, though one side of the elytron is indented indicating some trauma during eclosion, or before hardening of the elytral cuticle. The pronotal lateral marginal depressions are also narrower than in other specimens of *B. admirandum*, though broader than the similar *B. munroi*. However, dissection showed the male aedeagus median lobe, and greatly extended flagellar complex to completely match that of a bonafide specimen of *B. admirandum*, even agreeing in overall length of the median lobe, though the specimen is nearly 10% smaller in overall length. Thus, if this specimen represents a distinct species, that taxon would be the sister taxon to *B. admirandum*. Rather than inflate biodiversity based on dubious criteria, it is proposed that further specimens be sought from Mt. Kahili in order to better characterize that population.

Male Genitalia.—(n=3). Aedeagal median lobe broad dorsoventrally, ventral surface straight at midlength, apex downturned with narrowly rounded, slightly protruded tip (Fig. 4C), tip covered with numerous pore canals and very short longitudinal grooves; left paramere 1.3× as long as right, with truncate 3-setose projection medioapically, projection 3× as long as broad; right paramere also 3-setose, the medioapical setal articulatory socket spanning narrow apex, mesal of three setae subapical; flagellar complex greatly extended beyond base of median lobe, length of extended portion more than twice path of flagellum inside median lobe; secondary flagellar sclerite at about midpoint of extended portion of flagellum; flagellum length estimated to be 2.1-2.2 mm, compared to straight-line measure of 0.9 mm from base of medial lobe basal bulb to medial lobe apex.

Female Reproductive Tract.—(n=1). Bursa copulatrix broad overall, vagina bordered ventrally between gonocoxal bases by a cuticular fold bearing scallop-shaped sculpticells, bursa apically with spermathecal duct associated with right-lateral lobe, and common oviduct entering at medioapical constriction; spermathecal duct composed of thick, inflexible, translucent cuticle, duct base swollen (Fig. 6A), its diameter 5× duct diameter more apically near spermatheca (microslide preparation), total length of duct estimated to be 1.3 mm; spermathecal duct microsculpture in basal swollen area limited to rod-like region of transverse sculpticells along inner surface of basal curve, duct walls near base of narrow duct covered with transverse sculpticells, duct walls near spermatheca composed of polygonal four- to six-sided sculpticells, their transverse breadth relative to the duct subequal to slightly greater than their length; spermatheca ovoid with median constriction, spermathecal gland duct entering near constriction on side opposite spermathecal duct; gland atrium composed of approximately 72 taenidia-like coils; gland secretory complex subequal in length to atrium; gonocoxa broad (Fig. 7I), basal gonocoxite 1 with one to three lateroapical setae; apical gonocoxite 2 with broad base, falcate lateral margin and tightly rounded apex; gonocoxite 2 with two lateral ensiform setae along middle of lateral cutting margin, one dorsal ensiform seta dorsad apical lateral seta, and two moderately long apical nematiform setae.

In the dissected female, the spermathecal duct is filled with a purplish stained material (Chlorazol Black) from the duct-bursal junction to the completely looped portion of duct basad the spermatheca (Fig. 6A). This material is transversely broken in several places, and near the duct base includes a thin attenuated projection that protrudes into the bursa. The bursa copulatrix also contains a sinuous, slerotized structure floating free on the lumen. These structures are interpreted as the remnants of one or more male spermatophores.

Type.—Holotype female (BMNH) labeled "Metrocidium admirandum Type D.S. Kauai Perkins 682 // Type // …1904-336 // High Kauai Plat: Perkins VIII 96.

Distribution.—Kauai (Fig. 14): Halalea For. Res., Namolokama Mtn., 1305-1340 m el., High Plateau [Kaholuamano vicinity], R.C.L.P. lot 682, 1210 m el.; Mt. Kahili, 895 m el.; NaPali-Kona For. Res., Alakai Swamp Tr., 1160 m el., E of Kawaikoi Str., 1215-1230 m el., Pihea Tr., 1000 m el.

Habits.—Most individuals of this species have been encountered in terrestrial microhabitats, collected either

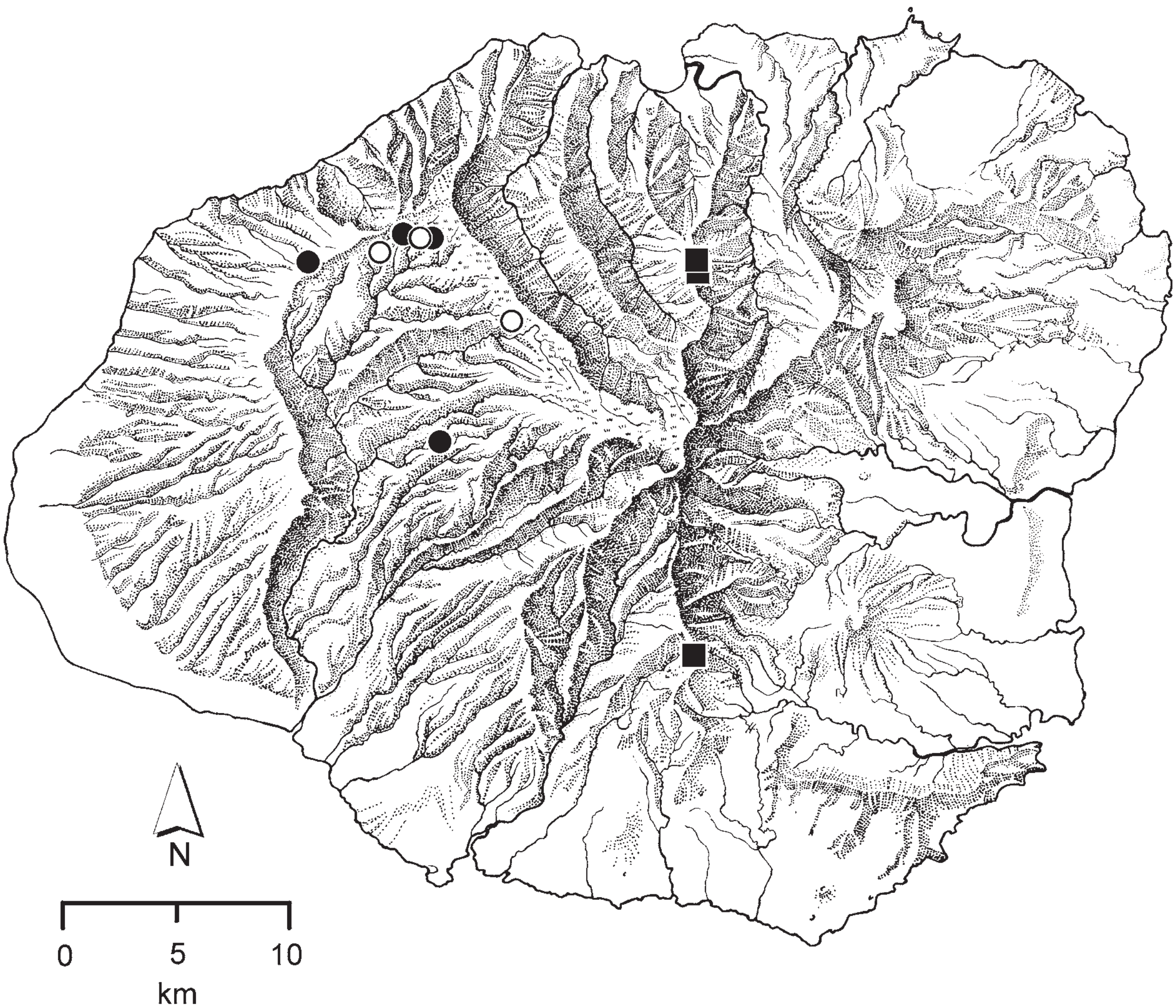


Fig. 14.—Distributional records in Kauai for: *B. admirandum* (■); *B. munroi* (●); both species (○).

from leaf litter extractions, or by hand-collecting as they walked on ground-level mossmats at night. Two individuals were obtained from moss-covered *Metrosideros* using pyrethrin insecticide.

Bembidion (Nesocidium) munroi (Sharp, 1903)
(Figs. 2B, 4D, 6B, 7J, 14)

Atelidium munroi Sharp, 1903:285.
Metrocidium brevicolle Sharp, 1903:285 (**New Synonymy**).
Atelidium munronis Seidlitz, 1904:164 (unjustified subsequent spelling).
Bembidion munroi: Britton, 1948:252.
Bembidion munroi var. *brevicolle:* Britton, 1948:252.

Diagnosis.—These small-bodied very convex beetles (Fig. 2B)—standardized body length 2.6-3.1 mm—are diagnosable by: 1, frons shiny between frontal grooves, very indistinct transverse lines loosely joined into a mesh in some individuals representing the most distinct indication of microsculpture, other individuals without micro-sculpture; 2, pronotum lacking lateral seta, pronotal hind angles setose or glabrous; 3, pronotal basolateral margin distinctly sinuate, lateral marginal depression very narrow throughout length, basal margin evenly arcuate between very obtuse hind angles; 4, elytral striae deeply incised, elytral intervals convex. Metathoracic flight wings vestigial, apex not extended beyond adjacent posterior margin of metanotum; metepisternum short, anterior and lateral margins of equal length; metasternal process broadly triangular, marginal bead slightly broader at apex than laterally.

Variation.—This precinctive Kauai species shows remarkable variation relative to that shown even in other much more geographically widespread Hawaiian species. The pronotal hind angle may be setose or glabrous, the latter condition the basis for Sharp's *Metrocidium brevicolle*.

The posterior dorsal elytral seta may be present or absent. This seta is monomorphically absent in *B. paratomarium*, *B. gagneorum* and *B. atomarium* of Oahu, *B. kamakou* of Molokai, and *B. haleakalae* of East Maui. Thirdly, the base of the sutural stria variously aligns with the parascutellar stria, making it appear that the parascutellar stria is absent. Alternately, the basal punctures and intermediate depressed regions of the sutural stria may be angled laterally and parallel to the parascutellar stria, allowing recognition of the latter as distinct. Elytral coloration also varies among individuals of *B. munroi*, with some individuals exhibiting concolorous brunneous to piceous elytra, and others possessing pale, rufous areas on the humeral and lateroapical margins. As in *B. ignicola*, this variation in melanization may be related to adult maturity, or it may have a genetic and/or population-level basis.

Male Genitalia.—(n=1). Aedeagal median lobe moderately broad dorsoventrally, ventral margin straight nearly to apex (Fig. 4D); median lobe tip narrow and tightly rounded apically, tip length twice breadth, its surface covered by numerous longitudinal strigae; left paramere 1.25× as long as right, apex 3-setose with short parallel-sided projection upon which setae are positioned; flagellar complex not extended from inside basal bulb of medial lobe; flagellum length estimated to be 0.6 mm, compared to straight-line measure of 0.7 from base of median lobe basal bulb to median lobe apex.

Female Reproductive Tract.—(n=1). Bursa copulatrix vase-shaped, basally narrower, apically expanded laterally, spermathecal duct entering to right of common oviduct (Fig. 6B); spermathecal duct composed of flexible, translucent cuticle, with curved basal expansion and narrow looping apical portion, basal expansion with longitudinal ridge of sclerotized cuticle on face nearest common oviduct, estimated length of duct 0.60 mm; apical portion of spermathecal duct covered with polygonal four- to six-sided sculpticells, their transverse breadth relative to duct orientation subequal to slightly greater than their length; spermatheca ovoid with median constriction, spermathecal gland duct entering near constriction on side opposite spermathecal duct; gland atrium composed of approximately 56 taenidia-like coils; gland secretory complex 1.5× length of atrium; gonocoxa broad (Fig. 7J), basal gonocoxite 1 with two small lateroapical setae; apical gonocoxite 2 with broad base, falcate lateral margin and narrow apex; gonocoxite 2 with two lateral ensiform setae near base along ridge just ventrad of lateral cutting margin, one slightly more apical dorsal ensiform seta, and two short apical nematiform setae.

Types.—For *Atelidium munroi* Sharp, lectotype female (BMNH) labeled " Atelidium munroi Type D.S. Kauai Perkins 256 // Type // …1904-336 // Mts. Waimea Kauai 4000 ft. Perkins V 1894" hereby designated. For *Metrocidium brevicolle* Sharp, lectotype female labeled "Metrocidium brevicolle Type D.S. Kauai Perkins 256 // Type // …1904-336 // Waimea Kauai 4000 ft. Perkins V 1894" hereby designated.

Distribution.—Kauai (Fig. 14): Kokee S.P., Ka Unu o Hua Ridge, 1298 m el.; NaPali Kona For. Res., Alakai Swamp Tr., 1160 m el., Alakai Swamp Tr. E Kawaikoi Str., 1230 m el., Alakai Swamp Tr.-Pihea Tr. Junction, 1180 m el., Mohihi Ridge Tr., 1255 m el.; Mts. above Waimea or High Plateau [Kaholuamano vicinity], R.C.L.P. lots 256, 528, 563, 631, 682, 1210 m el.

Habits.—This species exhibits terrestrial habits, occurring in leaf litter and in moss on roots and trunks of *Metrosideros*. Specimens have been collected by beating and sifting mossy substrates, and by grubbing.

Bembidion (Nesocidium) rude (Sharp, 1903)
(Figs. 2C, 4E, 5F, 7K, 15)

Nesocidium rude Sharp, 1903:283.
Bembidion rude: Britton, 1948:247.

Diagnosis.—The deep, indistinctly punctate elytral striae in combination with the bicolored elytra, wherein pale humeri, lateral margins, apex and sutural striae contrast with the piceous disc (Fig. 2C), serve to diagnose this species. Among Kauai species, *B. rude* is most similar to *B. waialeale* (Fig. 2D); however it can be diagnosed by: 1, broader pronotum and pronotal lateral margins; 2, more convex elytral intervals; 3, broader, more ovoid elytra. Frons with granulate isodiametric microsculpture; pronotal disc covered with transverse-mesh microsculpture; elytral intervals with indistinct transverse-mesh microsculpture, most evident in association with broadly depressed elytral striae; prosternal process with elevated apical triangle that fits into mesosternal notch, marginal bead of basal sides continuous and arcuate medially, defining base of raised apical triangle. Metathoracic flight wings vestigial; metepisternum subquadrate, anterior and lateral margins subequal. Standardized body length 2.8-3.4 mm.

Male Genitalia.—(n=1). Aedeagal median lobe broad dorsoventrally, heavily sclerotized flagellar sheath defining eudorsal surface near base of basal bulb, apex projected and evenly rounded, slightly more downturned than median shaft which is straight medioventrally (Fig. 4E); left and right parameres of subequal length, 3-setose; flagellar complex extended beyond basal margin of median lobe about 0.27× length of lobe measured from base of basal bulb to apex, csc and its articulation with flagellum exhibiting 90° dextral torsion (i.e. counterclockwise) relative to orientation of median lobe; flagellum supported in a heavily sclerotized ventral supporting sclerite just basad ostium; internal sac surface near ostium covered with isolated, papillate spicules; flagellum length estimated to be 0.7 mm, compared to straight-line measure of 0.7 mm from base of median lobe basal bulb to median lobe apex.

Female Reproductive Tract.—(n=2). Bursa copulatrix thinly membranous, short and broad, apically narrowed to broad spermathecal duct (Fig. 5F); spermathecal duct inflexible, with single large coil before spermatheca, cuticle transparent near bursa, heavily sclerotized

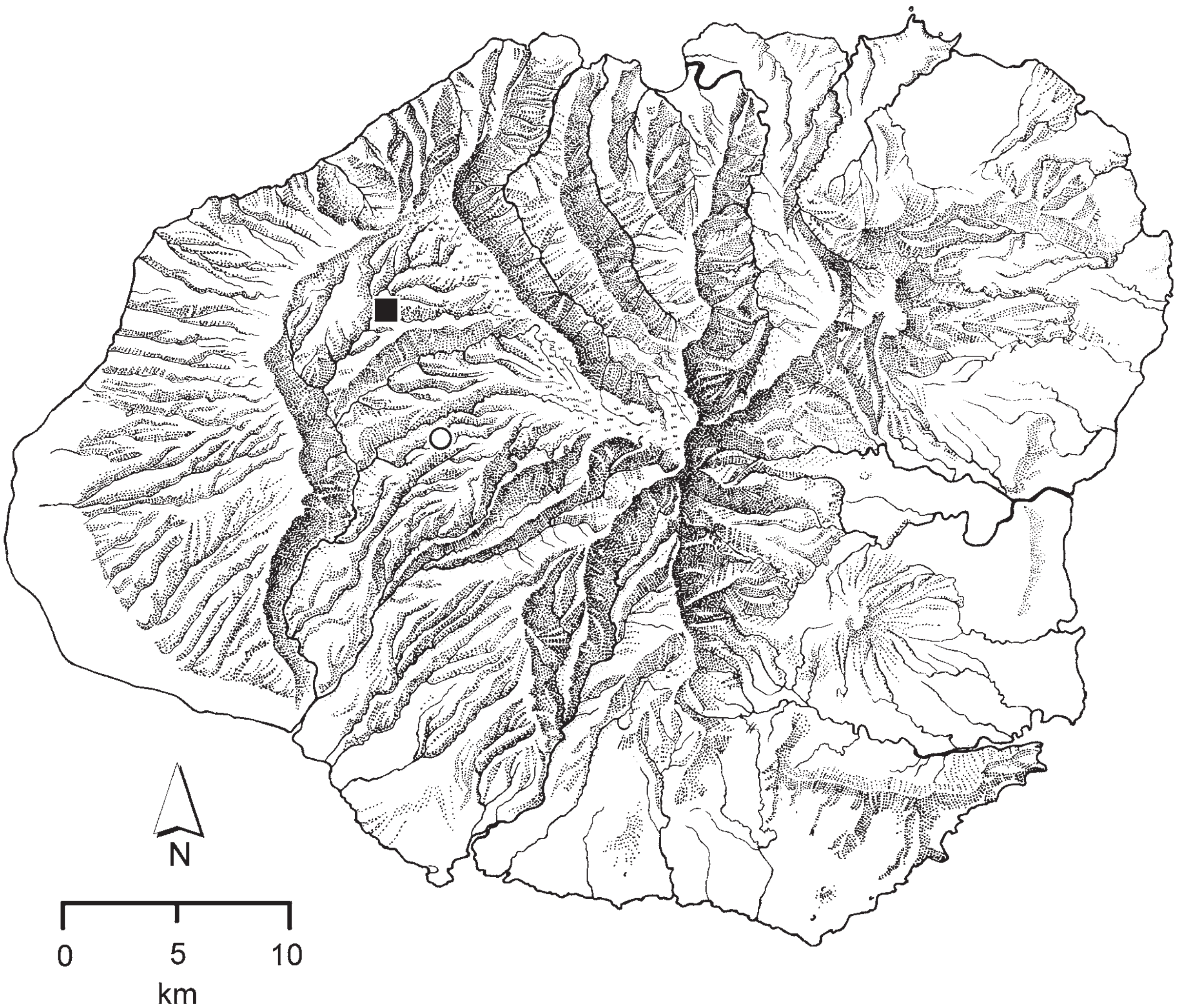


Fig. 15.—Distributional records in Kauai for: *B. rude* (■); *B. rude* + *B. perkinsi* + *B. pacificum* (○).

apically, in broader basal region covered with transverse rows of transverse, polygonal four- to six-sided sculpticells, in less-broad apical region scuplticells more quadrate, total duct length approximately 0.4 mm; spermatheca ovoid with medial constriction, spermathecal gland duct entering basad medial constriction on side opposite spermathecal duct; gland atrium composed of about 32 taenidia-like coils; gland secretory complex about 1.5× length of atrium; gonocoxa very narrow, basal gonocoxite 1 with one to two small lateroapical setae; apical gonocoxite 2 narrow basally, apex narrowly acuminate, with two small lateral ensiform setae, the more apical just dorsad lateral cutting margin, and an even smaller dorsal ensiform seta closer to apex; gonocoxite 2 with two short apical nematiform setae.

Type.—Lectotype male (BMNH) labeled "Nesocidium rude Type D.S. Kauai Perkins 682 // Type // … 1904-366 // High Kauai Plat. Perkins VIII 1896" hereby designated.

Distribution.—Kauai (Fig. 15): High Plateau [Kaholuamano vicinity], R.C.L.P. lots 528, 682, 1210 m el., Mohihi Ridge, south face.

Habits.—All we know of the habits of this species comes from Perkins' somewhat oblique comment regarding a collecting visit to Kauai: "Some special attention was given to collecting the very remarkable Bembidiids amongst which were *Nesocidium rude*, *Nesomicrops kauaiensis*, *Metrocidium admirandum* and *Macranillus caecus* [sic]. These turned up in a vain endeavour to discover the presence of the '*Cyclothorax'* group of ground beetles on Kauai, since they are found in such situations as one would search for some of these *Cyclothorax* on the other islands (Perkins 1896:2)."

***Bembidion (Nesocidium) waialeale*, new species**
(Figs. 2D, 4F, 6C, 7L, 16)

Diagnosis.—Slender beetles with body dorsum brunneous

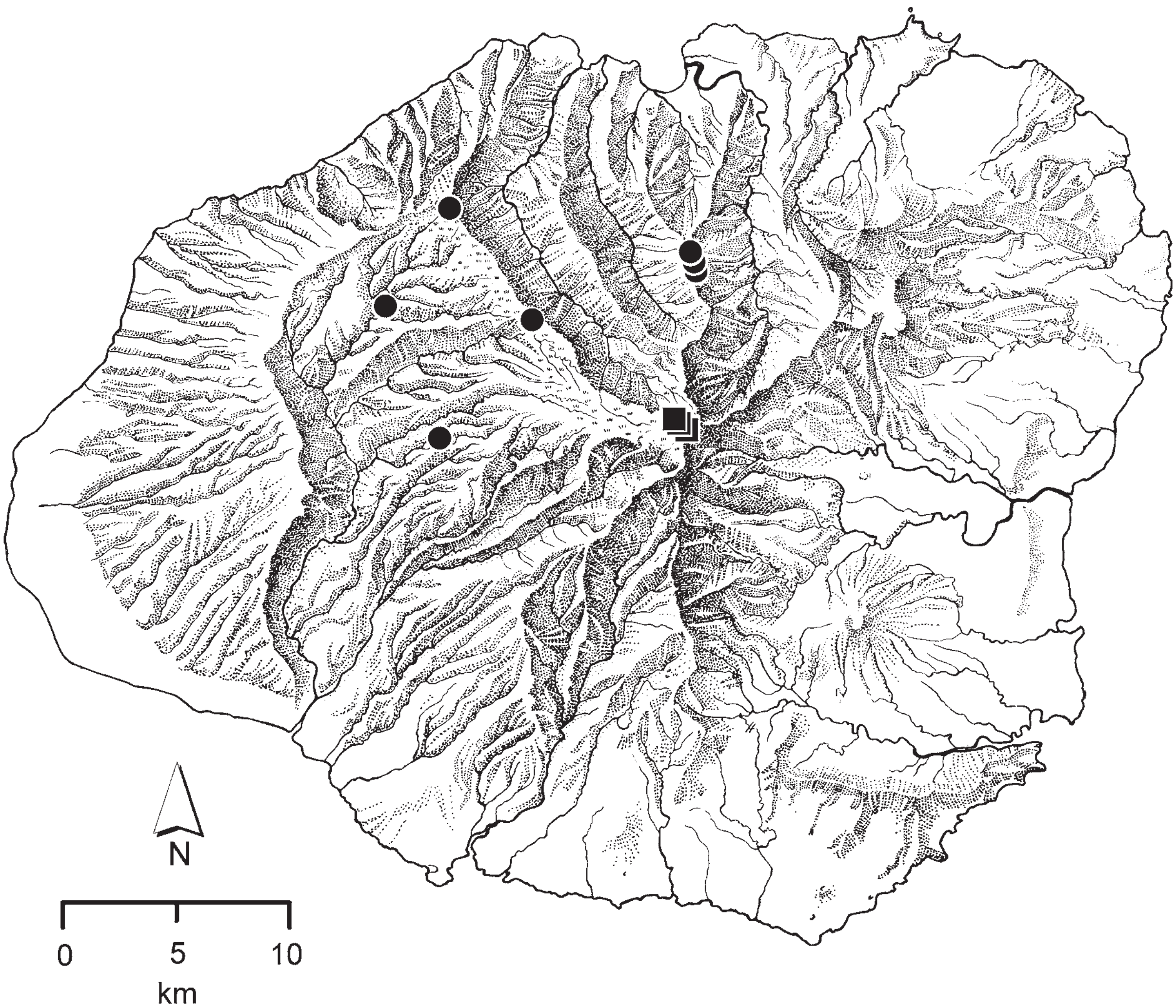


Fig. 16.—Distributional records in Kauai for: *B. waialeale* (■); *B. corticarium* (●).

and legs testaceous (Fig. 2D); eyes well developed, convex; frons with evident microsculpture consisting of slightly transverse sculpticells in transverse rows; pronotum elongate, lateral margin reflexed throughout length, broader at lateral pronotal seta; pronotal disc shiny, with indistinct transverse sculpticells over portions of surface; elytral striae shallow, striae 1-3 indistinctly punctate in basal half, striae 4-6 shallow and slightly wavy basally, stria 7 obsolete; standardized body length 3.1-3.4 mm.

Description.—Frons broadly convex between shallow but distinct frontal grooves that sinuously continue anterolaterally from frons onto clypeus to terminate on clypeal lateral margin just anterad antennal insertion; anterior supraorbital seta separated from frontal grooves by low, narrow ridge; posterior supraorbital seta posterad line drawn between hind margins of eyes; mentum tooth broadly triangular, apical marginal bead broadest medially. Pronotal basal setae inserted distinctly anterad hind angle, about halfway between angle and anterior termination of basolateral sinuation; pronotal base with approximately 8-10 shallow, indistinct indentations each side of midline, median longitudinal impression shallow on median base, discontinuous and partially obsolete on disc, anterior transverse impressions very shallow and broad; anterior marginal bead broadly obsolete medially, its margin gradually deepened toward rounded, non-protruded front angles; prosternal projection unmargined on ventral surface, broad apex tightly curved to upright posterior face. Elytra elongate-ovoid; basal groove absent tightly angled humerus; parascutellar stria shallow, with 4-6 punctures; parascutellar seta ed1 near basal junction of parascutellar and sutural striae; two free dorsal elytral setae (ed3, 5), both in depressions that span third interval and cause striae 2 and or 3 to converge slightly; two ed7 setae in position of obsolete stria 7; one ed8 seta near apex, closer to margin than to suture; lateral elytral setae of stria 8 grouped as four anterior setae (eo1-4), and four posterior setae (eo5-8), with stria 8 apically diverging from lateral margin just anterad subapical sinuation. Metathoracic flight wings vestigial; metepisternum short, anterior and lateral margins of equal length; metasternal process apex with upraised acuminate tip, sides directly basad tip more broadly divergent than basal sides adjoining posteromedial face of mesocoxal socket, marginal bead of process continuously arcuate medially, defining base of upraised acuminate tip.

Coloration.—In addition to diagnosis: maxillary and labial palpomeres with testaceous ground color and piceous infuscation, especially on penultimate palpomere; antennomeres 1 and 2 testaceous, antennomeres 3-4 darker, more infuscated, apical 7 antennomeres with smoky cast;

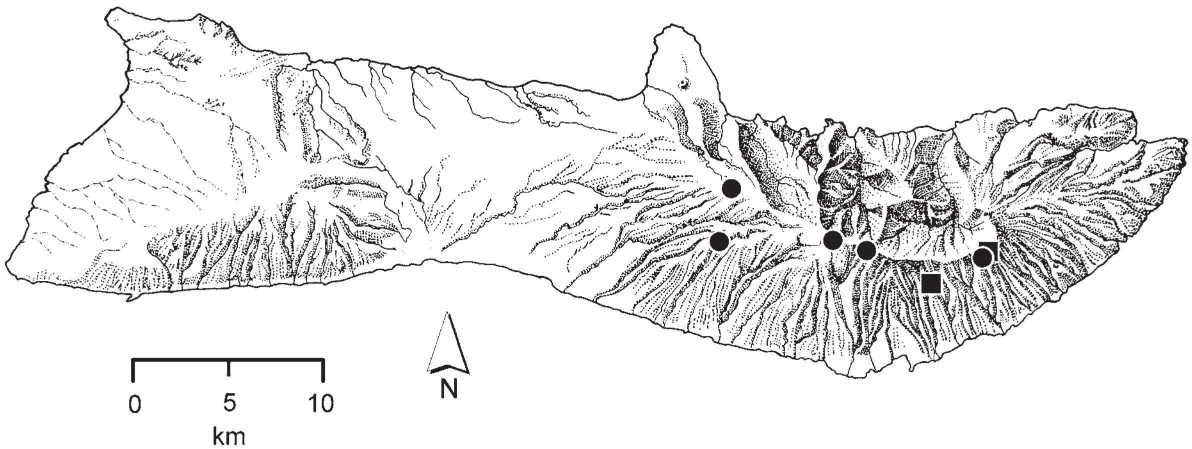


Fig. 17.—Distributional records in Molokai for: *B. smaragdinum* (●); *B. kamakou* (■).

ventrally, pronotal epipleura palest, rufoflavous, thoracic and abdominal ventrites and metacoxae rufobrunneous, inner margin of elytral epipleura paler to match pronotal epipleura, outer edge darker to match brunneous dorsum; legs including pro- and mesocoxae testaceous, tibiae and tarsi with slight smoky cast.

Male Genitalia.—(n=2). Aedeagal median lobe broad dorsoventrally, rounded, slightly protruded apex slightly downturned from curve of median shaft, ventral margin of shaft straight near middle of length (Fig. 4F); left paramere 1.2× as long as right, with narrow 3-setose tubular projection mesolaterally at apex, a fourth parameral seta along mesal margin at base of tubular projection; right paramere 3-setose, with two apical setae, and a third on mesal margin as far from apex as length of tubular projection on left paramere; flagellar complex extended beyond base of basal bulb about one-half length of median lobe measured from base of basal bulb to apex; base of secondary flagellar sclerite visibly protruded from base of median lobe basal bulb; flagellum estimated to be 1.2 mm long, compared to straight-line measure of 0.70 mm from base of medial lobe basal bulb to medial lobe apex.

Female Reproductive Tract.—(n=1). Bursa copulatrix thinly membranous, short and broad, truncate apex supporting moderately broad spermathecal duct and common oviduct (Fig. 6C); spermathecal duct well-sclerotized but somewhat flexible, basally curved, sinuous, apically curved into two loops, one side of duct in basal half with extremely evident slightly transverse sculpticells, the other half of diameter without evidence of heavy sclerotization, polygonal sculpticells completely surrounding duct near apex at spermatheca, duct length approximately 1.0 mm; spermatheca ovoid, gland atrium entering on side opposite spermathecal duct; gland atrium composed of 40 taenidia-like coils; gland secretory complex 1.5× length of atrium; gonocoxa of moderate breadth, basal gonocoxite 1 with a single larger lateroapical seta; apical gonocoxite 2 broadly expanded basally, constricted to narrowly acuminate apex, with two small lateral ensiform setae, one small dorsal ensiform seta, and two moderately long apical nematiform setae.

Type.—Holotype male (CUIC): HI: Kauai Waialeale summit 16-V-1995 lot 01 1515-1530 m beating mossy ohia J.K. Liebherr // Holotype Bembidion waialeale J.K. Liebherr 2007.

Paratypes.—Kauai (Fig. 16): Waialeale summit, beating mossy *Metrosideros*, 1524-1530 m el., 16-V-1995 lot 01, Liebherr (CUIC, 1), 17-V-1995 lot 01, Liebherr (CUIC, 1), beating mossy *Metrosideros* at night, 1524-1530 m el., 17-V-1995 lot 04 Liebherr (CUIC, 2); Waialeale summit, pyrethrin fog mossy *Dubautia*, 1570 m el., 18-V-2005 lot 01, Liebherr (CUIC, 1), Waialeale summit gulch, pyrethrin fog mossy *Dubautia*, 1530 m el., 18-V-2005 lot 05, Liebherr (CUIC, 14), pyrethrin fog *Cheirodendron/Metrosideros*, 1510 m el., 18-V-2005 lot 10, Polhemus (BMNH, 4; BPBM, 20; NMNH, 25).

Etymology.—The species epithet should be treated as a noun in apposition, as it is derived from the type locality of Mt. Waialeale.

Habits.—All specimens of this species have been associated with arboreal mosses growing on *Dubautia waialealae* Rock, *Metrosideros polymorpha*, and *Cheirodendron trigynum* (Gaud.) A. Heller. They have been collected by beating mossy branches, and via application of synthetic pyrethrin insecticide.

Bembidion (Nesocidium) smaragdinum (Sharp, 1903)
(Figs. 2E, 4G, 6D, 7M, 17)

Nesocidium smaragdinum Sharp, 1903:282.
Bembidion smaragdinum: Britton, 1948:253.

Diagnosis.—This plus *B. fulgens* and *B. auratum* constitute a trio of species consisting of small-bodied, brilliantly metallic beetles with ovoid elytra (Figs. 2E-G). *Bembidion smaragdinum* alone has the frons shiny between the frontal grooves, without evident microsculpture. This species differs from *B. fulgens* of Maui by larger body size, standardized body length 2.8-3.2 mm, and pronotum without evident discal microsculpture. It differs from *B. auratum* of Hawaii I. by the more convex elytral intervals, and the punctations of striae 1-4 that extend to the longitudinal position of the posterior dorsal elytral seta. Metathoracic flight wings vestigial, consisting of a triangular flap with sclerotized anterior margin, apex not extended beyond adjacent posterior margin of metanotum; metepisternum short, anterior and lateral margin subequal; metasternal process triangular, broadly margined, bead width at apex 3× as wide as bead width along sides.

Male Genitalia.—(n=1). Aedeagal median lobe broad dorsoventrally, median shaft evenly curved, apex slightly upturned relative to median shaft, apex protruded and evenly rounded (Fig. 4G); left paramere length about 1.2× right paramere length, both 3-setose, seta on mesal margin of each slightly more basal; flagellar complex extended beyond basal margin of median lobe about 0.25× length lobe measured from base of basal bulb to apex (flagellum is partially everted in Fig. 4G); brush sclerite short and broad, covered with very raised and undulated strigae; apex of flagellum resting in heavily sclerotized ventral supporting sclerite just basad ostium; internal sac covered with isolated papillate spicules near middle of shaft, spicules arranged as transverse ridges near ostium; flagellum length estimated to be 1.0 mm, compared to straight-line measure of 0.7 mm from base of median lobe basal bulb to median lobe apex.

Female Reproductive Tract.—(n=1). Bursa copulatrix thinly membranous, short, broad, apical lobe on right side supporting spermathecal duct, common oviduct entering at apical constriction (Fig. 6D); spermathecal duct flexible, cuticle transparent overall but with crescent-shaped region of granulate, opaque cuticle near entry to bursa, duct sinuously curved basally, looped (*in situ*) more apically near spermatheca, estimated length 1.0 mm; spermatheca ovoid, spermathecal gland duct entering in basal half, on side opposite spermathecal duct; gland atrium composed of about 35 taenidia-like coils; gland secretory complex 1.5× length of atrium; gonocoxa very broad (Fig. 7M), basal gonocoxite 1 with two lateroapical setae; apical gonocoxite 2 with broad base and terminal blade, apex broadly rounded; gonocoxite 2 with two large lateral ensiform setae near base set just ventromesad groove defining lateral cutting margin, one large dorsal ensiform seta, and two moderately long apical nematiform setae.

Type.—Lectotype female (BMNH) labeled "Nesocidium smaragdinum Type D.S. Molokai Perkins 345 // Type // …1904-336. // Molokai Perkins 11-VI-1893" hereby designated.

Distribution.—Molokai (Fig. 17): Molokai Mts. [Kaunuohua], R.C.L.P. lots 157, 159, 591, 1372 m el., [Onini Gulch], R.C.L.P. lot 175, Makakupaia R.C.L.P. lot 345, ~850 m el., R.C.L.P. lot 588, 915 m el.; Wailau Tr. at Wailau Vy. rim, 895 m el.

Habits.—The only Perkins' collection of this species for which a situation was noted is in lot "591. Molokai Mts. Carabidae all from boggy top mostly under moss on trees 4½-5·000 ft. … (Anonymous N.D.)." More recently one specimen was collected from a horizontal mossy log after application of pyrethrin insecticide.

Bembidion (Nesocidium) fulgens (Sharp, 1903)
(Figs. 2F, 4H, 6E, 7N, 18)

Nesocidium fulgens Sharp, 1903:282.
Bembidion fulgens: Britton, 1948:248.

Diagnosis.—Smallest of the species trio of brilliantly metallic beetles, standardized body length 2.6-2.7 mm. Also diagnosable from *B. smaragdinum* of Molokai by: 1, frons and vertex with evident transverse-mesh microsculpture; 2, pronotal disc with microsculpture consisting of transverse lines joined loosely into a transverse mesh on margins of pronotal laterobasal depressions. It can be told from *B. auratum* of Hawaii I. by the more convex elytral intervals and deeper, more punctate striae (Figs. 2F, G). Elytral striae 1-7 are broadly furrowed basally, with the distinct punctures restricted to the deepest portions. Metathoracic flight wings reduced to vestigial flaps with apex not extended beyond posterior margin of metanotum; metepisternum short, anterior and lateral margins subequal; metasternal process triangular, moderately broadly margined, width of bead at apex 2× bead width along sides.

Male Genitalia.—(n=1). Aedeagal median lobe broad dorsoventrally, median shaft even curved, apex straight on ventral surface, tip evenly rounded (Fig. 4H); left paramere length 1.2× right paramere length, both 3-setose, mesal setae of each slightly more basal; flagellar complex little hypertrophied, csc and bases of flagellum and flagellar sheath lying within basal bulb; brush sclerite short and broad, covered with very raised and undulated strigae; apex of flagellum associated with distinct, acuminate sclerotized area just basad ostium; internal sac covered with isolated papillate spicules near middle of shaft, spicules larger near ostium, but mostly isolated even in that area, forming only occasional transverse ridges; flagellum length estimated to be 0.6 mm, equal to straight-line measure from base of median lobe basal bulb to median lobe apex.

Female Reproductive Tract.—(n=1). Bursa copulatrix thinly membranous, short, broad, apically expanded, spermathecal duct entering bursa to right of common oviduct (Fig. 6E); spermathecal duct composed of flexible, transparent cuticle overall, with basal crescent of thicker, more sclerotized cuticle on one side of duct near bursa, duct sinuous, estimated length 0.7 mm; spermatheca ovoid with median constriction, spermathecal gland duct entering near constriction on side opposite spermathecal duct; gland atrium composed of about 30 taenidia-like coils; gland secretory complex 1.5× length of atrium; gonocoxa of moderate width (Fig. 7N), basal gonocoxite 1 with two lateroapical setae;

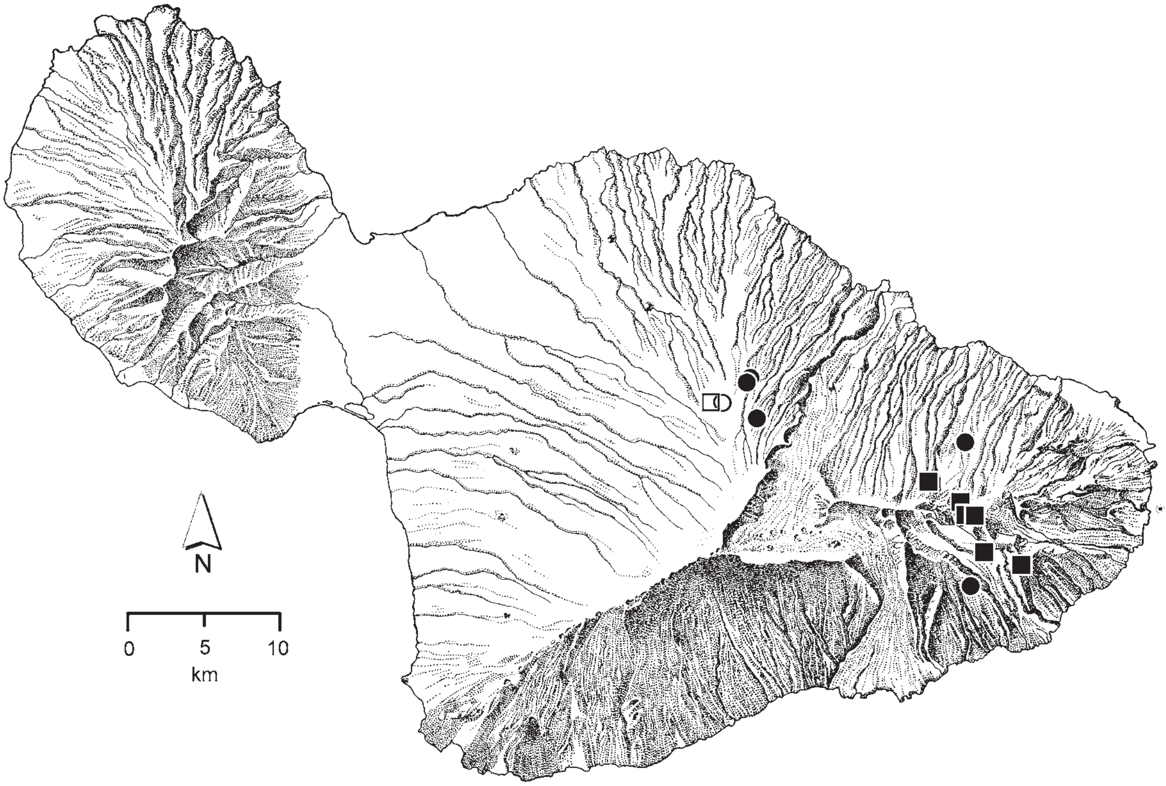


Fig. 18.—Distributional records in Maui for: *B. fulgens* (■); *B. haleakalae* (●); *B. fulgens* + *B. haleakalae* (○); *B. advena* + *B. fulgens* (□).

apical gonocoxite 2 with broad base, falcate lateral margin and narrow apex; gonocoxite 2 with two lateral ensiform setae near base and one dorsal ensiform seta of similar size, and two moderately long apical nematiform setae.

Type.—Lectotype female (BMNH) labeled "Nesocidium fulgens Type D.S. Haleakala Perkins 608 // Type // …1904-336 // Haleakala Maui 5000 ft. Perkins V 1896" hereby designated.

Distribution.—Maui (Fig. 18): Haleakala [Ukulele Camp vicinity], R.C.L.P. lots 120, 608, 1524 m el.; Haleakala N.P., Northeast Rift, Big Bog, 1670 m el., Midcamp Bog, 1660 m el.; Hana For. Res., Heleleikeoha Str., 1615 m el.; Hanawi N.A.R., Kuhiwa Vy., 1585 m el.; Kaumakani Peak, 1127 m el.

Habits.—Singletons of this species have been collected in various lots derived from sifting moss from trunks of *Metrosideros*, and from pyrethrin fogging of moss-covered *Metrosideros* logs and trunks. Two individuals were found under a rock on clay soil at a recently cleared helicopter pad in Hanawi N.A.R., at a site currently known as Po`ouli Cabin, indicating that terrestrial situations may be occupied in the vicinity of closed forest.

Bembidion (Nesocidium) auratum (Perkins, 1917)
(Figs. 2G, 12)

Nesocidium auratum Perkins, 1917:250.
Bembidion auratum: Britton, 1948:254.

Diagnosis.—Among the species consisting of beetles with uniformly metallic greenish to bluish body coloration and ovoid elytra (Figs. 2E-G), *B. auratum* is uniquely diagnosable by the flattened elytral intervals associated with shallow striae, the discal striae composed of rows of punctures more or less isolated from each other by cuticle that is nearly coplanar with adjoining intervals; anterior dorsal elytral seta in depression that spans third interval, posterior seta not in depression; standardized body length 2.6-3.0 mm. Metathoracic flight wing configuration not examined, but metepisternum short, lengths of anterior and lateral margins subequal, allowing a configuration of vestigial flight wings to be hypothesized; metasternal process triangular, moderately broadly margined, width of bead at apex 2× bead width along sides.

Variation.—The two known specimens differ in the development of the lateral elytral striae. The holotype has striae 4-6 represented basally by seven to eight serial punctures separated from each other by 3-4× their diameter. The second specimen has stria 6 represented by four and six isolated punctures (left and right side), and stria 7 is not indicated by any punctures.

Female Reproductive Tract.—This species is currently known from two female specimens, neither of which was dissected.

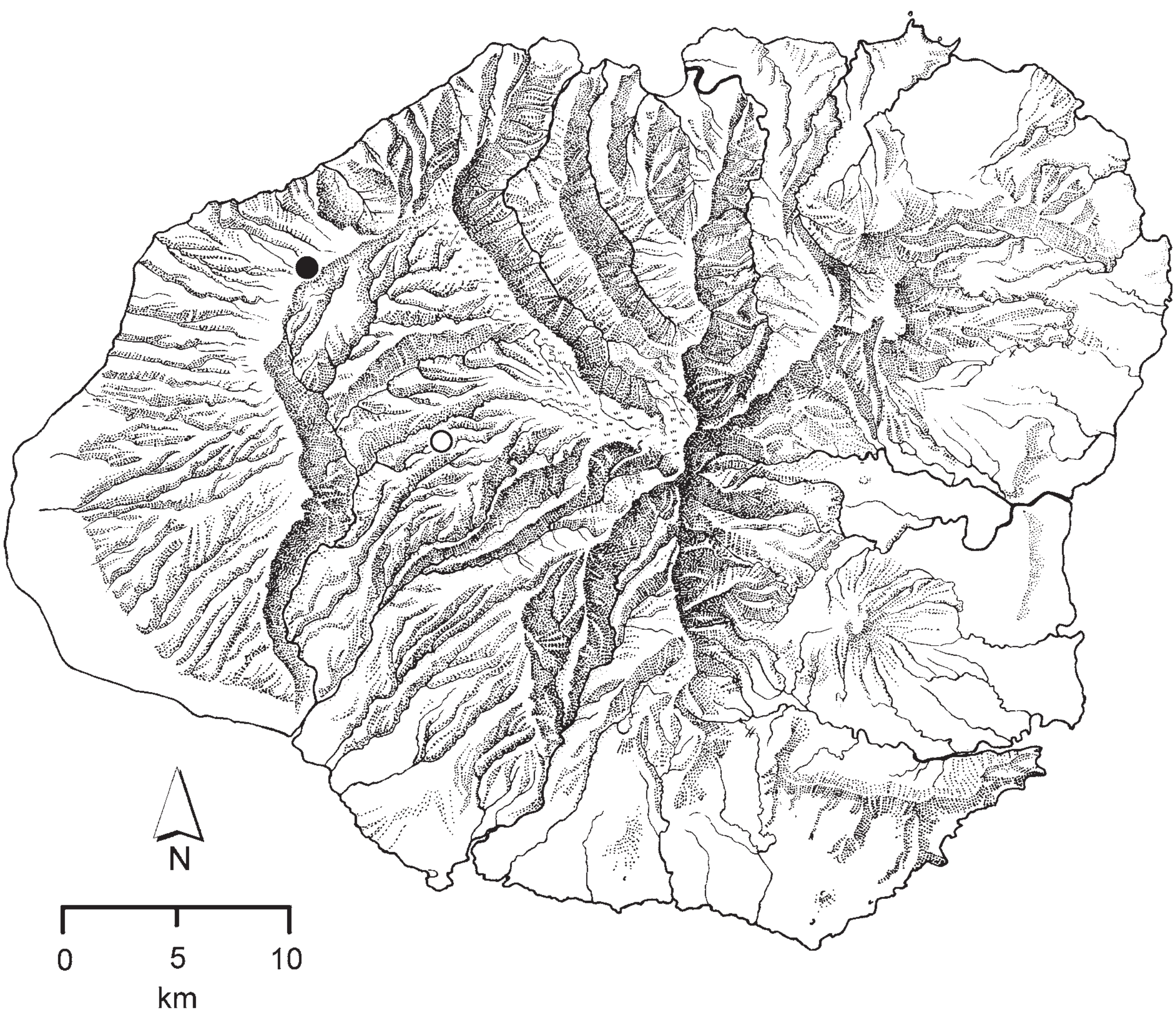


Fig. 19.—Distributional records in Kauai for *B. kauaiense* (○); *B. coecum* (●).

Type.—Holotype female (BPBM), platen-mounted with "Kil. Haw. VII. 06." on reverse // Nesocidium auratum Type. RCLP."

Distribution.—Hawaii (Fig. 12): Kilauea; Saddle Rd. 34.1 km [21.2 mi.] W Hilo, 1690 m el.

Habits.—In addition to the holotype, which Perkins (1917) collected from among decaying leaves, this species is known from a second specimen collected in a long-term pitfall trap set by Al Newton and Margaret Thayer (FMNH) in *Metrosideros*/*Acacia* mixed mesic forest along the Saddle Road (Fig. 12).

Bembidion (Nesocidium) kauaiense (Sharp, 1903)
(Figs. 2H, 19)

Nesomicrops kauaiensis Sharp, 1903:286.
Bembidion (*Nesomicrops*) *kauaiensis:* Britton, 1948:254.

Diagnosis.—One of two pallid Hawaiian *Bembidion* with extremely small eyes that do not protrude from curvature of ocular lobe (Fig. 2H), horizontal eye diameter crossing five ommatidia and measuring 0.10-0.12 mm; pronotal lateral marginal depression narrow, only slightly broader outside lateral pronotal seta, pronotal basolateral margin very briefly sinuate anterad basal seta; elytral striae broadly impressed and shallow, lined with shallow punctures separated by twice their diameter over basal two-thirds of elytral length, the intervening intervals very slightly convex; frontal grooves lined with evident transverse sculpticells, frons with flattened yet traceable transverse sculpticells, neck with evident transversely stretched isodiametric sculpticells in transverse rows; pronotal disc with transverse-mesh microsculpture, the sculpticells twice as broad as long; elytral intervals with isodiametric sculpticells arranged in irregular transverse rows; standardized body length 2.8-3.1 mm.

Female Reproductive Tract.—Neither the paralectotype female available to me for extended study (BPBM), nor a lightly sclerotized non-type female (R.C.L.P. lot 256) were dissected.

Type.—Lectotype female (BMNH) labeled "Nesomicrops kauaiensis Type D.S. Kauai Perkins 682 // Type // …1904-336 // high Kauai Plat. Perkins VIII 1896" hereby designated. Paralectotype females labeled identically (BMNH, 1; BPBM, 1). A fourth non-type female (BPBM) completes the specimens.

Distribution.—Kauai (Fig. 19): near Kaholuamano, R.C.L.P. lots 256, 682, 1210 m el.

Habits.—The only collecting information associated with this species is the inventory of Perkins' specimens that lists among lot 256, "Minute Carabids by grubbing…(Anonymous N.D.)." Presumably *B. kauaiense* was among those minute carabids.

Bembidion (Nesocidium) coecum (Sharp, 1903) (Figs. 2I, 19)

Macranillus coecus Sharp, 1903:287
Bembidion (*Nesomicrops*) *coecus*: Britton, 1948:287.

Diagnosis.—Smaller than the only other Hawaiian *Bembidion*—*B. kauaiense*—with extremely small eyes, standardized body length 2.3-2.5 mm; compound eyes remarkably small, horizontal diameter crossing three ommatidia and measuring 0.050-0.055 mm; frontal grooves broadly depressed, branched posteriorly to both converge on vertex and diverge laterally to terminate at posterior supraorbital seta; pronotum with lateral marginal depression narrow throughout, not widened outside lateral seta; pronotal hind angles right, protruded, basolateral margin anterad angles constricted enough to expose posterior portion of proepipleuron in dorsal view; pronotal basal marginal bead complete and very broad, broadest posterad inner linear margin of laterobasal depressions; parascutellar stria not distinguishable; elytral striae 1-5 in basal half consisting of series of elongate, shallow punctures irregularly separated by cuticle coplanar with intervals, striae 6-7 nearly obsolete, indicated by two to four isolated punctures; frons shiny, with indistinct transverse mesh microsculpture, frontal grooves with more evident, but still indistinct transverse sculpticells; pronotal disc shiny with only the faintest indication of transverse lines; elytral intervals shiny, occasional patches of cuticle with transverse mesh microsculpture traceable, the sculpticells 3-4× as broad as long.

Male Genitalia.—A single male (?) specimen, card-mounted with body associated but most legs broken off (BPBM) was not dissected.

Type.—Holotype female (BMNH) labeled "Nesomicrus coecus Type D.S. Kauai Perkins 631 // Type // …1904-336 // High Kauai Plat: Perkins VIII 1896."

Distribution.—Kauai (Fig. 19): High Plateau [Kaholuamano vicinity], R.C.L.P. lot 631, 1210 m el.; Kokee S.P., Ka Unu o Hua Ridge, 1280 m el.

Habits.—Elwood Zimmerman collected a series of five individuals (BPBM; four apparently dead as body parts are disassociated, the fifth with associated body but only one remaining leg) under stones on Ka Unu o Hua Ridge, 21-VII-1937. This site is directly west of the present-day Souza Center operated by the Kokee Natural History Museum.

Bembidion (Nesocidium) perkinsi (Sharp, 1903) (Figs. 2J, 15)

Nesocidium perkinsi Sharp, 1903:282.
Bembidion perkinsi: Britton, 1948:

Diagnosis.—Most similar in overall appearance to *B. rude*, but with humeral and lateroapical maculae arranged transversely in an "X" (Fig. 2J), humeral macula trapezoidally extended from humerus to its apex on elytral interval 5 just laterad anterior dorsal elytral seta, lateroapical elytral macula extended anteromedially from lateral margin just before the subapical sinuation to just posterad posterior dorsal elytral seta, disc between maculae brunneous, elytral apex darker, piceous; pronotal basolateral margins nearly parallel anterad obtuse hind angles, sinuation twice as long as distance of basal seta from basal margin; pronotal lateral marginal depression slightly broader outside lateral seta, narrowed anteriorly to rounded, slightly protruded front angles; elytral striae 1-7 broadly depressed in basal two thirds of elytral length, broad and shallow punctures depressing adjacent intervals, elytral intervals broadly convex; frontal grooves and frons between with distinct transverse-mesh microsculpture, transverse sculpticells on vertex less upraised but still distinct; pronotal disc shiny, indistinct transverse lines traceable over portions of disc; elytral intervals shiny, miscrosculpture obsolete; standardized body length 3.0-3.1 mm. Metepisternum short, anterior and lateral margins of equal length; metathoracic flight wings not examined, but presumably vestigial.

Male Genitalia.—As this species is extremely distinctive externally, the male paralectotype was not dissected.

Female Reproductive Tract.—For the same reason, the female lectotype was not dissected.

Type.—Lectotype female (BMNH) labeled "Nesocidium perkinsi Type D.S. Kauai Perkins" hereby designated. A single paralectotype male (BMNH) labeled "Nesocidium perkinsi Ind. Typ. D.S. Koholuamano Perkins.IV.95 // … // Khlm. K 15-4000 ft. IV.95.

Distribution.—Kauai (Fig. 15): Kaholuamano, 1210 m el.

Habits.—Nothing has ever been recorded concerning the biology of this species.

Bembidion (Nesocidium) koebelei (Sharp, 1903) (Figs. 2K, 9)

Nesocidium koebelei Sharp, 1903:282.
Bembidion koebelei: Britton, 1948:253.

Diagnosis.—Most similar in size and coloration to *B. ignicola*, with standardized body length 2.8 mm, but diagnosable by: 1, elytral humeri much narrower and more rounded (Figs. 1F, 2K); 2, dorsal body coloration more brunneous, without metallic reflection; 3, elytral intervals nearly flat between shallowly incised discal elytral striae; 4, third elytral interval not depressed at position of anterior dorsal elytral seta; 5, metepisternum short, anterior and lateral margins of equal length. Frontal grooves broad, shallow, lined with indistinct transverse-mesh microsculpture, frons between shiny, microsculpture obsolete, vertex covered with shallow transverse-mesh microsculpture near pronotum; pronotal disc shiny, indistinct transverse line intermittently traceable; pronotal lateral marginal depression slightly broader near lateral seta; basal pronotal seta located well before obtuse hind angle, near anterior limit of basolateral sinuation; elytral intervals shiny, microsculpture obsolete except near striae and punctures where transverse meshes may be traceable. Metasternal process narrowly triangular, marginal bead slightly broader at apex than along sides, tip slightly upraised but apex not distinct from more basal portion of process.

Female Reproductive Tract.—Neither the holotype female nor the only known second female were dissected.

Type.—Holotype female (BMNH) labeled “Nesocidium koebelei Type D.S. Honolulu Koebele.”

Distribution.—Oahu (Fig. 9): Honolulu mountains; Konahuanui.

Habits.—This species is known from only two specimens, the holotype collected by Albert Koebele and a second female collected by Otto Swezey on Konahuanui, 23-XI-1919 (BPBM). Though he was the sole person to discover many species, Koebele was notorious for not recording accurate collecting data (e.g. Sharp 1903:184, 289). Unfortunately, Swezey also did not elucidate anything of the habits of this species.

Bembidion (Nesocidium) corticarium (Sharp, 1903) (Figs. 3A, 4I-J, 6F, 7O, 16)

Nesocidium corticarium (Sharp), 1903:283.
Bembidion corticarium: Britton, 1948:248.

Diagnosis.—Small brunneous beetles with moderately convex eyes and broad, rounded humeri (Fig. 3A), standardized body length 2.8-3.0 mm, further distinguishable by: 1, pronotal lateral marginal depression of nearly equal width throughout length, slightly broader near lateral pronotal seta and narrowed to subangulate front angles; 2, pronotal base with broad, smoothly bordered marginal bead of nearly equal width across base, base otherwise smooth; 3, elytra with striae 1-5 evident, very shallow and containing small punctures that do not extend beyond striae, stria 6 only traceable basally, stria 7 obsolete; 4, two dorsal elytral setae. Metepisternum short with anterior and lateral margins of subequal length; metathoracic flight wings vestigial; metasternal process triangular, with small elevated apical area defined basally by medially arcuate bead that is continuous and slightly broader than marginal bead along sides of process. This species is most similar to *B. paratomarium* of Mt. Kaala, Oahu, but beetles of that species have only the anterior dorsal elytral seta, narrower humeri, and flatter eyes (Fig. 3C).

Male Genitalia.—(n=3). Aedeagal median lobe moderately broad, median shaft evenly arcuate to slightly upturned, tightly rounded apex, the tip protruded beyond ostial opening for distance equal to tip breadth (Figs. 4I, J); left paramere 1.3× as long as right, with narrow 3-setose projection at mesal margin of apex, its length 1-2× breadth; right paramere 3-setose, narrowed to rounded apex bearing two setae, third seta slightly subapical on mesal margin; flagellar complex extended beyond base of basal bulb for length subequal to median lobe length; brush sclerite short and broad, covered with dense longitudinal strigae that are coarsest near csc; secondary flagellar sclerite well-developed, its surface covered with dense longitudinal wrinkles; flagellum estimated to be 1.8 mm long, compared to straight-line measure of 0.8 mm from base of median lobe basal bulb to median lobe apex; flagellum supported by well-sclerotized, acuminate cuticular field just dorsad ostium. One specimen with the flagellum partially exerted was dissected (Fig. 4J). When the exerted flagellar apex was examined at 400× magnification, it was possible to observe torsion of the flagellum, whereby it completed about one-half rotation from ostial membrane to tip. Viewing the various faces shows that the flagellum is an elongate gutter-shaped structure, composed of a partially closed internal groove defined by a hemicircle of cuticle.

Female Reproductive Tract.—(n=1). Bursa copulatrix columnar, only slightly broader apically than basally (Fig. 6F); spermathecal duct composed of flexible translucent cuticle, with basal portion supported by longitudinal, sclerotized ridge on face nearest common oviduct, estimated duct length 1.8 mm; basal part of spermathecal duct to first loop (Fig. 6F) supported by longitudinal ribbon of polygonal sculpticells on side of duct far from common oviduct, more apical portion of duct completely surrounded by transverse, polygonal four- to six-sided sculpticells; spermatheca biovate, with deep median constriction, spermathecal gland duct entering near constriction on side opposite spermathecal duct; gland atrium composed of approximately 47 taenidia-like coils; gland secretory complex about twice length of atrium; gonocoxa moderately broad, apical gonocoxite 2 elongate (Fig. 7O); basal gonocoxite 1 with one lateroapical seta; apical gonocoxite 2

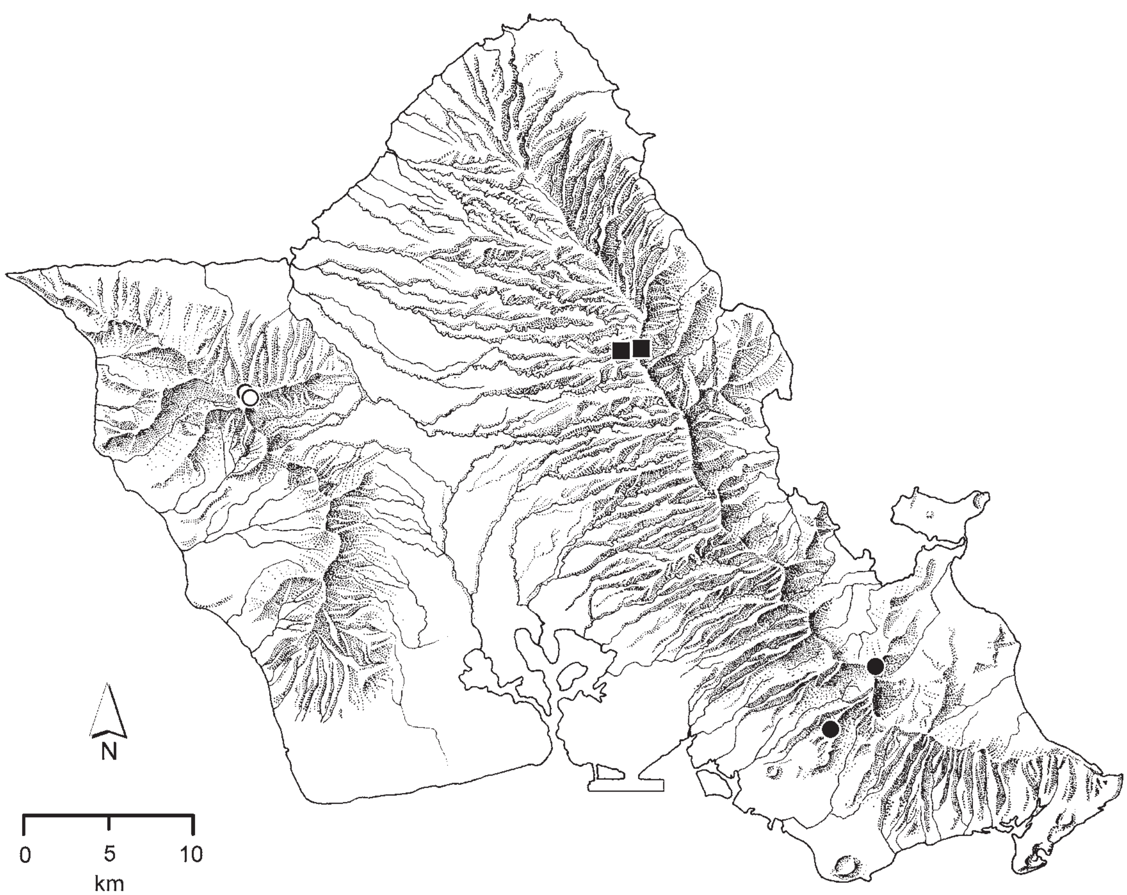


Fig. 20.—Distributional records in Oahu for: *B. gagneorum* (■); *B. paratomarium* (○); *B. atomarium* (●).

expanded basally, abruptly constricted to elongate lateral cutting margin, with two lateral ensiform setae near base of lateral margin, one dorsal ensiform seta just beyond longitudinal position of apical lateral seta, and two moderately long apical nematiform setae.

Type.—Lectotype male (BMNH) labeled "Nesocidium corticarium Type D.A. Kauai. IV.95 Perkins // Type // … 1904-336 // Khlm., K 15-4000 ft. IV 95" hereby designated.

Distribution.—Kauai (Fig. 16): Halalea For. Res., Namolokama Mtn., 1295-1340 m el.; NaPali Kona For. Res., Alakai Swamp, Kilohana, 1210 m el., Koaie Str. nr. Koaie Camp, 1120 m el., S of Mohihi Ridge; Mts. above Waimea [Kaholuamano], R.C.L.P. lots 256, 267, 1210 m el.

Habits.—Individuals of this species occur both in ground-level leaf and fern frond litter, and also on the mossy trunks, roots and nurse logs of *Metrosideros*.

***Bembidion (Nesocidium) gagneorum*, new species**
(Figs. 3B, 4K, 6G, 7P, 20)

Diagnosis.—Among the Hawaiian *Bembidion* lacking the posterior dorsal elytral seta, individuals of this species exhibit the most reduced elytral striation (Fig. 3B), with striae 1-3 shallow and indistinctly punctate on disc, striae 4-6 indicated by extremely shallow, isolated punctures in basal half, and stria 7 obsolete except for a few intermittent punctures, elytral intervals consequently only slightly convex on disc, flat laterally; frons with evident transverse-mesh microsculpture on lateral areas comprising mesal faces of frontal grooves, sculpticells less elevated but traceable medially; pronotum more transverse (Fig. 3B) than other species exhibiting single dorsal elytral seta (Figs. 3C-F), ratio of maximum width to median length 1.26-1.27; standardized body length 2.5-2.7 mm.

Description.—Frontal grooves parallel anteriorly on frons, broadly, arcuately divergent to posterior supraorbital setae; fossa of anterior supraorbital seta broad, deep, separated from frontal groove by indistinctly upraised carina; eyes small, slightly convex, horizontal diameter 0.17-0.18 mm; mentum tooth narrowly triangular, tip slightly acuminate. Pronotal basal setae in broad marginal bead defined mesally by arcuate lateral marginal depression that also extends for short distance along basal margin, setal position equidistant from basolateral and basal margin; pronotal basal marginal bead broad, narrowed each side to meet extension of lateral marginal depression; pronotal base smooth, impunctate; median longitudinal impression obsolete basally, indistinctly indicated on disc;

anterior transverse impressions extremely shallow, difficult to trace medially, more evident near subangulate, non-protruded front angles; anterior marginal bead broadly obsolete medially; lateral marginal depression narrow throughout; prosternal process unmargined ventrally, broadly curved to upright posterior face, median portion of posterior face indistinctly depressed. Elytra broadly ovate with broad base (Fig. 3B); basal groove absent on the subangulate humerus; parascutellar stria composed of three punctures; parascutellar seta (ed1) in base of sutural stria 1; the single dorsal elytral seta (ed3) in middle of interval 3, area around seta only slightly depressed; two ed7 setae; one ed8 seta near apex, closer to margin than to suture; lateral elytral setae grouped as four anterior setae (eo1-4), and four posterior setae (eo5-8), with stria 8 extended beyond posterior lateral seta parallel to elytral margin, evanescent apicad subapical sinuation to position of seta ed8. Metathoracic flight wings vestigial; metepisternum very short, anterior margin longer than lateral margin; metasternal process apex narrowly triangular, with upraised acuminate tip, lateromarginal bead of process arcuately continuous medially, defining base of upraised acuminate tip.

Coloration.—Uniformly brunneous dorsally, with mandibles, labrum, and basal antennomere slightly more flavous, subulate apical palpomeres testaceous; elytra concolorous, without any humeral or apical pale areas; venter of head capsule, pro- and mesosternum, and proepisternum brunneous, pro- and elytral epipleura paler, flavous; metathorax, abdominal ventrites and legs pale, rufoflavous, only profemora with slight infuscation.

Male Genitalia.—(n=1). Aedeagal median lobe moderately broad, median shaft straight on ventral surface, apical sixth of lobe subangulately downturned, tip slightly pointed (Fig. 4K); left paramere 1.1× as long as right, apex acuminate, 3-setose; right paramere 3-setose, narrowed to triangular tip bearing the setae, the lateral setae slightly subapical; flagellar complex extended beyond base of basal bulb for length subequal to median lobe length; apex of flagellar complex (csc and brush sclerite) rotated 90° counterclockwise (dextral torsion) relative to median lobe orientation (specimen photographed flattened under cover slip, Fig. 4K); secondary flagellar sclerite present, sclerotized area about as long as brush sclerite; flagellum estimated to be 1.5 mm long, compared to straight-line measure of 0.7 mm from base of median lobe basal bulb to median lobe apex. In the single specimen dissected, the flagellar apex exits from the supporting acuminate sclerotized area just dorsad the ostium, and recurves ventrally so the apex lies near the median lobe venter just inside the ostium. The apex of the associated sclerotized area also turns in this direction, suggesting that this rest position is not an artifact of specimen preparation.

Female Reproductive Tract.—(n=1). Bursa copulatrix urn-shaped, laterally with very thin, transparent membrane, membrane folded apically near entry of spermathecal duct and common oviduct (Fig. 6G); spermathecal duct inflexible, extremely convoluted, the duct coiling in alternate directions at each turn, duct base nearly twice diameter of more apical portion, estimated duct length 1.20 mm; basal portion of duct to second turn (Fig. 6G) supported by longitudinal ribbon composed of transverse sculpticells that lies along one side of duct, more apical portions of duct completely surrounded by transverse, polygonal four- to six-sided sculpticells; spermatheca ovoid with shallow median constriction, spermathecal gland duct entering just basad constriction on side opposite spermathecal duct; gland atrium composed of approximately 60 taenidia-like coils; gland secretory complex short, about half length of atrium; gonocoxa moderately narrow, apical gonocoxite 2 acuminate apically (Fig. 7P); basal gonocoxite 1 with one to two lateroapical setae; apical gonocoxite 2 moderately expanded basally, with two to three small lateral ensiform setae associated with ventral ridge some distance from lateral cutting margin, one small dorsal ensiform seta present directly dorsad more apical of the lateral ensiform setae, and two small apical nematiform setae.

Types.—Holotype female (BPBM): Poamoho Trail, 650 m Oahu // sifting ground litter // 11-VI-1972 W. C. Gagne BISHOP // Holotype Bembidion gagneorum J.K. Liebherr 2007. Paratypes. Oahu (Fig. 20): Poamoho Tr., sifting ground litter, 750 m el., 02-VI-1977, Howarth (BPBM, 3; CUIC, 2).

Etymology.—The species epithet collectively honors Drs. Wayne Gagné and Betsy Harrison Gagné for their efforts to conserve Hawaiian natural biological wonders.

Habits.—Individuals of this species are known to date to exclusively inhabit ground-level leaf litter situations.

Bembidion (Nesocidium) paratomarium, new species
(Figs. 3C, 4L, 20)

Diagnosis.—Of Hawaiian *Bembidion* with only the anterior dorsal elytral seta, individuals of this species are distinguishable by: 1, frons with indistinct microsculpture of transverse lines loosely joined in a mesh; 2, pronotum narrow basally, with basolateral margins nearly straight anterad basal seta (Fig. 3C); 3, elytral striae 1-7 evident, inner striae distinct, deeply punctate, the punctures depressing cuticle on adjacent intervals, discal intervals convex; 4, elytra concolorous overall, without humeral or apical pale areas. This potentially tenuous diagnosis relative to *B. atomarium* is forcefully corroborated by the male aedeagal configuration (Fig. 4L); flagellar complex extended only slightly from basal bulb, brush sclerite and csc rotated 90° relative to longitudinal axis of median lobe (for *B. atomarium* see Fig. 4M). Standardized body length 2.8-3.0 mm.

Description.—Frontal grooves parallel anterad line defined by hind margin of eyes, divergent posteriorly at nearly right angle to terminate at posterior supraorbital seta; fossa of anterior supraorbital seta deep, round, depression extended medially nearly to frontal groove; eyes small, little convex, horizontal diameter 0.14 mm; mentum tooth narrowly triangular. Pronotal basal setae in upraised basolateral marginal bead distinctly anterad obtuse hind angles; pronotal basal marginal bead broad, indistinctly defined by several transversely elongate punctures each side of midline; pronotal base with two to three punctures each side of midline anterad basal bead; median longitudinal impression continuous, traceable on disc; anterior transverse impressions broad, shallow, indistinct, evident only for very short distance mesad rounded, non-protruded front angles; lateral marginal depression broadest just anterad lateral seta, narrowed evenly to front angle and on basal half of length; prosternal process slightly, broadly depressed medioventrally, broadly curved to upright posterior face. Elytra with broadly rounded humeri, sides subparallel in middle of length (Fig.

3C); basal groove extended mesally from very obtusely angulate humerus, almost complete to base of parascutellar stria; parascutellar stria continuous, with three punctures; parascutellar seta (ed1) present between obsolete base of sutural stria 1 and parascutellar stria; the single dorsal elytral seta (ed3) in small depression on outer half of third interval, the depression not extended onto interval 4; two ed7 setae; one ed8 seta near apex, closer to margin than to suture; lateral elytral setae grouped as four anterior setae (eo1-4) and four posterior setae (eo5-8), with stria 8 extended beyond posterior lateral seta parallel to elytral margin, evanescent apicad subapical sinuation to position of seta ed8. Metathoracic flight wings vestigial; metepisternum short, anterior and lateral margins subequal in length; metasternal process with large apical triangle bordered posteriorly by broadly arcuate bead that is continuous with lateromarginal beads, apical triangle with upraised longitudinal keel.

Coloration.—The bodies of both specimens are uniformly brunneous dorsally, with mandibles, maxillary palpomeres and antennomeres 1-4 slightly more flavous; ventral sclerites generally paler, the flavous elytral epipleura palest, and pro- and mesosternum darkest, brunneous, abdominal sclerites and legs intermediate.

Male Genitalia.—(n=1). Aedeagal median lobe short and broad, median shaft evenly curved on ventral margin, ventral margin on apex slightly concave, tip broadly rounded, projected beyond ostial membrane for distance equal to width (Fig. 4L); left paramere 1.3× as long as right, gradually narrowed to 3-setose apex, mesal and lateral margins subparallel for short distance before parameral apex; right paramere narrowed to narrow, 3-setose apex, seta on mesal margin slightly subapical; csc left lobe and base of flagellum held completely within basal bulb; base of flagellar sheath stout and broad, extended for short distance beyond basal margin of basal bulb; brush sclerite compact, positioned between csc left lobe and flagellum, and with longitudinally strigose surface; an elongate patch of heavily sclerotized, longitudinal scales present along ventral internal margin of median lobe, and a smaller, distinct, elongate sclerite present just apicad brush sclerite (possibly the vsp; Maddison 1993); flagellum estimated to be 0.5 mm long, compared to straight-line measure of 0.7 mm from base of median basal bulb to median lobe apex.

Female Reproductive Tract.—The holotype female was not dissected.

Types.—Holotype female (BPBM): Mt. Kaala 1.17.32 Oahu // ex Astelia // F. X. Williams Collector // Nesocidium n. sp. (folded) // Holotype Bembidion paratomarium J. K. Liebherr 2007. Paratype. Oahu (Fig. 20): Mt. Kaala, *ex muscic in arboribus*, 22-VII-1917, Bridwell (BPBM, 1 male).

Etymology.—The adjectival species epithet is derived from the Latinized Greek atomus, or small particle, with the similarity of this species and *B. atomarium* denoted by the prefix par.

Habits.—The occurrence of both specimens in arboreal situations—an *Astelia* plant and arboreal moss—suggests a climbing lifestyle. Then again, the type and only known locality, Mt. Kaala, is topped by a well-collected summit bog. Thus eventual collection of this species by sifting litter should not be ruled out.

Bembidion (Nesocidium) atomarium (Sharp, 1903) (Figs. 3D, 4M, 20)

Nesocidium atomarium Sharp, 1903:284.
Nesocidium scydmaenoides Sharp, 1903:284 (synonymy Britton 1948).
Bembidion atomarium: Britton, 1948:250.

Diagnosis.—The third species in this sequence of Oahu *Bembidion* taxa characterized by a single dorsal elytral seta, individuals of this species have: 1, body dorsum shiny piceous, legs and antennae brunneous with distinct piceous infuscation; 2, frons very shiny, covered with indistinct transverse lines, frontal grooves with indications of microsculpture only in deepest linear portion; 3, pronotal basal marginal bead absent, base distinctly punctate, with five to six punctures each side of midline; 4, pronotal basal seta in lateral marginal bead just anterad obtuse hind angle; 5, elytral striae deeply punctate, but intervening areas of striae shallow, elytral intervals very broadly and indistinctly convex; 6, pronotal and elytral discs brilliantly reflective, without any indication of microsculpture. Metathoracic flight wings vestigial; metepisternum short, anterior and lateral margins of equal length. Standardized body length 2.4-2.7 mm.

Male Genitalia.—(n=1). Aedeagal median lobe short and broad, median shaft straight ventrally, apical fifth of lobe subangulately downturned to tightly rounded tip that does not protrude beyond ostial sac (Fig. 4M); left paramere 1.3× as long as right, apically with 3-setose projection that extends from broader portion of paramere with length about twice its breadth; right paramere evenly narrowed in apical two-thirds of length, apex 3-setose; flagellar complex extended beyond basal margin of basal bulb for distance less than half path length of flagellum inside median lobe; brush sclerite triangular, secondary flagellar sclerite held inside median lobe and covered with longitudinal, shingled sculpticells; flagellum and flagellar sheath curved ventrally at apex of acuminate sclerotized area that terminates inside the median lobe just dorsad ostium (as in specimen of *B. gagneorum*, Fig. 4K); flagellum estimated to be 1.1 mm long, compared to straight-line measure of 0.6 mm from base of median lobe basal bulb to median lobe apex.

Female Reproductive Tract.—No female of this species was available for dissection.

Types.—For *Nesocidium atomarium* Sharp, lectotype male (BMNH) labeled "Nesocidium atomarium Type D.S. Honolulu Perkins 785" hereby designated. For *Nesocidium scydmaenoides* Sharp, holotype male (BMNH) labeled "Nesocidium scydmaenoides Type D.S. Honolulu Perkins // Type // …1904-336 // Ridge N of Nuuanu Pali Oahu 2000 ft. 25-10-92."

Distribution.—Oahu (Fig. 20): Honolulu [Tantalus summit], R.C.L.P. lot 710, 605 m el.; Honolulu Mts., R.C.L.P. lots 785, 786; ridge N Nuuanu Pali [Puu Lanihuli].

Habits.—Sharp (1903:284) noted that the type series of *B. atomarium* was collected from *Pipturus*, indicating a propensity to climb vegetation at some point in the life cycle.

Bembidion (Nesocidium) kamakou, new species
(Figs. 3E, 4N, 17)

Diagnosis.—Of Hawaiian *Bembidion* characterized by presence of only a single dorsal elytral seta (ed3), *B. kamakou* is distinguishable by that seta being situated in a depression that spans the third elytral interval (Fig. 3E). In addition, individuals of this species may be determined by the following combination; 1, frons and frontal grooves covered with distinct transverse-mesh microsculpture, the transverse sculpticells very distinct with visible, upraised margins on vertex near pronotum; 2, elytral striae 1-7 evident, deeply punctate, striae 1-4 continuous on disc, punctures of striae 5-7 intermittently connected by depressed portions of striae; 3, elytral apex pale, lateral margin flavous from lateral elytral seta eo5 (anterior seta in posterior group of eo5-8) to elytral suture, the rufoflavous pale area broader near suture, and contrasted with piceous disc. Contrasted with the evident microsculpture of the frons, the pronotal disc is covered with very shallow, indistinct transverse lines; elytra with transverse lines limited to the depressed portions of the striae, intervals shiny with only occasional transverse lines. Standardized body length 2.5-2.6 mm.

Description.—Frontal grooves shallow, especially laterally where they are separated from fossa of anterior supraorbital seta by very low ridge, parallel between eyes and angularly divergent to posterior supraorbital setae; eye diameter small—horizontal diameter 0.16 mm—and convex, the outer surface defined by curved surface at posterior of ocular lobe; mentum tooth very narrow, sides parallel before acuminate apex, longitudinally keeled. Pronotal basal seta in broadened lateral marginal bead just anterad projected, slightly obtuse hind angle; sinuation of basolateral margin defined principally by setal articulatory socket, basolateral margin straight to convex anterad seta; pronotal basal marginal bead very broad, indistinctly defined anteriorly by transvserve row of intermittent, elongate punctures; median base with circular depression each side of midline defined by five to seven shallow punctures; median longitudinal impression obsolete on base, very finely incised on disc; anterior transverse impressions shallow, broad, evidenced laterally as carinae that extend mesad 0.10× anterior width from each rounded, non-protruded front angle; lateral marginal depression broadest just posterad lateral seta, evenly narrowed to hind angle, narrowed anteriorly except for slight expansion at front angle; prosternal process slightly depressed ventromedially, broadly curved to upright posterior face. Elytra ovoid, base straight for short distance laterad pronotum, humeri broadly angulate; pronotum tightly articulated with elytra and covering position of basal groove; parascutellar stria defined by four punctures; parascutellar seta (ed1) present just mesad base of sutural stria 1; two ed7 setae; one ed8 seta near apex, distance to apical margin 0.33× distance to sutural margin; lateral elytral setae grouped as four anterior setae (eo1-4) and posterior setae (eo5-8), stria 8 extended beyond posterior lateral seta parallel to elytral margin, evanescent apicad subapical sinuation to position of seta ed8. Metathoracic flight wings vestigial; metepisternum short, anterior and lateral margins subequal in length; metasternal process with large apical triangle bordered posteriorly by broadly arcuate bead that is continuous with lateromarginal beads, apical triangle with upraised longitudinal keel.

Coloration.—Head capsule, pronotum and elytra shiny brunneous, elytral sutural stria more rufous, lateroapical border pale, rufoflavous; mandibles and antennomeres 1 and 2 paler, rufoflavous, palpomeres and outer antennomeres infuscated, brunneous with a smoky cast; pro- and elytral epipleura rufous, thoracic and abdominal ventrites, and metacoxae brunneous; legs rufoflavous, femora with darker brunneous infuscation in basal four-fifths.

Male Genitalia.—(n=1). Aedeagal median lobe moderately broad, ventral surface evenly curved apicad parameral articulations, straight in apical half to evenly rounded tip that protrudes only slightly beyond membrane ventrad ostium (Fig. 4N); left and right parameres of subequal length; left paramere with apical, parallel-sided 3-setose process that is 3× as long as broad; right paramere with broad base and dorsally angulate 3-setose apical process that is 3× as long as broad; csc left lobe and its articulation with base of flagellum directly at basal margin of median lobe basal bulb, stout base of flagellar sheath extended slightly beyond basal margin; brush sclerite elongate, surface longitudinally undulated; flagellar and flagellar sheath apices lying ventrad markedly transversely ridged acuminate sclerotized region dorsad ostium, tips of flagellum and sheath curved ventrally to middle of median lobe just inside ostium; sinuous sclerotized area with longitudinally undulated surface just apicad brush sclerite (possibly the vsp, Maddison 1993); flagellum estimated to be 0.7 mm long, compared to straight-line measure of 0.6 mm from base of median basal bulb to median lobe apex.

Type.—Holotype male (NMNH): HI: Molokai Puu Lua summit Wailau Vy. rim 16-VI-1999 lot 1 970 m el. 21°06′28″N 156°48′48″W D.A. Polhemus pyr. fog Metrosideros // Holotype Bembidion kamakou J.K. Liebherr 2007. Paratype. Molokai (Fig. 17): Puu Lua summit ridge, leaf litter fern/Ohia/Olapa, 970 m el., 16-VI-1999, Ewing (UHEM, 1 male); above Makalihua, sift *Cibotium* litter, 880 m el., 19-V-2004 lot 02, Liebherr (CUIC, 1 male).

Etymology.—The species epithet kamakou is derived from the volcano defining eastern Molokai, and should be treated as a noun in apposition.

Habits.—This species is known both from arboreal mossy microhabitats, and also from mesic leaf litter derived from tree ferns.

Bembidion (Nesocidium) haleakalae, new species
(Figs. 3F, 4O, 6H, 7Q, 18)

Diagnosis.—Sharing the single anterior dorsal elytral seta and pale elytral apex with *B. kamakou* but diagnosable by: 1, pronotum with elongate basolateral sinuation, the basolateral margins subparallel for 3× distance from basal seta to basal margin (Fig. 3F); 2, pronotal disc with evident, though shallow transverse-mesh microsculpture, the regularly arranged sculpticells most visible on convex surface mesad lateral seta; and 3, anterior dorsal elytral seta ed3 in small depression that extends only over outer half of third interval. Frons with evident transverse microsculpture, most evident in frontal grooves and on vertex near pronotum; pronotal disc with indistinct transverse lines over portions of surface; elytral intervals very shiny, with only irregular wavy transverse lines disturbing the highly reflective surface. Standardized body length 2.5-2.9 mm.

Description.—Frontal grooves parallel, shallow anteriorly where they are bordered laterally by a thin, elevated ridge, terminated posteriorly in a deep, round depression centered on an equilateral triangle the vertices of which are otherwise defined by the two suprorbital setae; eyes somewhat variable (see Variation below), longest diameter 0.15-0.23 mm (most individuals with eyes < 0.20 mm diameter), anterior margin nearly vertical, much less convex than remainder of perimeter, outer surface little convex; mentum tooth narrowly triangular, longitudinally keeled. Pronotal basal seta in lateral marginal bead distinctly anterad hind angle, lateral margins parallel behind seta and subparallel for short distance before (Fig. 3F), lateral marginal sinuation terminated about 0.20× median length before hind angle, margin convex in anterior 0.80 of length; basal marginal bead indistinctly defined by transverse line of irregularly spaced punctures that terminate laterally in arcuate laterobasal depressions; pronotal base with irregular depression each side of midline defined by three to five shallow punctures; median longitudinal impression distinct, finely incised from median base to before anterior transverse impressions; anterior transverse impressions broad, shallow, but traceable by longitudinal wrinkles and irregular punctures that isolate an anteromedial triangle along anterior margin of pronotum, impressions distinct mesad rounded, non-protruded front angles; lateral marginal depression narrow except for short distance surrounding lateral seta; lateral seta positioned in lateral marginal bead; prosternal process slightly depressed ventromedially, broadly curved to upright posterior face. Elytra elongate ovoid (Fig. 3F), base extended laterally, humeri angulate with basal groove continuing medially, traceable as change in elytral curvature to parascutellar stria, which is defined by three punctures; parascutellar seta (ed1) just mesad sutural stria 1 nearest anterior puncture of parascutellar stria; striae 1-6 continuous and distinctly punctate on disc, obsolete near base, stria 7 represented by about 10 isolated punctures in anterior half of elytra; discal elytral intervals broadly convex; two ed7 setae; one ed8 seta near apex, distance to posterior elytral margin 0.25× distance to sutural margin; lateral elytral setae grouped as four anterior setae (eo1-4) and four posterior setae (eo5-8), with stria 8 terminated just mesad subapical sinuation. Metathoracic flight wings vestigial; metepisternum short, anterior and lateral margins subequal in length; metasternal process with apical triangle bordered posteriorly by broadly arcuate bead that is continuous with lateromarginal beads, apical triangle with upraised median keel.

Coloration.—Head capsule and pronotum shiny brunneous, elytral disc piceous, median basal third, humeral margin and sutural stria brunneous, lateroapical area posterad seta eo5 pale, flavous, the pale area of fusiform shape in dorsal view; mandibles, palpomeres, and antennomere 1 and 2 more flavous, but with intense infuscation, outer antennomeres darker, smoky brunneous; body venter uniformly brunneous, except for legs, including pro- and mesocoxae, that are rufoflavous.

Male Genitalia.—(n=2). Aedeagal median lobe broad, ventral surface indistinctly, evenly curved apicad parameral articulations, straight apically to slightly upturned, evenly rounded tip that protrudes only slightly beyond ostial membrane (Fig. 4O); left and right parameres of subequal length; left paramere with apical parallel-sided process that is 4× as long as broad; right paramere with apical 3-setose parallel-sided process that is 3× as long as broad; flagellar complex extended beyond basal margin of median lobe basal bulb, csc left lobe centered ventrad dorsal basal margin, and flagellum and flagellar sheath extended for distance equal to 0.25× median lobe length; flagellar base and csc rotated 90° counterclockwise (dextral torsion) relative to orientation of median lobe; brush sclerite elongate with longitudinally undulated surface; apex of flagellum and flagellar sheath resting ventrad a markedly transversely ridged acuminate sclerotized region; flagellum estimated to be 0.8 mm long, compared to straight-line measure of 0.6 mm from base of median basal bulb to median lobe apex.

Female Reproductive Tract.—(n=1). Bursa copulatrix urn-shaped, laterally with very thin, transparent membrane, membrane folded apically near entry of spermathecal duct and common oviduct (Fig. 6H); spermathecal duct inflexible, sinuously curved with one complete loop basad spermatheca, base broad, diameter 4× that close to spermatheca, estimated length 0.5 mm; basal portion of spermathecal duct covered with transverse sculpticells, narrower apical portion of duct covered with more quadrate polygonal four- to six-sided sculpticells; spermatheca ovoid with shallow median constriction, spermathecal gland atrium entering basad constriction (Fig. 6H) on side opposite spermathecal duct; gland atrium composed of approximately 50 taenidia-like coils; gland secretory complex lost from dissection; gonocoxa moderately narrow, apical gonocoxite 2 narrowed apically (Fig. 7Q); basal gonocoxite 1 with two to three lateroapical setae; apical gonocoxite 2 moderately expanded basally, base extended laterally relative to falcate lateral cutting margin; apical gonocoxite 2 with two small lateral ensiform setae on ventral ridge some distance from lateral margin, one small dorsal ensiform seta present directly dorsad more apical of the lateral ensiform setae, and two small apical nematiform setae.

The dissected female has a broad, asciform object that stains purple in Chlorazol Black lodged in the first curve of the spermathecal duct. The structure has an acuminate basal end of granulate appearance. This asciform structure is interpreted as the remnants of a male spermatophore.

Variation.—The eyes vary among individuals of this species. Most individuals from Waikamoi and Kuhiwa Valley exhibit eyes with longest diameters ranging from 0.15-0.19 mm. One large male—2.9 mm standardized length—from Kula Pipeline Road (BPBM) has large eyes of 0.23 mm diameter. The opposite extreme is represented in a moderately sized 2.8 mm female—the lone specimen known from Kaapahu (BPBM)—that has eyes of only 0.13 mm diameter. Though these specimens vary in eye configuration, they all exhibit the microsculpture, pronotal shape, and elytral maculation diagnostic for the species, necessitating the conclusion that eye development varies infraspecifically. More specimens from Kaapahu will test whether the range of variation in that population differs from that exhibited in the more westerly populations.

Types.—Holotype female (CUIC): HI: Maui Haleakala NW slope Waikamoi Pres. Trans. 3 @ 1700 m el. 10-IV-1991 sifting litter J. K. Liebherr // Holotype Bembidion haleakalae J.K. Liebherr 2007. Paratypes. Maui (Fig. 18): Waikamoi Nature Conservancy Preserve, Honomanu drainage, transect 3, sifting litter, 1700 m el., 10-IV-1991 lot 01, Liebherr (CUIC, 3), Ukulele Pipeline, pyrethrin fog mossy *Metrosideros*, 1534 m el., 07-V-1998 lot 02, Liebherr (CUIC, 1); Hanawi

N.A.R., Kuhiwa Vy. E rim, pyrethrin fog steep streambank, 880 m el., 10-VI-1999 lot 01, Polhemus (NMNH, 4), *Cibotium chamissoi* dead fronds, 900 m el., 10-VI-1999 lot 07, Ewing (UHEM, 1), ohia lehua litter, 900 m el, 10-VI-1999 lot 08, Ewing (UHEM, 1); Koolau F.R., Kula Pipeline Rd., pyrethrin fog *Metrosideros*, 1265 m el., 18-V-2003 lot 08, Polhemus (BPBM, 3; NMNH, 4), pyrethrin fog log 1305 m el., 18-V-2003 lot 09, Polhemus (NMNH, 1); Haleakala National Park, Kaapahu, 1200 m el., 08-IV-2004 lot 01, Kaholoa`a (HALE deposited in BPBM, 1).

Etymology.—The species epithet is derived from the volcano Haleakala, with that name treated as a first declension noun.

Habits.—This species has been found both in ground-level leaf litter and humus, and also in moss associated with logs and trunks.

RESULTS AND DISCUSSION

Genitalic Specialization.—Both male and female internal genitalic and reproductive structures vary greatly among Hawaiian *Bembidion* species. The greatly hypertrophied male aedeagal flagellar complex serves to define the monophyly of this radiation, and connects the Hawaiian fauna to *Bembidion* (*Ananotaphus*) *errans* of Australia. The degree of hypertrophy varies from slight, as in *B. paratomarium* (Fig. 4L) to extreme, as in *B. pacificum*, *B. teres*, and *B. admirandum* (Figs. 4A-C). As *B. pacificum* and *B. teres* share a body form and associated wing configuration, as well as coloration pattern with *B. errans*, a preliminary hypothesis that they best represent the ground-plan of the Hawaiian radiation can be made. Thus well-developed hypertrophy of the male aedeagus appears to have evolved early in the radiation of the Hawaiian species. This hypertrophic condition in the uneverted aedeagus transforms radically when the aedeagal internal sac is everted. Maddison (1993) demonstrated that the flagellum protrudes from the apical membranous portion of the internal sac, articulating with the left lobe of the central sclerite complex. This complex lies to the left of the orifice that defines the apex of the male sperm duct.

The length of the female spermathecal duct is highly associated with length of the male aedeagal flagellum in Hawaiian *Bembidion* beetles (Table 1). In two instances—*B. ignicola* and *B. fulgens*—the estimated lengths of the male flagellum are about 10-15% less than the estimated spermathecal duct length. The opposite situation is reported for *B. pacificum*, *B. waialeale*, and *B. gagneorum*, wherein the estimated male flagellar length is slightly longer than the female spermathecal duct. Such minor disparities may be related to body size of the sampled individuals, and also to measurement error, especially for highly convoluted spermathecal ducts such as in *B. gagneorum* (Fig. 6G). There are only three taxa—*B. admirandum*, *B. rude* and *B. haleakalae*—within which measurements of the male and female structures differ greatly, and in each instance the male flagellum is much longer than the female spermathecal duct.

TABLE 1. Estimated lengths of the male aedeagal flagellum and female spermathecal duct for Hawaiian *Bembidion* species in which specimens of both sexes have been dissected (species sequence as in taxonomic treatment).

Species	Male flagellum length (mm)	Female spermathecal duct length (mm)
B. ignicola	1.0	1.1
B. pacificum	3.0	2.8
B. teres	2.8	2.8
B. admirandum	2.1-2.2	1.3
B. munroi	0.6	0.6
B. rude	0.7	0.4
B. waialeale	1.2	1.0
B. smaragdinum	1.0	1.0
B. fulgens	0.6	0.7
B. corticarium	1.8	1.8
B. gagneorum	1.5	1.2
B. haleakalae	0.8	0.5

In carabid beetles that transfer sperm within a male spermatophore, the spermatophore is secreted by the male accessory glands, formed inside the internal sac, and deposited into the female when the sac is everted inside the female bursa copulatrix (Jeannel 1941, Gerber 1970). Spermatophore emplacement within the spermathecal duct has been shown to be one function of the flagellum in cicindeline carabid beetles (Freitag et al. 1980, Schincariol and Freitag 1986, Rodríguez S. 1999, Freitag et al. 2001), a function also demonstrated for staphylinid beetles in the genus *Aleochara* Gravenhorst (Gack and Peschke 1994, 2005). In both of these groups, the flagellum also facilitates the clearing of previous male spermatophores and sperm from the spermatheca and its duct, either by direct action, or through placement of a spermatophore that displaces prior sperm (Gack and Peschke 1994). Schuler (1959) previously reported a similar association between male aedeagal flagellar length and female spermathecal duct length among species in the *Bembidion* subgenus *Microserrulula* Netolitzky. All evidence thus points directly to an intimate association of the male flagellum and female spermathecal duct in copulating *Bembidion* beetles. However, last-male sperm predominance, as reported in *Aleochara*, does not seem to occur in *Bembidion*, if we can generalize from Kaufmann's (1986) report that *Bembidion* (*Odontium*) *confusum* Hayward females are inseminated by up to five males, with sperm of successively mating males mixing in the spermatheca.

Evidence for the use of a spermatophore for sperm transfer between male and female Hawaiian *Bembidion* beetles rests on the finding of opaque, granulate structures blocking the base of the spermathecal ducts in individuals of *B. teres* (Fig. 5E), *B. admirandum* (Fig. 6A), and *B. haleakalae* (Fig. 6H), and the presence of loose, sinuous cuticular fragments in the bursa of the *B. teres* and *B. admirandum* females. It remains to be shown whether these various structures represent multiple spermatophores or different regions of single more complex spermatophores. If the putative spermatophores of Hawaiian *Bembidion* are organized in the same manner as previously studied adephagan and staphyliniform spermatophores, i.e. with an neck-like extension that enters the spermathecal duct and a bulbous sperm sac that remains in the bursa (Gerber 1970, Gack and Peschke 1994, Rodríguez S. 1999), then it follows that the granulate structures lodged in the spermathecal duct represent the remains of the filiform neck-like extension. Spermatophores of Tenebrionidae are arranged in a reverse manner, with an apical sperm cap that distends and breaks, releasing the sperm at the base of the spermathecal duct, and a long, basal, more heavily sclerotized tail that remains in the bursa copulatrix unassociated with the spermathecal duct after copulation (Fedina 2007). Phylogenetic affinity would predict the former arrangement. However direct observations and dissections of mating Hawaiian *Bembidion* are the most parsimonious means to sort out the possibilities.

The correspondence of male flagellum and female spermathecal duct length is maximal for those species characterized by female spermathecal ducts of more or less equal diameter throughout their length (Figs. 5C-E, 6B-G, Table 1). For the three species with males that exhibit a flagellum that is substantially longer than the female spermathecal duct—*B. rude* (Fig. 5F), *B. admirandum* (Fig. 6A), and *B. haleakalae* (Fig. 6H) (Table 1)—the base of the spermathecal duct is much broader than the more apical region. In *B. admirandum*, the female of which exhibits the most basally swollen spermathecal duct, the male flagellum is nearly twice the linear length of the spermathecal duct. Given the functional constraints of inserting a very narrow, whiplike flagellum into a large cavity, it seems likely that the flagellum hugs the spermathecal duct walls, possibly spiraling up the duct toward the narrow apical portions of the duct and the terminal spermatheca. The apical torsion visible in the partially everted flagellum of *B. corticarium* (Fig. 4J)—and also observed in the flagellum of subgenus *Bracteon* Bedel males (Maddison 1993)—supports a contention that the flagellum may experience torsion along its length as it is inserted.

The intimate evolutionary association of an intromittent male structure with a corresponding female receptive structure strongly supports the action of sexual selection during diversification of these beetles. The basis for this selection has been recently characterized as either: 1, females maximizing their fitness through choosing superior males, i.e. female choice (Eberhard 1985, 1997); or 2, antagonism between females and males during mating associated with resistance to mating by females, leading to exaggerated mating structures in males, i.e. sexual conflict (Gavrilets et al. 2001, Chapman et al. 2003). In Hawaiian *Bembidion*, there is a close association of flagellar to spermathecal duct length, with the only exceptions occurring in species with basally swollen spermathecal duct conformations hypothesized to mechanically require a longer flagellum to reach the vicinity of the spermatheca. Thus any apparent exaggeration of male structures in the three species with overly long male flagella seems explainable via functional constraints imposed by the associated female structures. If that proves to be so—testable by preserving pairs of those species *in copula*—the present data will not support the sexual conflict model.

If the male flagellum is associated with clearing old spermatophores from the spermathecal duct and flushing old sperm from the spermatheca, as suggested by Freitag et al. (2001) for cicindeline carabid beetles and demonstrated by Gack and Peschke (1994) in *Aleochara curtula* Goeze, then successful male mating will ensure, for the moment, enhanced male paternity. This situation would lead to a prediction that successful males will subsequently guard a female to preclude matings by another male.

It is also possible that recently emplaced spermatophores will plug the spermathecal duct, preventing removal during immediately subsequent mating attempts. Active ejection of male spermatophores by females, as demonstrated in *Pseudoxychila tarsalis* Bates (Rodríguez S. 1999), or at least modification of a plugging structure enough to allow passage of sperm, is a necessary adjunct to mating in any case, as the spermathecal duct must conduct sperm to fertilize the eggs. These conflicting functions of the spermathecal duct—as a structure that could be modified to guard sperm for the short term, and as a conduit for the conveyance of sperm to the egg in the longer term—suggest that timing of mating and oviposition must be highly choreographed. It would be in the female's best genetic interest to resist any matings when eggs are ready for fertilization, as the presence of a spermatophore might preclude, or at least presumably impede that operation. It is also possible that the elongate, convoluted spermathecal ducts test sperm on their outward journey to the fertilization site, and so sperm from multiple males (Kaufmann 1986) may still undergo a collective, selective test during their passage to the egg's micropyle and nucleus.

Flight-Wing Reduction.—Like other major beetle radiations in Hawaii (Perkins 1913, Zimmerman 1948) and other long-studied island systems such as the Atlantic islands (Wollaston 1865, 1867), the Hawaiian *Bembidion* include a great predominance of taxa characterized by rudimentary metathoracic flight wings (Table 2). *Bembidion* radiations on other islands have followed this same pattern. Wollaston (1877) described 12 endemic *Bembidion* from St. Helena, all of which are vestigially winged, and Lindroth (1980) grouped and revised five vestigially winged New Zealand species under the generic-level taxon *Zecillenus*. For the Hawaiian *Bembidion*, novel information relating wing configuration to overall diversity concerns the vestigialized wing configurations of all five newly described species: *B. waialeale* of Kauai, *B. paratomarium* and *B. gagneorum* of Oahu, *B. kamakou* of Molokai, and *B. haleakalae* of East Maui. This situation is predicated on the extreme

TABLE 2. Islands inhabited (including numbers of species precinctive to each island), and metathoracic flight-wing configurations for native Hawaiian *Bembidion* species.

Islands scored as major groups that have been united in the recent geological past (Carson and Clague 1995). Flight wings scored as macropterous and functional (+), polymorphic, including wings of both volant and non-flying form (±), and vestigial (-). Species are in sequence of taxonomic treatment.

Species	Flight-wings	Kauai	Oahu	Maui Nui	Hawaii I.
B. spurcum	+	+	+	+	-
B. blackburni	-	+	+	+	-
B. advena	-?	-	-	+	-
B. ignicola	±	+	+	+	+
B. pacificum	+	+	+	-	-
B. teres	+	+	+	+	-
B. admirandum	-	+	-	-	-
B. munroi	-	+	-	-	-
B. rude	-	+	-	-	-
B. waialeale	-	+	-	-	-
B. smaragdinum	-	-	-	+	-
B. fulgens	-	-	-	+	-
B. auratum	-	-	-	-	+
B. kauaiense	-	+	-	-	-
B. coecum	-	+	-	-	-
B. perkinsi	-	+	-	-	-
B. koebelei	-	-	+	-	-
B. corticarium	-	+	-	-	-
B. gagneorum	-	-	+	-	-
B. paratomarium	-	-	+	-	-
B. atomarium	-	-	+	-	-
B. kamakou	-	-	-	+	-
B. haleakalae	-	-	-	+	-
Total no.of Bembidion spp./island		13(8)	9(4)	9(5)	2(1)

provincialism of many of the brachypterous taxa, with, for example, the species triplet *B. paratomarium*, *B. gagneorum*, and *B. atomarium* of Oahu (Figs. 3B-D) dividing up the island into three definable areas; the western Waianae Range, the northern Koolau Range, and the southern Koolau Range (Fig. 20). Though a phylogenetic hypothesis has yet to be developed, among the species described as of now several putative clades can be proposed, all of which include representative vestigially winged taxa on adjacent islands. These clades include: 1, *B. koebelei* of Oahu (Figs. 2K, 9), *B. smaragdinum* of Molokai (Figs. 2E, 17), *B. fulgens* of East Maui (Figs. 2F, 18), and *B. auratum* of Hawaii I (Figs. 2G, 12); and 2, the Oahu triplet mentioned above, plus *B. kamakou* of Molokai (Figs. 3E, 17) and *B. haleakalae* of East Maui (Figs. 3F, 18). The former quartet is supported by similar, derived convex elytral margins, and for the two species with male and female genitalic data, by very similar aedeagal flagellar complexes and female spermathecal ducts (Figs. 4G, H; 6D, E). The latter pentuplet is supported by the shared convex body form (Figs. 3B-F) and loss of the posterior dorsal elytral seta, though the male flagellar complex exhibits two states within these species. *B. paratomarium*, *B. kamakou*, and *B. haleakalae* share a very short flagellar configuration (Figs. 4L, N, O), and individuals of *B. gagneorum* and *B. atomarium* exhibit long flagella (Figs. 4K, M). To the level of current knowledge, taxa composed of vestigially winged individuals are related to allopatric representative species on other islands, other mountains ranges, or other massifs. Conversely, parallel distributions of winged taxa illustrate a very different level of populational fragmentation. In all instances, macropterous taxa share at least part of their distributional range with all other macropterous taxa (Table 2). Thus, in species comprised totally of winged individuals, all speciation events, presumably occurring via allopatric speciation in these host-generalist species, have been followed by secondary establishment of sympatry.

Loss of flight wings is associated with loss or reductions of other structures. This is repeatedly observed in reduction of compound eyes, best exemplified by the suite of characters associated with cave troglobites (Barr 1968), including greatly reduced or eliminated eyes, and the hypertrophy of tactile setae for use in a constant-dark environment. All macropterous Hawaiian *Bembidion* species also exhibit eyes that are convex and more than 0.20 mm in horizontal diameter. Among the vestigially winged taxa, *B. kauaiense* and *B. coecum* stand out for the extensive reduction of their eyes, with the latter's eyes reduced to a nearly flat surface, with a horizontal diameter crossing only three ommatidia and measuring about 0.05 mm. Nine other vestigial winged taxa exhibit eyes that range in diameter from 0.13-0.19 mm, resulting in a total of 11 out of 19 vestigially winged species with reduced compound eyes. This evolutionary reduction can most likely be assigned to common ancestors once a phylogenetic hypothesis is produced; however the evolutionary association appears significant.

Unlike the troglobite syndrome, wherein hypertrophied setae serve as tactile substitutes for vision, or can be used to determine air movements in order to assess preferred ecological conditions (Jeannel 1926:17), Hawaiian *Bembidion* characterized by wing loss and eye reduction also exhibit loss of several ground-plan setae. Evolutionary loss of the lateral pronotal seta characterizes *B. admirandum* and *B. munroi*. Five other species lack the posterior dorsal elytral seta, and a sixth—*B. munroi*—has this seta absent in some individuals. Thirdly, the only species to exhibit polymorphism for the basal pronotal seta—*B. munroi* again—is also in this group of taxa composed of visually impaired, sedentary individuals. These seven species also exhibit very convex body forms (Fig. 2A, B; 3B-F), again because elytral anatomy is freed from constraints inherent in setting wings for flight. The convex body shape in these beetles suggests that they have become highly effective wedge-pushers (Evans 1977) in their leaf litter and moss microhabitats. It is tempting to speculate that residence in such confines reduces the evolutionary advantage to tactile setae, as the dorsal and ventral body surface would be in direct contact with the substrate.

Biogeography, Ecology, and Conservation.—If we were to suggest those species with more generalized habits, we should pick those with the largest geographic distributions, as such species would be the most successful colonists of novel, isolated habitats. In the instance of Hawaii, we should use the unitary oceanic islands in the archipelago—Kauai, Oahu, Maui Nui, and Hawaii I. (Carson and Clague 1995)—as the islands that must be colonized over a barrier, not via range expansion within continuous habitat. We might also unite Oahu and Maui Nui, as the Penguin Bank connected Oahu with western Molokai (Carson and Clague 1995, Price and Elliott-Fisk 2004). However, the Kauai Channel between Kauai and Oahu, and the Alenuihaha Channel between Maui and Hawaii I. have never been breached by land, and so colonization among the three island units of Kauai, Oahu+Maui Nui, and Hawaii I. must have been over water. All but one of the Hawaiian *Bembidion* species to be distributed on both sides of one or the other of these water barriers include individuals with fully developed flight wings. *Bembidion blackburni* could be said to represent the sole, remarkable exception to this rule, as individuals of this species are vestigially winged, yet this species is distributed on Kauai, Oahu, and Maui Nui. Conversely, given that only five other instances of overwater colonization are required to explain the geographic distributions of all macropterous or wing-polymorphic species, we might alternately conclude that winged dispersal may not be the sole means by which *Bembidion* species traverse water barriers within Hawaii. Such an interpretation gains credence if the proposed phylogenetic affinities among several groups of vestigially winged taxa are corroborated by cladistic analysis. These groups include the proposed four-species clade of *B. koebelei* + *B. kamakou* + *B. haleakalae* + *B. auratum*, the last of which presumably colonized Hawaii I. from Haleakala volcano. Secondly, if the polymorphic occurrence of the posterior dorsal elytral seta in *B. munroi* is evidence of affinity to the five-species clade characterized by this seta's absence (*B. paratomarium* + *B. gagneorum* + *B. atomarium* + *B. kamakou* + *B. haleakalae*), then the Kauai Channel would have been crossed by a vestigially-winged ancestor.

Of the current Hawaiian Islands from which *Bembidion* are known, Kauai houses both the highest overall species diversity, and also the greatest number of precinctive species (Table 2). Maui Nui and Oahu exhibit secondary levels of overall diversity and endemicity. Given this pattern, Kauai—the oldest high island at an age of at least 5.2 Ma (Carson and Clague 1995) would appear to be the portion of the present range occupied longest by Hawaiian *Bembidion*. This interpretation is bolstered by species distribution patterns within the islands. On Kauai, 11 of the 13 resident species are broadly sympatric along the western margins of the Alakai Swamp and headwaters of the Waimea River (Figs. 8, 14, 15, 16, 19). The sole exceptions include *B. teres*, known only from a Kauai island record and probably also sympatric, and *B. waialeale*, narrowly allopatric at the highest elevations of the island on Mt. Waialeale (Fig.16). Conversely, on Oahu the four precinctive species are allopatrically arrayed in three distinct areas (Figs. 9, 20), the southern Koolaus, northern Koolaus, and Waianae Range. Similarly, Maui Nui houses two representative Molokai-Maui species pairs, *B. smaragdinum* and *B. fulgens*, and *B. kamakou* and *B. haleakalae* (Figs. 17, 18), each members of larger, putatively monophyletic groups. It may be that the island geology has underlain these patterns, as Kauai is a large, single volcano reduced to a wheel of spoke-like ridges (e.g. Fig. 16). However widespread species distributions—as in *B. corticarium* (Fig. 16) that includes Namolokama Mountain (the "spoke" to the north of the Waialeale "hub"), and *B. admirandum* (Fig. 14) that includes Namolokama and Mt. Kahili (the southern "spoke")—argue for establishment of ranges before the rampant erosion that cut the intervening Lumahai and Wainiha River Valleys along Kauai's northern coast.

The macropterous and flight-wing polymorphic Hawaiian *Bembidion* species exhibit broad ecological preferences. Individuals of these species have been collected from the margins of lower-order montane streams on sand and gravel substrates, in and on mosses along these stream margins, and also in leaf litter, moss, and damp places on the forest floor. On Kauai, vestigially winged taxa such as *B. admirandum*, *B. munroi*, and *B. kauaiense* appear to have retained preference for ground-level habitats. The only reliable collecting record for the minute-bodied, stenophthalmic *B. coecum* is from soil under a rock. This suggests occupation of deep soil cracks by these beetles, and would explain the general rarity of specimens. Conversely, many of the more highly specialized species characterized by vestigial wings on Oahu, Molokai and Maui have been found most often in arboreal and semiarboreal mossy microhabitats, often in deep moss growing on vertical living tree trunks and on dead, horizontal logs that serve as nurseries for *Cibotium* tree ferns or other trees. Thus at the level of the archipelago, this radiation exhibits a transition from terrestrial to deep soil, and from terrestrial to arboreal microhabitats. This pattern is consistent with the taxon cycle (Wilson 1959, 1961) and taxon pulse (Erwin 1985), each presaged by Darlington's (1936, 1943) transformational model that hypothesized evolution of brachypterous, montane, mesophilic and geophilic taxa from flighted, lowland, streamside or riparian taxa. If we were able to hypothesize unambiguously concerning the sister group of the Hawaiian radiation, we could determine whether the origin of this radiation establishes a groundplan for Hawaiian *Bembidion* consistent with these ecological transformation series (Liebherr and Hajek 1990).

Based on their comparatively well-developed, elongate male flagellar complexes, the most suitable candidates, given present knowledge, for closest relatives of the Hawaiian radiation include *B. errans* of Australia, and the *Zecillenus* group of New Zealand. Darlington (1962) reported collecting *B. errans* from coastal estuarine habitats from across Australia indicating that this macropterous taxon is not only widespread geographically, but also a denizen of at least partially or temporarily saline habitats. Similarly, all *Zecillenus* species "are coastal, living on sand within or just above the tide-water zone (Lindroth 1980)." At this time then, given current best estimates regarding the adelphotaxon to Hawaiian *Bembidion*, it would appear that the ancestor arrived in Hawaii, and established in coastal habitats that may have included some saline component. Our knowledge of such habitats is mitigated by the extensive disturbance to coastal Hawaiian ecosystems. However Blackburn's note that the habitat of *B. pacificum* extended "from the sea level to an elevation of about 3000 feet (1878)" suggests that even extant, or possibly historically extinct species occurred very close to the seashore.

Given a current taxonomic revision that is based on all historical taxonomic specimens plus a substantial amount of newly collected material, the potential loss of Hawaiian biodiversity due to disturbance and replacement of native ecosystems (Howarth 1990) can now be assessed for Hawaiian *Bembidion*. Liebherr (2004) listed eight *Bembidion* species that have been absent from one or more of the islands in their range for more than 100 years. Of these, *B. blackburni* and *B. teres* have been absent from collections on Kauai, but found repeatedly over time on Oahu, Molokai, or Maui. *Bembidion pacificum*, last seen on Oahu in 1920, has been absent from Kauai collections since 1894. *Bembidion admirandum* was considered uncollected since Perkins collected the unique specimen in 1896, but this interpretation was based on misidentifications of several 20th Century specimens. Concerted Kauai fieldwork in 2005 recovered a large series of this species from leaf litter samples in the Alakai Swamp, allowing a robust evaluation of variation within the species relative to *B. munroi*. Given that, we now know that *B. admirandum* is extant, and can be found in shallow leaf litter on higher, drier spots of the forest floor within the bog forest. And finally, disassociated specimens of *B. coecum* collected by Elwood Zimmerman in 1937 were found within unidentified material (BPBM). Thus recent taxonomic activities leave a biodiversity balance sheet that includes only three species missing since R.C.L. Perkins' *Fauna Hawaiiensis* survey: *B. kauaiense* and *B. perkinsi* of Kauai, and *B. advena* of Haleakala, Maui. Concerted leaf litter extraction, soil flotation, and "plain old" grubbing are the likely means to rediscover these elements of the Hawaiian *Bembidion* fauna.

Using the information now at hand, the Hawaiian *Bembidion* can bolster, in their own small way, the definition of areas of endemism that should be targeted for conservation. On Kauai, the allopatric distribution of *B. waialeale* in the summit bog of Mt. Waialeale reaffirms the importance of this site for conserving highly distinctive representatives of Hawaiian biotic diversity. Among carabid beetle taxa, Mt. Waialeale has already been recognized as unique, for it is the only home of *Blackburnia waialeale* Liebherr (Liebherr and Zimmerman 2000) and *Blackburnia riparia* Liebherr and Short (2006). The latter *Blackburnia* lives on unique hygropetric habitats consisting of a cyanobacterial flux coating vertical rockface waterfalls that are also home to the micropterous, Waialeale endemic hydrophilid beetle, *Limnoxenus waialeale* Short and Liebherr (2007).On Oahu, the division of the Koolau Range into distinct northern and southern areas of endemism is paralleled in Hawaiian *Blackburnia* carabid beetles (Liebherr 2006b). Protection of these areas as State Forest Reserves is a first step toward comprehensive conservation management of the Koolau Range. The long-recognized biotic uniqueness of Mt. Kaala, reflected in designation of the summit bog as the Mt. Kaala Natural Area Reserve

(State of Hawaii D.O.F.A.W. 2007) indicates that *Bembidion* species are exhibiting a biogeographic pattern congruent with many other taxa. On Maui an extensive network of State Natural Area and Forest Reserves, The Nature Conservancy of Hawaii Waikamoi Preserve, Haleakala National Park, and the East Maui Irrigation District are managed to conserve both the Maui watershed and its native biodiversity. The single area defined by an endemic Hawaiian *Bembidion* that would appear outside the umbrella of coordinated conservation management is in eastern Molokai, where *B. kamakou* is distributed from the southeastern rim of Wailau Valley across the southeastern face of Kamakou volcano (Fig. 17). This Wailau-Puu Ohelo area of endemism is also the only home for *Blackburnia gastrellariformis* Liebherr (2001), nine species of the psydrine carabid beetle genus *Mecyclothorax* Sharp (Liebherr 2007), two species of Hawaiian *Drosophila*—*D. bostrycha* Hardy and *D. musae* Hardy (Hardy 1965)—plus a recognized but not yet formally described new species of the curculionid weevil genus *Nesotocus* Perkins (Solomon 2004).Once again, a biogeographic pattern of Hawaiian *Bembidion* diversity mirrors that of other sympatric taxa, and in this case adds an element that could be conserved through coordinated land management practices that mitigate the threats and impacts of invasive species (Fornwall and Loope 2004), in order to maintain the natural mosaic of habitat types in the area.

ACKNOWLEDGMENTS

This paper constitutes my heartfelt tribute to Professor George E. Ball on the occasion of his 80th birthday. This presentation of *Bembidion* beetles constitutes a foray into a group new to me, and I felt able to initiate it based on confidence instilled by Dr. Ball, who has always exhibited immense support for work conducted by scientific colleagues. Moreover, his personal willingness to wade into uncharted waters in order to educate our community on the evolutionary wonders of all manner of carabid beetles has been a consistent beacon showing us how to encounter and report on hitherto unknown or poorly known taxa.

For permission and assistance to access lands they administer, I thank Betsy Harrison Gagné, Fern Duvall, Bill Evanson, Jon Giffin, and Alvin Kyono of the State of Hawaii, Department of Land and Natural Resources; Wayne Souza of Kokee State Park; Ed Misaki of The Nature Conservancy of Hawaii, Molokai Preserves; Kalani Fronda of Kamehameha Schools; Randy Bartlett and Hank Oppenheimer of West Maui Land and Pineapple Co.; Raina Takumi Kaholoa`a of Haleakala National Park; and David Foote of Hawaii Volcanoes National Park. I also thank Kip Dunbar and the Dunbar family for their hospitality and access to Kainalu Ranch. Neal Evenhuis, B. P. Bishop Museum and Hawaii Biological Survey facilitated logistical support of field research. I acknowledge the professionalism of the many helicopter pilots—Steve Chilton, Howard Estabrook, Tom Hauptmann, Eric Pacheco, Don Shearer, and Cowboy—for getting us into and out of inaccessible places where these beetles live. Dan A. Polhemus, Curtis P. Ewing, and Art Medeiros are thanked for their considerable efforts in the field. The irony of using modern technology to protect taxa endangered by other aspects of modern technology is not lost on any of us. I thank James E. Hayden, Jr., for his assistance in the laboratory, and Marty Schlabach for access to the invaluable rare literature in the Comstock Memorial Entomology Library. Terry L. Erwin and David R. Maddison provided very helpful reviews of the manuscript while sharing the extensive understanding of Bembidiini. This research was funded by the American Philosophical Society, National Geographic Society awards 4431-90 and 5929-97, and National Science Foundation awards DEB-9208269, DEB-9806349, and REVSYS award DEB-0315504.

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