CSIRO PUBLISHING
Invertebrate Systematics, 2015, **29**, 191–213
http://dx.doi.org/10.1071/IS14047

Reassembling a lost lowland carabid beetle assemblage (Coleoptera) from Kauai, Hawaiian Islands

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Abstract. A late Holocene but prehistoric carabid beetle fauna from the lowland Makauwahi Cave, Kauai, is characterised. Seven extinct species – *Blackburnia burneyi*, *B. cryptipes*, *B. godzilla*, *B. menehune*, *B. mothra*, *B. ovata* and *B. rugosa*, spp. nov. (tribe Platynini) – represent the first Hawaiian insect species to be newly described from subfossil specimens. Four extant *Blackburnia* spp. – *B. aterrima* (Sharp), *B. bryophila* Liebherr, *B. pavida* (Sharp), and *B. posticata* (Sharp) – and three extant species of tribe Bembidiini – *Bembidion ignicola* Blackburn, *B. pacificum* Sharp and *Tachys oahuensis* Blackburn – are also represented. All subfossil fragments are disarticulated, with physical dimensions and cladistic analysis used to associate the major somites – head, prothorax and elytra – for description of the new species. The seven new Makauwahi Cave species support recognition of a lowland area of endemism adjoining Haupu, a low-stature 700 m elevation ridgeline in southern Kauai. Four of the extinct *Blackburnia* are adelphotaxa to extant species currently found at higher elevations in Kauai. Addition of these lowland specialists to the phylogenetic hypothesis undercuts applicability of the taxon cycle for interpreting evolutionary history of these taxa. Two of the extinct species are Kauai representatives in clades that subsequently colonised younger Hawaiian Islands, enhancing support for the progressive biogeographic colonisation of the archipelago by this lineage. And three of the extinct *Blackburnia* species comprised larger beetles than those of any extant Kauai *Blackburnia*, consistent with the evolution of island gigantism in the lowland habitats of Kauai.

Additional keywords: adaptive radiation, Carabidae, insect extinction, phylogenetic analysis, Polynesian colonisation.

Received 27 August 2014, accepted 20 November 2014,

> 'Fossil insects would probably tell us interesting tales – if there were any fossils!' (Zimmerman 1948: 47).

Introduction

The Hawaiian Islands, home to a fascinating array of adaptive radiations (Zimmerman 1970), have suffered rampant extinction upon human colonisation due, in part, to biological attributes of the extremely endemic, very diverse resident biota (Sadler 1999), and second to the wholesale conversion of formerly forested lowland habitats and concomitant introduction of alien species (Burney *et al*. 2001). For example, the Hawaiian avifauna underwent two waves of extinction associated first with Polynesian colonisation and the introduction of the Pacific rat (*Rattus exulans* (Peale)), followed by extensive introduction by European colonists of other invasive species such as avian malaria (Boyer 2008; Athens 2009). These extinctions reduced the number of native bird species by at least half (Olson and James 1982*a*); that finding made possible only by the extraordinary number of extinct, fossil birds discovered throughout the Hawaiian Islands (Olson and James 1982*b*, 1991; James and Olson 1991, 2006; Iwaniuk *et al*. 2009). Up until now our knowledge of insect extinctions has been based on the historically documented loss of insect diversity since the initial explorations of European entomologists (Blackburn and Sharp 1885; Sharp 1913; Liebherr and Polhemus 1997; Liebherr 2005). In this contribution we describe an assemblage of carabid beetle species excavated from dominantly pre-Polynesian colonisation aged deposits in Makauwahi Cave, Kauai; a large sinkhole on the southern coast of Kauai (Burney *et al*. 2001). Seven of the species discovered in these deposits are not known from any historically collected specimens, supporting the conclusion that these species suffered extinction through the agencies of Polynesian agricultural land conversion and introduction of invasive predators such as the Pacific rat. All extinct species are assignable to the genus *Blackburnia* Sharp, tribe Platynini. Several of these species have their closest phylogenetic relative on Kauai, allowing elucidation of the geographic factors associated with their speciation. Others are related to species on the geologically younger islands of Maui Nui and Hawaii, with their phylogenetic position reinforcing the hypothesis of progressive biogeographic colonisation of the island chain during evolutionary diversification (Liebherr and Zimmerman 1998, 2000). Seven other species in the assemblage are represented in the present-day fauna, though historical range contractions have significantly influenced the distributions of these species as well. For extant species restricted to Kauai, recent collections have been restricted to habitats at least 600–1000 m elevation higher than Makauwahi Cave. One other species is geographically widespread, occurring on other Hawaiian islands, though its occurrence in the Makauwahi Cave deposits stands in stark contrast to its absence from present-day Kauai. Thus the composition of this lowland assemblage, with numerous extinct species, one species extirpated from Kauai, and several species that occurred at elevations much lower than occupied today, sheds new light on the biogeographic history of the Kauai carabid beetle fauna from before human colonisation to the present day.

Materials and methods

Site description, stratigraphy and sampling

Makauwahi Cave is a limestone sinkhole situated just west of Kamala Point, along Kauai's south-east coast (Fig. 1*A*). The rim of the sinkhole lies at less than 7 m elevation. Details of the Makauwahi Cave site, its setting, stratigraphy, sedimentology, chronology and general palaeoecology are documented in Burney *et al*. (2001); here, we briefly provide details relating to the context, collection, processing and nature of the sequence relating specifically to the insect sampling regime conducted by Nick Porch in collaboration with David Burney. Examination of Makauwahi Cave sediments initially demonstrated the presence of well-preserved insect material in waterlogged deposits at the site. These small samples demonstrated that the insect material recorded a similar sequence to non-insect taxa described by Burney *et al*. (2001), with an indigenous, lowland biota in the lower part of the sequence, and materials representing human colonisation through the prehistoric and into the historic era throughout the upper part of the record. Like the bird, land snail and plant record already known from the site (Burney *et al*. 2001), indigenous insect taxa were predominantly found in the prehuman and early Polynesian parts of the sedimentary sequence.

Material examined in this paper is mainly derived from currently ongoing North-west (NW) Pit excavations near the locations of auger hole 2 and piston core 3 in the North Cave (Burney *et al*. 2001: fig. 1), with an additional four samples obtained from archived East Pit material. Here the sedimentary sequence reflects the same key features Burney *et al*. (2001) described, based on extensive coring, augering and excavation across the site (Fig. 1*B*). The Makauwahi Cave sequence can be considered to be composed of three generalised components:

1. The prehuman sedimentary record (unit I–unit V of Burney *et al*. 2001) composed of inorganic terrestrial sediments (units I, II), marine sediments deposited during sea level rise around 7000 years ago (unit III) and dominantly, by volume, organic sediments including peaty sands, sandy

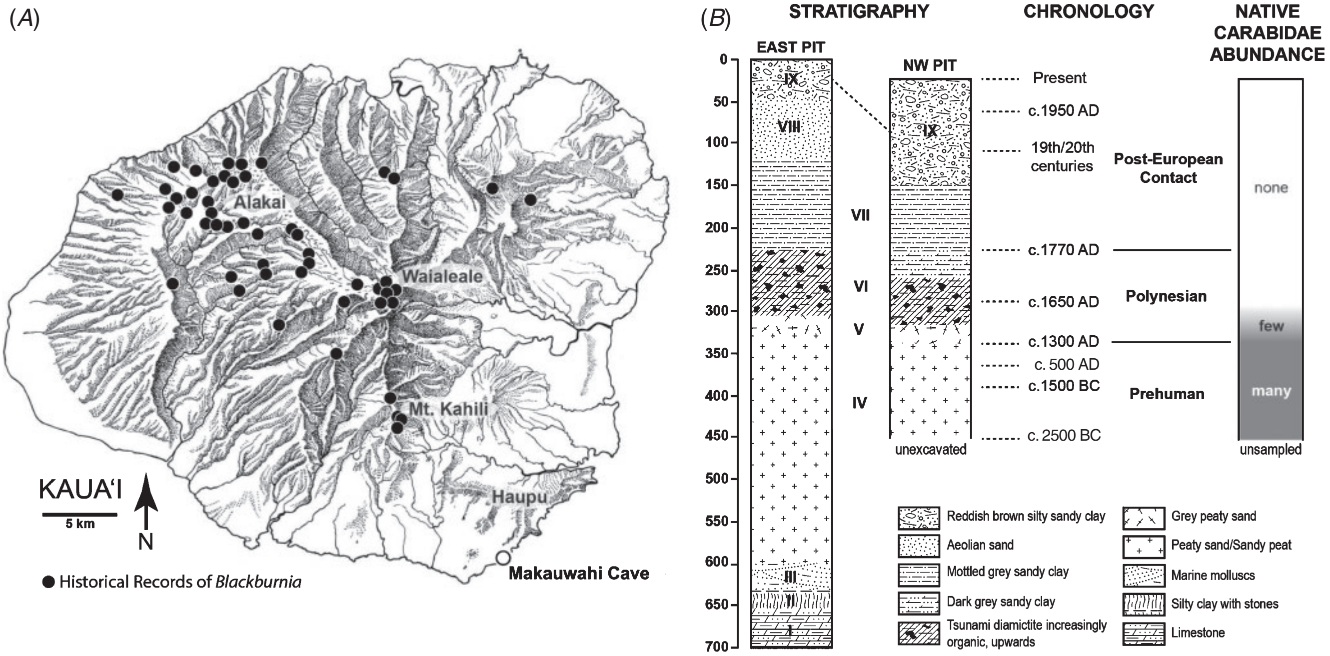

Fig. 1. Distribution of native Carabidae on Kauai. (*A*) Geographical distribution of sites from which native Carabidae have been sampled on Kauai throughout the history of entomological exploration, and Makauwahi Cave locality (○). (*B*) Depth below site datum, stratigraphy and chronology of sediments in Makauwahi Cave East Pit and North-west Pit; East Pit stratigraphy modified after Burney *et al*. (2001: fig. 4). Native carabid subfossils have been predominantly found in prehuman deposits, with the shallowest native specimens found at 290 cm in East Pit and 310 cm in North-west Pit within the tsunami layer that also includes anthropogenic materials deposited subsequent to Polynesian colonisation (see text for detailed explanation). This pattern applies to larger carabids like *Blackburnia*; it is possible that examination of <1.0 mm sediment fractions will reveal the presence of native bembidiine carabids at shallower depths. Chronology is based on Burney *et al*. (2001) and Porch's unpublished radiocarbon dates.

peats and algal gyttja which accumulated in a freshwater-brackish lake (units IV, V). More than 25 radiocarbon dates demonstrate that this sequence is largely 7000–1000 years old. In NW Pit this sequence ranges in depth from 450 to 330 cm below site datum (BSD) (Fig. 1*B*). It is possible that the uppermost part of unit V in NW Pit belongs to the following component.

(2) The Polynesian sedimentary record (unit VI–base of unit VII of Burney *et al*. 2001). Unit VI contrasts with the underlying organic sequence by its coarseness. Burney *et al*. (2001: 619) interpret this unit as the result of 'a severe marine overwash event, probably a tsunami,' sometime in the 15th to 17th centuries AD. Throughout the site there is evidence that this event truncated the prehuman sedimentary sequence and mixed prehuman and Polynesian material into a single deposit (unit VI). This complicates the use of depth in the sedimentary sequence as a proxy for age of material in this part of the sequence. Indeed, radiocarbon dating of individual insect sclerites (N. Porch, unpubl. data) shows that it is likely that at least the larger taxa of indigenous beetles (Lucanidae : *Apterocyclus* Waterhouse; Carabidae : *Blackburnia*) from this layer are reworked prehuman inclusions. In NW Pit this layer ranges from 330 to 270 cm BSD (Fig. 1*B*).

(3) The historic sedimentary record (unit VII–unit X of Burney *et al*. 2001). Within unit VII historical artifacts begin to occur. Decreasingly organic clayey sediment derived from the historically degraded catchment dominates the sedimentary record in NW Pit. No indigenous carabid material has been recovered from this part of the sequence and the depauperate insect fauna is dominated by introduced taxa.

Sampling for insect material was undertaken across all three components described above, but limited in extent in the prehuman part of the record by the shallow depth of NW Pit excavations at the time of sampling. Nonetheless, extensive sampling of all three components was accomplished with a focus on the Polynesian and prehuman parts of the record.

Coarse organic remains, such as insect subfossils, make up a relatively small component of Makauwahi Cave sediments, and carabid remains a small percentage of the insect remains. In order to recover reasonable quantities of infrequent insect types, and especially of larger taxa, the organic fraction of the sediment was concentrated in the field, reducing the volume of sediment to be returned to the laboratory by more than 90%. This was accomplished by using density separation in water. Sediment, recovered during excavation of a 10 cm excavation level was placed in 20 L plastic buckets. Water was added to the sediment and physical disaggregation was accomplished using hose water pressure and/or gentle mechanical breakdown by hand. The resultant light organic slurry was washed through a 0.25 mm sieve. This process was repeated until all that remained in the bucket was heavy clastic sediment – this was discarded after recovery of other palaeoecological and/or archaeological material. In the field the light >0.25 mm organic fraction was washed and placed in labelled plastic bags for return to the laboratory.

Laboratory techniques

In the laboratory organic material recovered by gravity separation in water (see field methods above) was sieved through nested sedimentological sieves ranging from 4 mm to 0.25 mm. All sieve fractions ranging from 4 mm to 1 mm were completely sorted, in water, using a binocular microscope. The recovered insect material was stored in vials containing 70% EtOH. Beetle material for each sample was sorted to family and carabid subfossils concentrated in bulk lots, by sample, in 70% EtOH. These bulk samples of carabid subfossil fragments were sorted by fragment type and stored temporarily in 1 mL clear shell vials with starplug stoppers. Each vial was provided with a sample label, and species determinations were recorded on that label. Specimens were viewed under alcohol until prepared for photography, when the photographic subject was removed to air and placed on a Whatman filter paper disc in a Syracuse dish, with the filter paper disc dampened with 70% EtOH. The paper disc was restocked with 70% EtOH using a dropping bulb as needed to avoid drying out of the subfossil fragment and the associated curling that occurs when these fragments are dried. Specimens were photographed using a Microptics (now Visionary Digital) macrophotography setup with Nikon D1x camera-back mounting Infinity Photo-Optical Co. K2 lenses. Illumination was provided by three fibre-optic wands mounted on a Microptics ML1000 light source powered by a Dynalite 2000 w/s flash generator.

Taxonomic materials

Subfossil specimens excavated from NW Pit (North Cave) and East Pit of Makauwahi Cave (Burney *et al*. 2001: fig. 1) are labelled using a grid system relevant to each pit, with grid numbers presented below solely to allow association of specimens found within the same sample. Depth of the sample within the stratigraphic column is also presented to establish the likely age of deposition of the specimens (Fig. 1*B*). Excavated subfossil specimens were compared to specimens collected alive in the field to determine whether the subfossil fragments were representative of extant or extinct species. This determination was facilitated by the extensive record of historically collected Carabidae from Kauai (Fig. 1*A*), comprising 4716 specimens of native Carabidae sampled during the latter part of the 19th century (Blackburn and Sharp 1885; Sharp 1903), and throughout the 20th century (Liebherr and Zimmerman 2000; Liebherr 2008). Comparative extant specimens were drawn from: the Cornell University Insect Collection, Ithaca, NY (CUIC); Bernice P. Bishop Museum, Honolulu, HI (BPBM); and the National Museum of Natural History, Washington, DC (NMNH).

Linnaean rules of nomenclature (International Code of Zoological Nomenclature 1999) are followed for all scientific names. Based on the cladistic analysis below, 13 separate kinds of somites representing extinct taxa – four heads, four prothoraces and five elytra – are grouped into four distinct convex sets of terminals on the cladogram. Each of these distinct convex sets of terminals are composed of complementary somites – e.g. head, pronotum plus elytra, head plus elytra, or pronotum plus elytra – that are grouped phylogenetically in the context of all extant taxa. Each convex set of somites is considered to represent a distinct species, with the species' delimitations supported by the cladistic hierarchy. To ensure unambiguous species assignment should the cladistic hypothesis be modified by additional information, specimens of only one somite of each set of associated somites are treated as types, with taxonomic material representing the second and potentially third somites treated as cladistically associated non-type material.

Holotypes are deposited in the CUIC, with representative cladistically associated non-type specimens also deposited there. All non-type material cladistically associated as extinct species is explicitly iterated in each description. Additional paratypes and non-type specimens, as well as subfossil specimens of extant species are distributed among the BPBM, CUIC and NMNH. Specimens are archivally preserved in 70% EtOH within 1 mL shell vials with cotton stoppers; these microvials inverted in two dram patent-lip flint glass vials containing the type and locality labels. For the primary types deposited in the CUIC these two dram vials are themselves held inverted inside metal-bale terrine canning jars – 'La Parfait' style – with an outer cap label denoting the contents of the various specimen vials.

Cladistic analysis

The newly described species of *Blackburnia* were analysed cladistically by adding them to the previously developed cladistic dataset based on Liebherr and Zimmerman (1998), that matrix subsequently modified by Liebherr (2001, 2003, 2006) and Liebherr and Short (2006). The original matrix included information based on 206 characters, with those characters described in Liebherr and Zimmerman (1998). Twenty-six of those characters were not relevant to analyses presented in Liebherr and Zimmerman (2000) *et seq*., as their states pertained to outgroup taxa excluded from those analyses. Six characters relevant to fossil taxa have been added to this analysis, resulting in 186 unit-coded characters. Descriptions of the six new characters follow, the characters numbered as the Winclada (Nixon 2002) default.

Character 180: standardised body length 4.6–16.0 mm (0); standardised body length >16.0 mm (1). Body size was estimated for all fossil somites through comparison with somites of extant species. This character was added to recognise the much greater size of the head, thoracic and elytral somites assigned to *B. godzilla*, sp. nov. Standardised body length for *B. godzilla* is at least 18.0 mm based on dimensions of head capsules, pronota and elytral fragments available for examination.

Character 181: cuticle thinner, less sclerotized (0); thicker, more heavily sclerotized (1). Though previous presentation of the *Blackburnia* radiation (Liebherr and Zimmerman 2000) noted the thicker cuticle of many brachypterous species assigned to subgenus *Blackburnia* (Division 1 of Sharp 1903), this character was not included in the analysis. The thickness and opacity of the cuticle was easily scored for the subfossil fragments, and assessed for extant taxa through gentle flexure of elytral apices.

Character 182: median area of frons smoothly or irregularly convex between frontal grooves (0); frons trisulcate, three distinct impressions present between frontal grooves (1). Both *B. cryptipes*, sp. nov. and *B. menehune*, sp. nov. exhibit a distinctly trisulcate frons with those depressions separated from the more lateral frontal grooves (Fig. 5*B*, *I*).

Character 183: basal pronotal setal position not associated with well defined lateral marginal bead, being situated mesad the bead (0); basal seta placed within well defined lateral marginal bead (1). Most *Blackburnia* species exhibiting basal pronotal seta have the seta situated mesad the marginal bead, e.g. *B. godzilla* (Fig. 3*C*), or further separated in the middle of the lateral depression, e.g. *B. rugosa*, sp. nov. (Fig. 4*G*). Less commonly the seta is situated directly in the lateral bead; e.g. *B. mothra* (Fig. 4*C*) and *B. ovata*, sp. nov. (Fig. 5*F*).

Character 184: sutural interval flat mesad elytral basal groove (0); sutural interval upraised mesad elytral basal groove, continuous with an elevated elytral basal carina (1). Most commonly in *Blackburnia* the sutural interval is not elevated at its base mesad the elytral basal groove (Fig. 3*B*, *G*), with the interval extended smoothly onto the elytral base. In *B. menehune*, sp. nov., and related species *B. micantipennis* (Sharp) and *B. waialeale* Liebherr, the sutural interval is elevated basally, and in the instance of *B. menehune*, continuous with a distinctly elevated basal elytral carina (Fig. 5*H*).

Character 185: elytral basal groove smooth, without pits at bases of striae 3 and 5 (0); basal groove with deep depressions or pits at bases of striae 3 and 5 (1). *Blackburnia menehune* exhibits distinct pits at the bases of striae 3 and 5 (Fig. 5*H*). Less distinct though still evident depressions are observed at these specific positions basad striae 3 and 5 in all species of the *B. blaptoides* and *B. elegans* (Sharp) clades excepting *B. kipahulu* Liebherr (Fig. 2).

The 15 different forms of subfossil fragments – four heads, five pronota and six different elytra – were first analysed separately, with each fragment coded for relevant characters leaving all other unscorable characters coded as ambiguous. This matrix thus included 149 taxa scored for 186 characters.

Physical dimensions of all fragments were also measured, with special attention given to measurements that functionally associate topologically adjacent somites. These measurements included, from head to elytra: (1) basal width of head capsule at cervical collar; (2) anterior foramen of pronotum, measured between front angles of pronotum, or across opening of proventrites if available; (3) posterior foramen of pronotum, measured across posterior angles of notum or opening between proventrites; and (4) width of basal articulatory extension of elytron, that width doubled to estimate mesonotal width. If one or more somites were of dimensions compatible with morphological association, their cladistic relationships were examined to determine whether cladistic affinity was supported by the analysis.

Once putative cladistic associations were made for the various sets of somites, those somite terminals were fused in the data matrix, and the analysis re-run. For this dataset the fusion resulted in 141 taxa analysed for 186 characters. Tree lengths were compared for trees generated under separated somites versus fused sets of somites, with cladistic associations of somites confirmed if the latter set of fused trees were of the same length as trees generated with somites analysed independently.

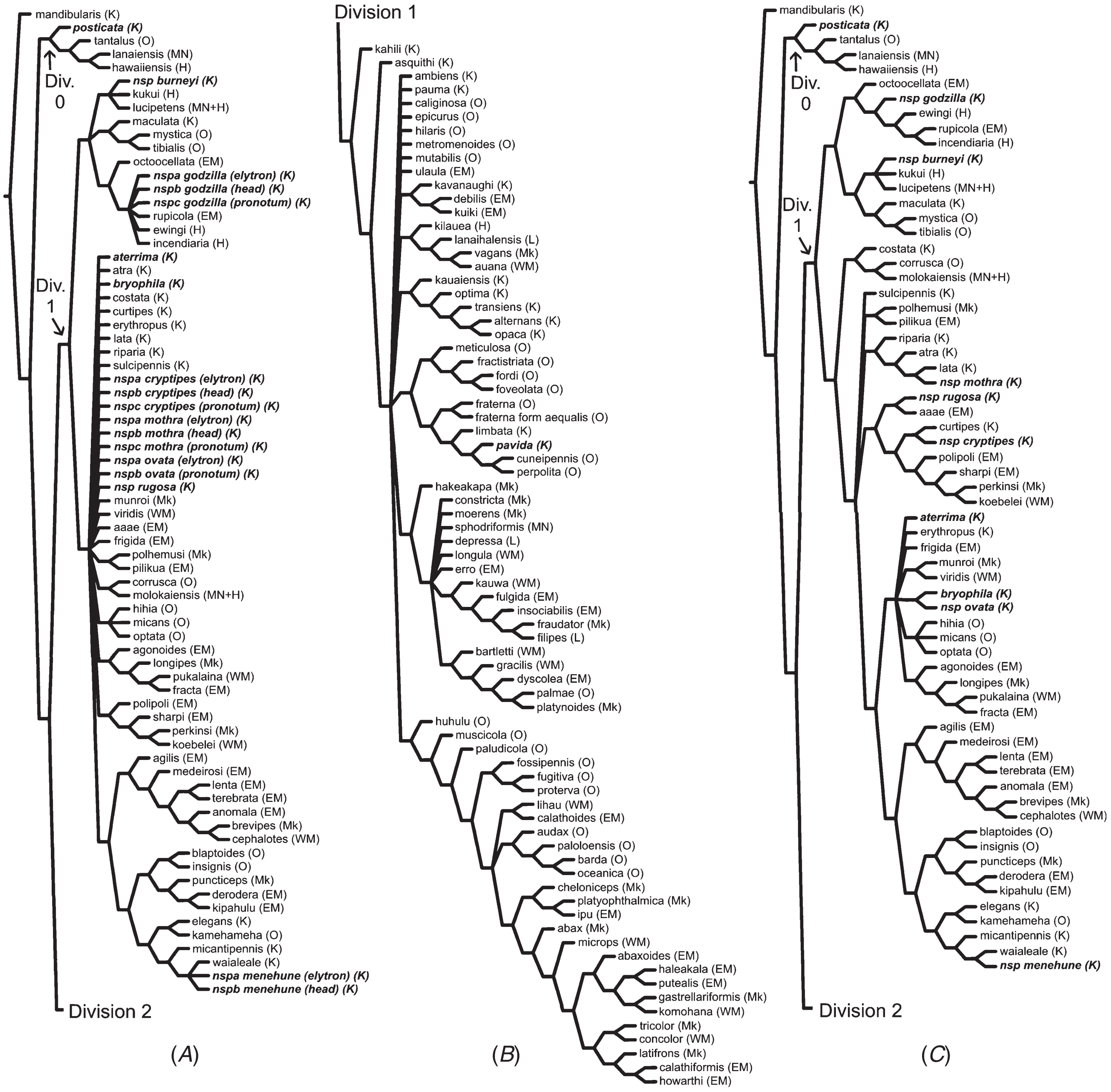

Fig. 2. Cladograms of *Blackburnia* species in Hawaii. Species represented in Makauwahi Cave deposits in bold italics; new species described from Makauwahi Cave designated with 'nsp' prefix. (*A*) Strict consensus of cladistic relationships within subgenera *Protocaccus* (*B. mandibularis*), *Colpocaccus* (Division 0) and *Blackburnia* (Division1; Liebherr and Zimmerman 2000) obtained when subfossil heads, pronota and elytra of extinct species are analysed independently. Somite assignments to distinct species as reflected in alphabetically variant terminals (nspa, nspb, etc.) supported by physical dimensions and subsequent cladistic association (see Fig. 2*C*). (*B*) Strict consensus of cladistic relationships within subgenus *Metromenus* (Division 2; Liebherr and Zimmerman 2000) obtained in both analyses; i.e. subfossil representatives analysed independently and somites cladistically associated (fused) into distinct species. (*C*) Strict consensus of cladistic relationships within divisions 0 and 1 (Liebherr and Zimmerman 2000) obtained when subfossil heads, pronota and elytra of extinct species are fused and collectively assigned to distinct species based on physical dimensions and cladistic association. The alphabetically variant terminals of Fig. 2*A* are here represented by single species names. Island distributions parenthetically follow species names: EM, East Maui; H, Hawaii I; K, Kauai; L, Lanai; Mk, Molokai; O, Oahu; MN, Maui Nui; WM, West Maui.

All analyses implemented Winclada (Nixon 2002), using the ratchet (Nixon 1999) and NONA (Goloboff 1999) for tree search. This initial analysis was based on 10 000 ratchets, with the resultant trees hard collapsed to remove unsupported nodes. The strict consensus of all trees was used to evaluate the range of cladistic placements of both separately analysed and

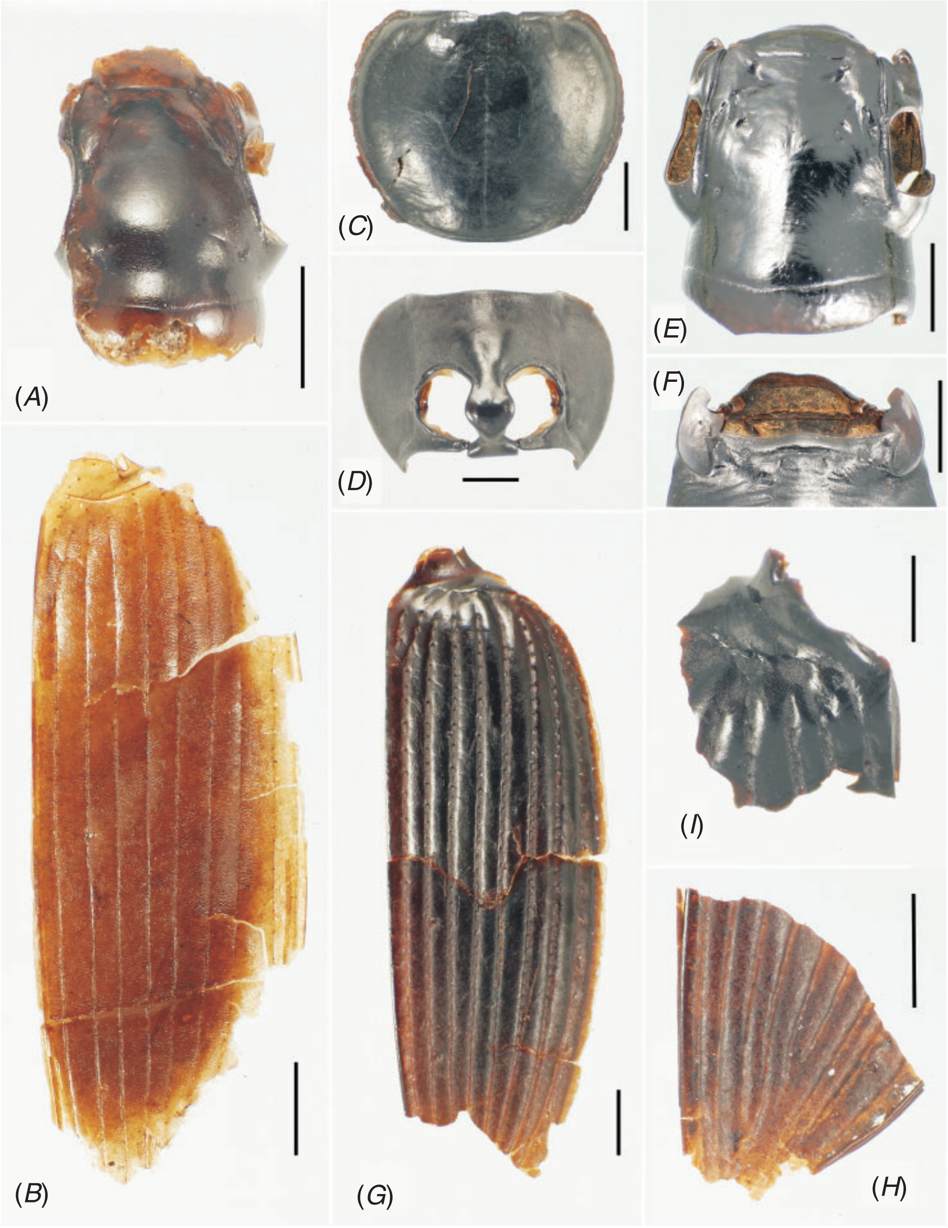

Fig. 3. Subfossil fragments of *Blackburnia* spp. from Makauwahi Cave, Kauai: (*A*) *B. posticata* head capsule, dorsal view; (*B*) *B. posticata* right elytron, dorsal view; (*C*) *B. godzilla* pronotum, dorsal view; (*D*) *B. godzilla* prothoracic ventrites, including prosternum, proepisterna, and proepimera, ventral view; (*E*) *B. godzilla* head capsule, dorsal view; (*F*) *B. godzilla* head capsule, including submentum and gula, ventral view; (*G*) *B. godzilla* right elytron, two fragments, dorsal view; (*H*) *B. godzilla* right elytron apex, dorsal view; (*I*) *B. godzilla* left elytron basal fragment including doubled parascutellar setae. Scale bars for A, B, I = 0.5 mm; scale bars for C–H = 1.0 mm.

cladistically associated subfossil fragments. The data matrix was also analysed using TNT (Goloboff *et al*. 2008) to determine whether the ratchet had found the most parsimonious trees. The TNT search included the default sectorial search, default ratchet, driven search, find minimum tree length 100 times, 5 initial add sequences, and random seed 1. Text renditions of the files comprising the data matrices in NONA format, listings of the 186 characters and states, and resultant equally most parsimonious trees are presented as Supplementary Materials S1 (follow directions in file 'S1_New_fossil_25IV2014.txt' for the separate analysis), and S2 (start with file 'S2_Fused_fossil_28IV2014.txt' for the fused analysis).

Results

The prehistoric Makauwahi Cave fauna comprises seven extant carabid beetle species, plus subfossil fragments comprising 15 different somites assignable to seven extinct species of

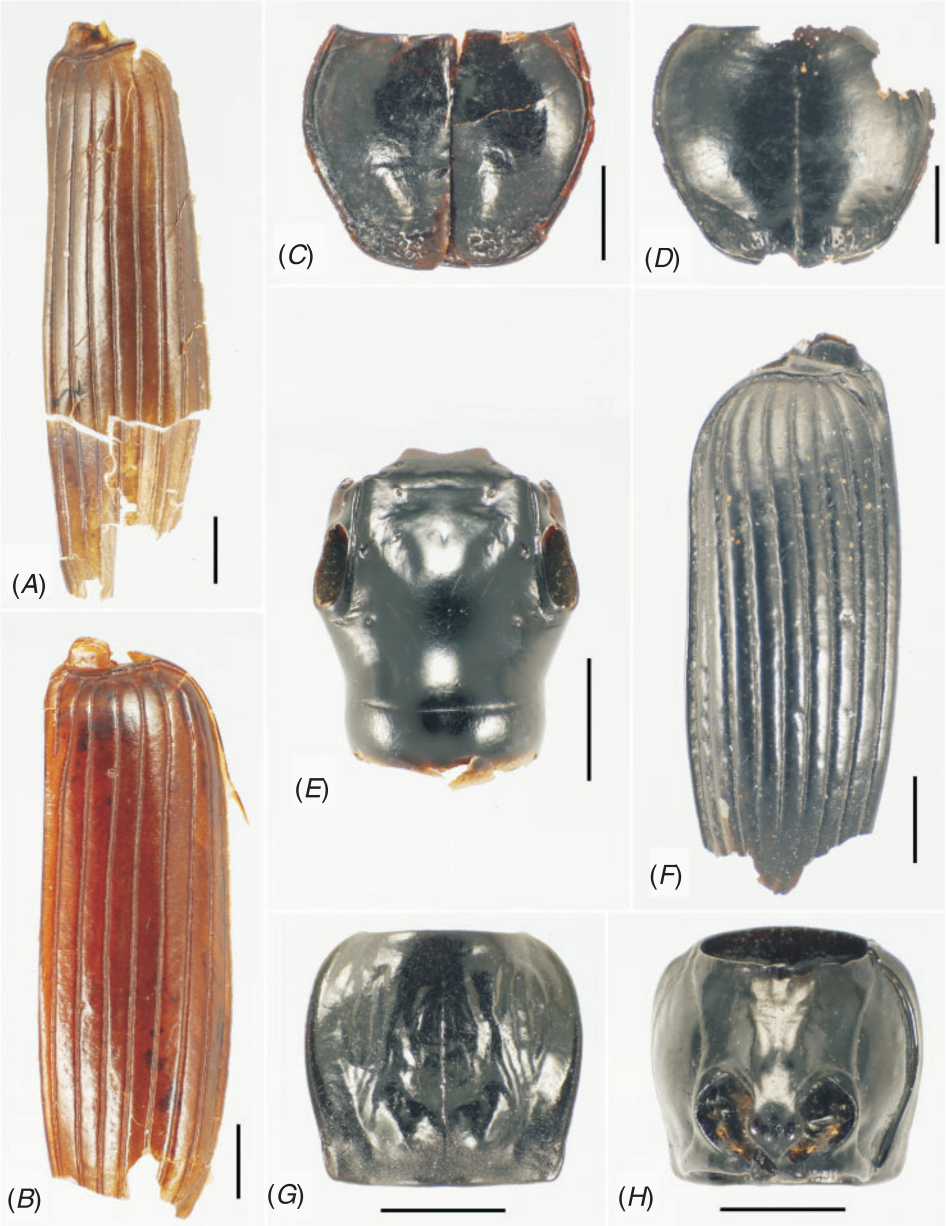

Fig. 4. Subfossil fragments of *Blackburnia* spp. from Makauwahi Cave, Kauai: (*A*) *B. burneyi* right elytron, three fragments, dorsal view; (*B*) *B. burneyi* right elytron, dorsal view; (*C*) *B. mothra* pronotum, two matching fragments broken along midline, dorsal view; (*D*) *B. mothra* pronotum, dorsal view; (*E*) *B. mothra* head capsule, dorsal view. (*F*) *B. mothra* left elytron, dorsal view; (*G*) *B. rugosa* pronotum, dorsal view; (*H*) *B. rugosa* prothorax, including ventrites (prosternum, proepisterna and proepimera) articulated with pronotum, left pronotal epipleuron visible, ventral view. Scale bars = 1.0 mm.

Blackburnia. Species occurrences were restricted to strata from 290 cm to 450 cm depth (Table 1). Species treatments are presented taxonomically, with the extinct *Blackburnia* interpolated among the extant species based on phylogenetic relationships.

Phylogenetic analysis

When subfossil fragments are analysed separately, 10 000 ratchet runs result in 4760 trees of 1137-step length (CI = 16, RI = 72). After hard collapse of trees with unsupported nodes, 1986 trees remain, with the strict consensus of those trees (Fig. 2*A*, *B*) of 1381 step length (47 nodes are collapsed on the consensus of the MEPT). These trees were confirmed as shortest using TNT, with the program examining 1 547 474 391 trees while finding the shortest 1137-step trees 17 times.

Cladistic association of subfossil fragments was accomplished under three situations. *Blackburnia burneyi* is represented solely by elytra paraphyletically grouped with two extant taxa, so *B. burneyi* is described from elytra only. For *B. godzilla*, and *B. menehune* the strict consensus paraphyletically groups sets

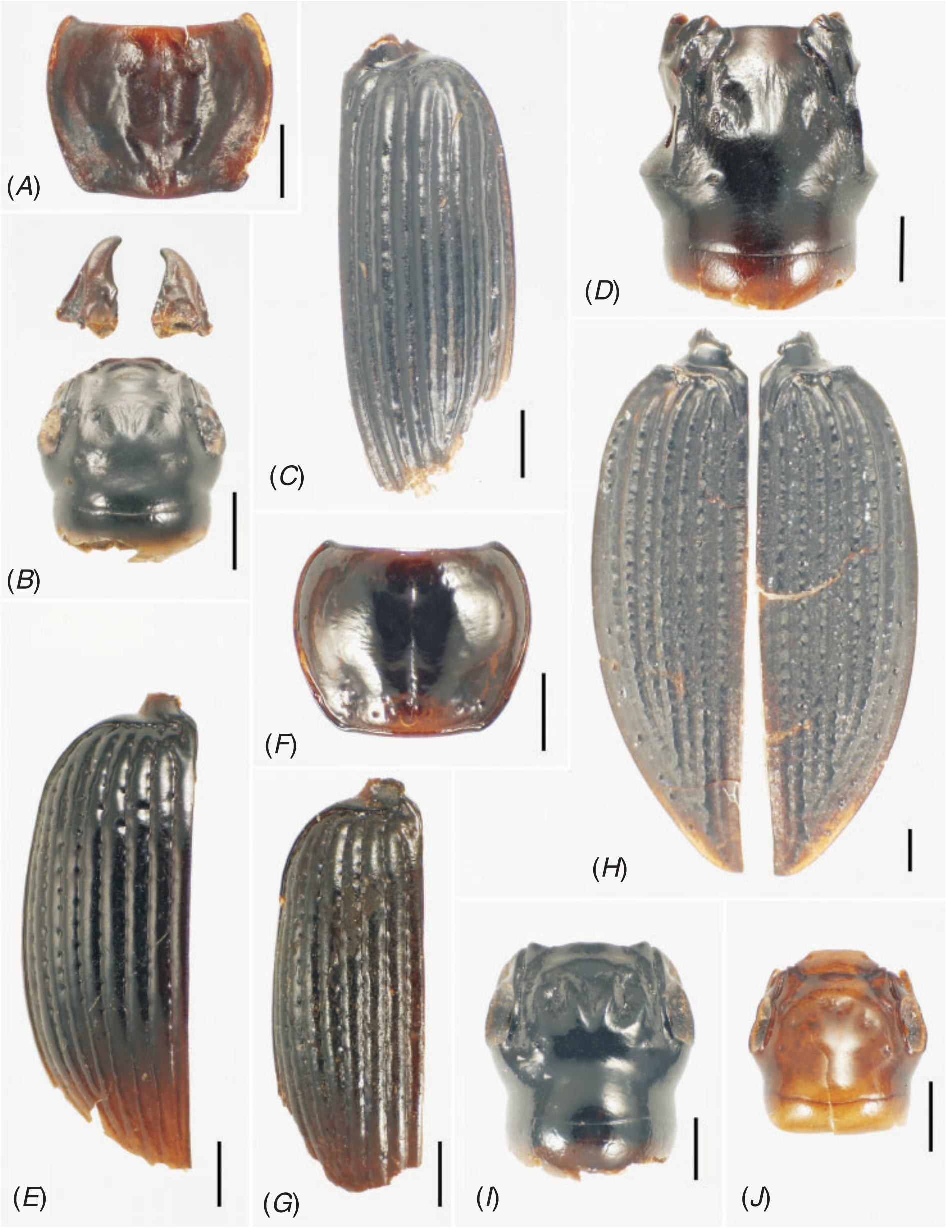

Fig. 5. Subfossil fragments of *Blackburnia* spp. from Makauwahi Cave, Kauai: (*A*) *B. cryptipes* pronotum, dorsal view; (*B*) *B. cryptipes* head capsule and associated mandibles (see text), dorsal view; (*C*) *B. cryptipes* right elytron, dorsal view; (*D*) *B. aterrima* head capsule, dorsal view; (*E*) *B. bryophila* left elytron, dorsal view; (*F*) *B. ovata* pronotum, dorsal view; (*G*) *B. ovata* left elytron, dorsal view; (*H*) Paired elytra of *B. menehune* derived from the same sample (left is holotype, right a paratype), dorsal view; (*I*) *B. menehune* head capsule, dorsal view; (*J*) *B. pavida* head capsule, dorsal view. Scale bars = 0.5 mm.

of somites of the extinct taxa with extant species represented by complete specimens. Thus cladistically associating the somites for these two extinct species was straightforward (Fig. 2*A*). Physical dimensions of the somites assigned to these two species were checked to confirm that these cladistically associated somites were anatomically compatible. The remaining fragments that were ultimately associated and assigned to *B. cryptipes*, *B. mothra*, *B. ovata* and *B. rugosa* took part in a massive polytomy in the strict consensus (Fig. 2*A*), thus they could not be unambiguously associated cladistically based only on relationships shared by all trees. Instead, they were secondarily sorted based on physical dimensions (described below under taxonomy). Physical size suggested that both *B. mothra* and *B. cryptipes* were represented by heads, pronota and elytra, whereas the smaller sized *B. ovata* was represented by pronota and elytra. This left the pronotum described as *B. rugosa* odd-somite out, with this taxon thus represented by only one somite. Based on the biological

Table 1. Stratigraphic distribution of carabid beetle species in the well sampled Makauwahi Cave North-west Pit sediments; globally extinct species (†), locally extirpated species presently not resident on Kauai but extant elsewhere in Hawaiian Islands (*)

Species	Stratigraphic distribution (cm)
Blackburnia posticata	330–410
Blackburnia godzilla†	330–450
Blackburnia burneyi†	330–450
Blackburnia mothra†	310–450
Blackburnia rugosa†	310–450[A]
Blackburnia cryptipes†	330–390
Blackburnia aterrima	400–450
Blackburnia bryophila	310–390
Blackburnia ovata†	330–390
Blackburnia menehune†	310–450[A]
Blackburnia pavida	370
Bembidion ignicola	330–450
*Bembidion pacificum**	320–450
Tachys oahuensis	320–450

[A] Taxa have been sampled upwards to 290 cm in the East Pit excavation; i.e. a level stratigraphically equivalent to 310 cm in the North-west Pit.

associations resulting from sorting by physical dimensions (presented in the descriptions below) the fused dataset, when analysed using parameters identical to those of the initial analysis, produced 2136 trees of 1137-step length (CI = 16, RI = 72). When these trees were hard collapsed removing unsupported nodes, 609 trees remained. The strict consensus of these trees (Fig. 2*C*, *B*) is 1225 steps long, with 26 nodes collapsed. TNT corroboration of the shortest tree length was based on examination of 1 915 941 143 rearrangements, with the best score of 1137 hit 22 times. Thus the relationships of subfossil taxa presented in the fused analysis tree (Fig. 2*C*) were also represented in some of the equally parsimonious trees generated when subfossil fragments were analysed separately (Fig. 2*A*).

Taxonomic results

Tribe **PLATYNINI**

Genus ***Blackburnia*** Sharp, 1878

Diagnosis

Among their closest relatives, species of the genus *Blackburnia* are characterised by the presence of a ring of setae on the apex of the second antennomere (Liebherr and Zimmerman 1998). As antennae are not associated with any of the disarticulated subfossil somites, other characters must be used to place these subfossils as members of the tribe Platynini, and genus *Blackburnia* as the tribe's sole native Hawaiian representative. For head capsules these include the presence of two supraorbital setae (Figs 3*E*, 4*E*, 5*B*, *I*), a gracile head capsule with moderately expanded ocular lobes, and a shallow neck constriction that is visible dorsally. Elytra of Platynini lack an internal plica, and when dorsal elytral setae are present, the anterior seta is associated with the third stria, whereas the posterior two or more setae are more closely associated with the second stria (Figs 3*G*, 4*A*, *B*, *F*). *Blackburnia* pronota exhibit substantial variation among the 133 extant species. Nonetheless the pronota assigned to extinct species (Figs 3*C*, 4*C*, *D*, *G*, 5*A*, *F*) all share characters of setation, shape, margination and microsculpture with extant phylogenetic relatives (Fig. 2*A*, *C*). The highly nested phylogenetic positions of the extinct species (Fig. 2*C*) are indicative of numerous synapomorphies shared with extant species, corroborating assignment of these taxa to *Blackburnia*. These synapomorphies are noted in the descriptions below.

Blackburnia (Colpocaccus) posticata (Sharp)

(Fig. 3*A*, *B*)

Material examined

Head capsule including gula and clypeus. BAC (site code; Burney *et al.* 2001)-Makauwahi Cave , NW Pit, HH-75 (grid reference for Makauwahi Cave excavation unit; Burney *et al.* 2001: 618), 390–400 cm depth (one, CUIC).

Elytron. BAC-Makauwahi Cave, NW Pit, HH-75, 400–410 cm depth (right basal 3/4, CUIC); MC-07 (grid reference for Makauwahi Cave excavation unit; Burney *et al.* 2001: 618), 330 cm depth (median dorsal fragment, CUIC).

Identification

Cuticle relatively thin, lightly sclerotized. Head capsule with eye sockets large, gena short and protruded behind eye (Fig. 3*A*); frontal grooves broad, shallow, moderately convergent; vertex microsculpture transversely stretched. Elytra with smooth striae, intervals slightly convex, interval width 0.15 mm (Fig. 3*B*); intervals covered with isodiametric microsculpture, the sculpticells in transverse rows; ninth interval along lateral margin as well as apex flavous, paler than rufobrunneous disc; parascutellar seta present; three dorsal elytral setae present, the anterior in stria 3, the posterior two associated with stria 2.

Distribution

Specimens collected in historical time span habitats ranging from 600–1375 m elevation, geographically distributed across several isolated ranges in Kauai, including the Alakai Plateau of north-western Kauai, Namolokama Mountain in northern Kauai, the Makaleha Mountains in the north-east, and Mt Kahili in the south. Relative to Makauwahi Cave, Mt Kahili represents the most proximate present-day locality known to house native Carabidae. This species is known from three horizons throughout the sample Makauwahi Cave deposits: 330 cm, 390–400 cm and 400–410 cm. It is likely that before the human colonisation of Hawaii this species occurred across Kauai from sea level to high altitude.

Blackburnia (s. s.) godzilla, sp. nov.

(Fig. 3*C*, *D*)

urn:lsid:zoobank.org:act:A6057254-E726-42C0-BBEA-25E357DB886B

Material examined

Holotype. BAC-Makauwahi Cave, NW Pit, HH-76, 370 cm (pronotum, CUIC).

Paratypes. BAC-Makauwahi Cave, NW Pit, MC-07, 330 cm (pronotum, chips out of front and back, NMNH; paired pronotal halves, broken at midline, BPBM; prosternum, episterna and epimera and prosternal process, CUIC); MC-07, HH-75, 340 cm (pronotum right posterior quarter fragment, CUIC); HH-76, 380–390 cm (pronotum with left margin damaged, CUIC; pronotal hind angle fragment, CUIC).

Diagnosis

This species is the largest-bodied *Blackburnia* known, extant or extinct, with maximum pronotal width 4.9 mm and pronotal length 3.85–4.05 mm. The pronotum shares moderately broad lateral marginal depressions and nearly obsolete, rounded hind angles (Fig. 3*C*) with *B. octoocellata* (Karsch), *B. ewingi* Liebherr, *B. rupicola* (Blackburn) and *B. incendiaria* (Blackburn). The pronotal basal margin is completely beaded and convex medially, with a concave sinuosity immediately mesad the rounded hind angle; a state shared with *B. ewingi*. The disc is covered with transverse mesh microsculpture with sculpticell margins unraised, in contrast to the granulate discal microsculpture of *B. ewingi*, *B. rupicola* and *B. incendiaria*.

Description

Pronotum transverse, maximum pronotal width/pronotal length = 1.34; median base smooth, broad transverse wrinkles laterally delimiting disc (Fig. 3*C*); median longitudinal impression fine, slightly irregularly impressed; lateral marginal depression broad, broadly upraised to margin that is more distinctly beaded in the basal half of pronotum; lateral seta absent, basal seta present and situated before rounded hind angle; laterobasal depression broad, with indistinct transverse wrinkles, lined with isodiametric microsculpture that contrasts with smoother transverse microsculpture of disc. Proventrite assembly width measured across dorsal margins of proepisterna 4.75 mm; prosternal process broad, robust, ventral surface slightly convex, indistinct and irregular depressed areas laterally (Fig. 3*D*); posterior face of prosternal process rounded.

Physical dimensions

The occipital foramen of the prothorax, based on the dimensions of the single proventrite assembly, is of 2.55 mm diameter, consistent with the 2.45–2.62 mm cervical diameters observed for the cladistically associated heads below. The mesothoracic foramen is somewhat less than 3.0 mm wide at the most distant curvature of the proepimeral hind margin; i.e. this distance occurs on the single known specimen that also has a sprung proepimeral–prosternal joint (Fig. 3*D*). The width of each elytron, from midline to the lateral margin of the basal articulatory extension, is ~1.6 mm (Fig. 3*G*), a dimension compatible with the 3-mm wide posterior pronotal foramen that would have lain anterad to the mesonotum and associated articulatory sclerites of the elytra.

Distribution

This species is continuously represented in the Makauwahi Cave depositional sequence from 330 cm to 450 cm.

Etymology

The large body size exhibited by these beetles led us to colloquially name the species after Godzilla (Honda 1954). We validate that moniker here. The epithet is to be used as a noun in apposition.

Cladistically Associated Head

(Fig. 3*E*, *F*)

Material examined

Non-type material. BAC-Makauwahi Cave, NW Pit, MC-07, 330 cm (head capsule, NMNH); HH-75, 340–350 cm (head capsule, NMNH); HH-76, 370 cm (vertex and genae posterad eyes, NMNH); HH-76, 390 cm (right side of vertex and gena, BPBM); S. wall, 390–420 cm (head capsule, BPBM); BAC-Makauwahi Cave, NW Pit, (excavation grid cell) GG-74 sump, 400–450 cm (head capsule, CUIC).

Identification

Head large, frons width 2.00–2.18 mm (Fig. 3*E*); head capsule basal width horizontally across the cervical collar 2.40–2.62 mm, length from clypeal margin to cervical collar 3.0 mm; ocular ratio – distance across outer surfaces of eyes over minimum frons width – estimated to be ~1.4; neck with evident dorsal impression; frons convex and smooth between frontal grooves; ocular lobe protruded, defined dorsally by deep groove that extends forward along frons margin, and posteriorly by shallow indentation that vertically crosses gena; two supraorbital setae, the latter situated mesad the hind margin of eye; submentum with two setae each side (Fig. 3*F*); cuticle thick, robust; frons with evident isodiametric microsculpture, the surface glossy over portions but sculpticells traceable; fine micropunctures sparsely distributed across the frons and vertex.

Distribution

Just as with the pronotum, head capsules have been found from 330 cm to 450 cm depth.

Cladistically Associated Elytron

(Fig. 3*G*–*I*)

Material examined

Non-type material. BAC-Makauwahi Cave, NW Pit, MC-07, 330 cm (right elytron basal half, CUIC); HH-75, 340–350 cm (left elytron basal fragment, CUIC); 2007, 370 cm (left elytron basal half, NMNH); HH-75, 380 cm (right elytron basal 3/4, CUIC); HH-75, 380–390 cm (right elytron basal half, BPBM); HH-75, 390–400 cm (right elytron apical half, CUIC; right elytron apical 1/4, NMNH); GG-74 sump, 400–450 cm (right elytron, CUIC).

Identification

Elytron width 3.5 mm, elytron length 10.7 mm based on 9.75 mm long fragment lacking apex (Fig. 3*G*) complemented by apical elytral fragment (Fig. 3*H*); articulatory base of elytron mesad basal juncture of fifth stria and basal groove 1.6 mm wide; humerus narrowly rounded, lateral margin curved posteriorly outside the base of the fifth stria; elytral disc flattened medially; elytral intervals moderately convex basally, less upraised in apical half (Fig. 3*H*), striae deep and broad, distinctly punctate in basal half, smoother apically, basal punctures only slightly expanding strial breadth; parascutellar seta present; three dorsal elytral setae, anterior in third stria, posterior two in medial half of third interval; subapical sinuation reduced, margin slightly sinuate; 19 lateral elytral setae in largest fragment (arranged as nine in anterior series, two medial and eight in posterior series), with two more setae likely lost from abraded apex; microsculpture isodiametric in transverse rows, more well developed, upraised apically.

Distribution

These cladistically associated elytra exhibit the same stratigraphic distribution as heads and pronota assigned to *B. godzilla*; 330–450 cm depth in Makauwahi Cave deposits.

Additional associated sclerites

Mesosternum of basal width 3.0 mm (Fig. 3*D*; GG-74 sump, 400–450 cm, CUIC); metasternum of 4.0 mm width (HH-76, 390 cm, CUIC); basal three abdominal ventrites of 3.9 mm width (HH-76, 370 cm, CUIC). These three sets of ventrites are associated with *B. godzilla* based on their large size, and their well developed isodiametric microsculpture that matches the microsculpture on the proventrite assembly. A basal left elytral fragment is also assigned (Fig. 3*I*; HH-75, 340–350 cm, CUIC) based on isodiametric microsculpture, size, and the punctation of the striae. This fragment has the parascutellar seta doubled, interpreted here as a variant of the normal unisetose parascutellar seta.

Phylogenetic placement

In the initial cladistic analysis with subfossil somites analysed independently, the three somites associated as this species are placed together in an unresolved bush with *B. rupicola*, *B. ewingi* and *B. incendiaria* (Fig. 2*C*). The somites are placed in this clade based on characters unique to each, with rounded hind angles of the prothorax, lack of a subapical sinuation on the elytra, and large body size providing grouping information. When the three subfossil somites are fused, the strict consensus of equally parsimonious trees places *B. godzilla* as the adelphotaxon to the three species listed above.

Blackburnia (s. s.) burneyi, sp. nov.

(Fig. 4*A*, *B*)

urn:lsid:zoobank.org:act:36ED3E03-47DE-4D77-9AEC-0A569EA0E44B

Material examined

Holotype. BAC-Makauwahi Cave, NW Pit, HH-75, 340–350 cm (right elytron, two pieces, CUIC).

Paratypes. BAC-Makauwahi Cave, NW Pit, MC-07, 330 cm (right elytron, NMNH); 2007, 330 cm (elytral lateral fragment, CUIC); HH-75, 340–350 cm (three elytral fragments, CUIC); HH-76, 370 cm (elytral fragment, CUIC); HH-75, 380 cm (right elytral scutellar fragment, CUIC); HH-76, 390 cm (elytral median fragment, CUIC); GG-74 sump, 400–450 cm (right elytron, BPBM; right elytron lateral fragment, CUIC).

Diagnosis

This species was likely macropterous based on the parallel-sided elytra, with broad humeri, flattened disc and thin cuticle (Fig. 4*A*, *B*). Among winged *Blackburnia* species, this shares nearly flat elytral intervals and smooth, deep, impunctate elytral striae with *B. kukui* Liebherr and *B. lucipetens* (Blackburn). *Blackburnia burneyi* can be diagnosed from those by the somewhat narrower elytral intervals – 0.30 mm wide on the discal intervals – versus the wider, 0.35 mm intervals of the other two species. Also, the elytral basal groove is deeper in this species, though the bases of elytral striae 3–6 are shallower near their juncture with the basal groove than observed in *B. kukui* and *B. lucipetens*.

Description

Broad rounded humerus leading to a subparallel shape (Fig. 4*A*, *B*), each elytron ranging in width from 2.45 mm to 2.60 mm; elytral striae deep, broad, smooth, of equal development across width, and apparently throughout length based on available specimens; parascutellar striole deep, elongate, indistinctly punctured; parascutellar seta present; three dorsal elytral setae, the anterior immediately mesad third stria, the posterior two adjoining second stria; lateral marginal setal series including six anterior setae posterad humerus, followed by two setae just anterad midlength, with an estimated 10 setae comprising the posterior series posterad the position of the middle dorsal elytral seta (based on counts made on two complementary elytral fragments), leading to a total count of lateral elytral setae of 18; colouration uniformly rufobrunneous (though apices abraded); microsculpture a reduced isodiametric mesh in transverse rows intermixed with transverse sculpticells most visible near the striae, intervals medially glossy.

Physical dimensions

Though this species is known only from elytra, the basal width of the articulatory elytral extension at 1.0 mm breadth suggests an associated pronotum with a mesothoracic foramen of ~2.0 mm diameter. Based on cladistic placement, such a pronotum may be predicted to appear similar to those of *B. kukui* or *B. lucipetens* (Liebherr and Zimmerman 2000: fig. 40A, B).

Distribution

Representative subfossils of this species are found throughout the Makauwahi Cave sequence from 330 cm to 450 cm.

Etymology

The patronymic epithet burneyi honours David A. Burney for his long-standing dedication to preserving the Makauwahi Cave site, and developing it as an educational resource presenting the natural and cultural history of Kauai.

Phylogenetic placement

This species is placed at an unresolved trichotomy with *B. kukui* and *B. lucipetens* based on the presence of thin cuticle, nearly flat elytral intervals, and subparallel elytral shape due to the broad humeri. Based on the slightly narrower elytral intervals in this species versus *B. kukui* and *B. lucipetens*, this species is estimated to exhibit a slightly smaller overall body length. This estimate is supported by the most complete elytral fragment being 8.1 mm long, far shorter than the elytral length of 10.2 mm of *B. kukui* (CUIC). The discovery of *B. burneyi* in Kauai geographically complements the Hawaii Island resident distribution of the other two species of this triplet.

***Blackburnia* (s. s.) *mothra*, sp. nov.**

(Fig. 4*C, D*)

urn:lsid:zoobank.org:act:5C83E188-5373-47E0-9A49-54BF3A84952B

Material examined

Holotype. BAC-Makauwahi Cave, NW Pit, MC-07, 330 cm (matching pronotal halves, broken at midline, CUIC) (Fig. 4*C*).

Paratypes. BAC-Makauwahi Cave, NW Pit, HH-76, 370 cm (pronotum, NMNH) (Fig. 4*D*); HH-76, 390 cm (pronotum right half, BPBM).

Diagnosis

This species is uniquely diagnosed by large size – pronotal maximum width 3.2 mm, length 2.9 mm – in combination with the presence of both lateral and basal pronotal setae (Fig. 4*C, D*). Among *Blackburnia*, the consistent presence of both setae occurs only in the much smaller bodied *B. ambiens* (Sharp). The single known specimen of *B. lata* Liebherr unilaterally exhibits both setae on its left side, and only the lateral seta on the right.

Description

Pronotum orbicular with hind angles rounded, the lateral margins anterad the hind angles straight (Fig. 4*C*); pronotal base completely margined, its surface smooth medially and distinctly punctate laterally, the punctures extended into the shallow laterobasal depression; median longitudinal impression finely inscribed (Fig. 4*D*), anterior transverse impression shallow, indistinct, finely punctate; front angles distinct, a fine anterior marginal bead joining the lateral bead at nearly a right angle; lateral marginal depression narrow, the margin beaded, that bead broader and more rounded posteriorly near the basal seta; articulatory socket of basal seta immediately adjoining the marginal bead, a raised tubercular area surrounding the mesal margin of the socket; disc smooth, glossy, with reduced transverse microsculpture, lateral marginal depression with evident transverse-mesh microsculpture; laterobasal depression with a mixture of transverse and isodiametric sculpticells, their arrangement interrupted by rugose punctures along base.

Physical dimensions

The widths of the pronotal occipital foramen range from 1.8 to 1.9 mm (Fig. 4*C, D*), compatible with the 1.78–1.80 mm basal diameters of the cladistically associated heads (Fig. 4*E*). The mesothoracic foramen of the two complete pronota measures 1.8 mm, equivalent to the 1.8 mm width across the basal articulatory extensions of the elytra (Fig. 4*F*).

Distribution

This highly distinctive species is represented by only three specimens found at 330 cm, 370 cm and 390 cm horizons.

Etymology

Among the Kauai *Blackburnia*, beetles of this species exhibit a body size second only to *B. godzilla*, leading to use of the epithet mothra (Honda 1961, 1964), Godzilla's cinematic companion. The epithet is to be used as a noun in apposition.

Cladistically Associated Head

(Fig. 4*E*)

Material examined

Non-type material. BAC-Makauwahi Cave, NW Pit, MC-07, 330 cm (head capsule, CUIC) (Fig. 4*E*); BAC-Makauwahi Cave, NW Pit, HH-76, 370 cm (head capsule, NMNH).

Identification

Frons width 1.65–1.70 mm, basal width at cervical collar 1.78–1.80 mm, head capsule length from clypeal margin to cervical collar 2.25 mm; eyes small, ocular lobe broadly expanded, gena elongate behind small eyes, ocular ratio estimated to be ~1.45 mm based on lobe configuration near eye; neck impression broad, evident; frontal grooves broad, arcuate, defining a central raised callus on frons with a slight, irregular median impression; inner margin of eye bordered by deep, narrow impression that extends deeply to antennal articulation; two supraorbital setae, the posterior seta mesad point where intraocular groove extends ventrally behind eye; two submentum setae each side; frons microsculpture of transversely stretched isodiametric sculpticells in transverse rows, sculpticells evident over portions of frons, cuticle glossy over other portions. The head assigned to *B. mothra* shares the broad arcuate frontal impressions mesad the eyes observed in *B. lata*, though *B. lata* differs by being smaller with much shallower intraocular grooves, and by the placement of the posterior supraorbital seta well posterad the position of the intraocular groove behind the eye.

Distribution

The two had capsules are found in samples at 330 cm and 370 cm within the same grid locations as two of the pronota.

Cladistically Associated Elytron

(Fig. 4*F*)

Material examined

Non-type material. BAC-Makauwahi Cave, East Pit, concentrate, 310 cm (left elytron fragment, NMNH); BAC-Makauwahi Cave, NW Pit, HH-75, 340–350 cm (left elytron basal half, BPBM); HH-75, 360–370 cm (left elytron humeral fragment, CUIC); 2007, 370 cm (left elytron basal third, CUIC); BAC-Makauwahi Cave, NW Pit, HH-76, 380 cm (left elytron in two pieces, CUIC); HH-75, 380–390 cm (left elytron basal 4/5, NMNH) (Fig. 4*F*); GG-74 sump, 400–450 cm (right elytron humeral fragment, BPBM).

Identification

Heavily sclerotized, convex, uniformly piceous, elytral width 2.5 mm; articulatory base mesad basal juncture of fifth stria and basal groove 0.9 mm broad; humerus narrowly rounded, basal groove evenly recurved, smooth; elytral striae punctate, punctures laterally expanding striae; strial punctures reduced apically, equally developed across width; elytral intervals rounded, discal intervals 0.35 mm wide; parascutellar seta present; three to four dorsal elytral setae, the anterior associated with the third stria, the posterior setae in the second stria or on the third interval; one setae in apical half of fifth stria in one individual; >16 lateral elytral setae, 14 setae in one fragment of 2/3 elytral length, 14 in a second fragment of 4/5 length, 12 setae in a third fragment of 1/2 length; microsculpture on discal intervals a fine transverse mesh, sculpticell breadth 2–3× length.

Distribution

These elytra have been found throughout the Makauwahi strata, at 310 cm, 340–350 cm, 360–370 cm, 380–390 cm and 400–450 cm.

Phylogenetic placement

In all trees of the independent analysis, the head and elytron assigned to *B. mothra* are grouped with *B. lata*. The cladistic position of the pronotum is more varied, with it alternately placed at the unresolved polytomy along with *B. lata*, or placed at two progressively more inclusive positions along the clade also including *B. riparia* Liebherr & Short, and *B. atra* Liebherr. Cladistic instability in the *B. pilikua* Liebherr + *B. polhemusi* Liebherr species pair allows that clade to move to a different clade inside *B. sulcipennis* (Sharp) thereby collapsing all somites of *B. mothra* to the massive polytomy headed by *B. aterrima* (Fig. 2*A*). However, because the association of all three somites into one taxon in a fused analysis costs no extra steps, *B. mothra* is circumscribed using these three somites. The cladistic placement of *B. mothra* as sister to *B. lata* is supported by the presence of lateral pronotal setae in both taxa – a reversal from the condition in *B. riparia* and *B. atra* – plus the ambiguous unilateral presence of a basal seta in *B. lata* paired with unambiguous bilateral presence of basal setae in. *B. mothra.*

Blackburnia (s. s.) rugosa, sp. nov.

(Fig. 4*G, H*)

urn:lsid:zoobank.org:act:34940B94-B5E4-496E-B34D-BB11E5B84390

Material examined

Holotype. BAC-Makauwahi Cave, NW Pit, HH-76, 370 cm (associated pronotum, prosternum, proepisternum and proepimeron, CUIC).

Paratypes. BAC-Makauwahi Cave, East Pit, FF-40, 290–330 cm (pronotum, NMNH); NW Pit, HH-75, 320–330 cm (pronotal right half fragment, BPBM); MC-07, 330 cm (two whole, three half pronota, CUIC); 2007, 330 cm (pronotal right half, NMNH); HH-75, 340–350 cm (pronotum, BPBM); 2007, 350 cm (pronotum, right apex broken, NMNH); HH-75, 360–370 cm (pronotum, partial right half, CUIC); HH-76, 370 cm (pronotum, BPBM); HH-75, 380 cm BPBM); HH-75, 380–390 cm (pronotum, CUIC); HH-76, 390 cm (pronotum right half, two pronotal fragments, CUIC); GG-74 sump, 400–450 cm (prosternum and prosternal process, CUIC).

Diagnosis

The broadly quadrate pronotum with thickly raised lateral margins is unique within *Blackburnia* (Fig. 4*G*), though the placement of the basal pronotal seta well before the hind angle and the coarsely rugose disc are observed in the closely related *B. curtipes* (Sharp). Based on an associated specimen, the prosternal process is broad and slightly depressed medially (Fig. 4*H*). The range of pronotal maximum width values spans 2.25–2.40 mm, similar to widths observed in *B. erythropus* (Sharp) and *B. aterrima* (Sharp), suggesting overall body length to be ~8.0–11.0 mm.

Description

Pronotum quadrate, maximum width subequal to median length; discal surface with broad longitudinal rugosities, smaller and more closely packed along the lateral margins of disc, larger medially, with a distinct pair of upraised calli immediately anterad the flat median base, and a pair of sinuous calli anteriorly framing the middle of the disc (Fig. 4*G*); basal margin without bead, median base nearly coplanar with very shallow, broad laterobasal depressions; median longitudinal impression finely inscribed, irregularly expanded by minute punctulae; anterior edge unmargined, nearly straight with front angles not protruded; lateral marginal depression obsolete behind front angle, broadened posteriorly, upraised and beadlike in basal half; only basal pronotal seta present, placed 0.12× length anterad the hind angle, the lateral margin slightly indented laterad basal seta; prosternum broadly depressed anteromedially, flat to slightly convex mesad anterior margins of coxal cavities; prosternal process unmargined, depressed medially (Fig. 4*H*); pronotal disc with very reduced microsculpture, the elevated portions glossy with indistinct isodiametric sculpticells visible in depressed areas; median base broadly covered with well developed, upraised isodiametric mesh, the surface sparsely pocked with micropunctures; sternal sclerites smooth, glossy, the surface bearing sparsely distributed micropunctures.

Physical dimensions

Based on a complete prothorax (Fig. 4*H*) the occipital foramen is of 1.30 mm diameter, and the mesothoracic foramen is of 1.40 mm diameter.

Distribution

This is among the most well represented subfossils in Makauwahi Cave, no doubt based on its robust sclerotization. Specimens have been found in all horizons, from 290 cm to 450 cm.

Etymology

The adjectival species epithet rugosa signifies the well developed rugosities across the pronotal disc.

Phylogenetic placement

Based on the unmargined pronotal base and the very shallow laterobasal depressions, this species is placed as the sister species to the Haleakala Cave species, *Blackburnia aaae* (Liebherr & Samuelson) in a clade that also includes *B. curtipes*. Given its many autapomorphies, *B. aaae* has always been difficult to place phylogenetically (Liebherr and Zimmerman 1998, 2000), and the characters associated with the pronotal base may very well be homoplasious. Phyletic proximity to *B. curtipes* and *B. cryptipes*, sp. nov. is supported by the shared rugose pronotal disc and placement of the basal pronotal seta.

Blackburnia (s. s.) cryptipes, sp. nov.

(Fig. 5*A*)

urn:lsid:zoobank.org:act:0C7C31EA-7B77-48CE-8A7D-A070C15E038B

Material examined

Holotype. Pronotum: BAC-Makauwahi Cave, NW Pit, HH-76, 390 cm (one pronotum, CUIC).

Diagnosis

Pronotum much like *B. curtipes*, moderately transverse – maximum pronotal width/pronotal length = 1.30 – with obtuse-rounded hind angles and lateral margin straight before the angle, the basal pronotal seta placed well before the angle (Fig. 5*A*), but differing in the lack of a mediobasal marginal bead, and smooth, not distinctly punctate laterobasal depressions as in *B. curtipes*. The pronotum is also smaller; maximum pronotal width 1.50 mm versus 1.65 mm in *B. curtipes*.

Description

Pronotal basal margin slightly convex medially, broadly recurved just mesad hind angle; pronotal median impression finely impressed, disc elevated each side of median line; front angles slightly protruded, apically rounded; pronotal marginal depression moderately narrow, the flat depressed area mesad beaded margin lined with isodiametric microsculpture; lateral pronotal seta absent; microsculpture reduced over portions of disc, microsculpture irregularly transverse in depressions, more isodiametric near anterior margin and in laterobasal depressions.

Physical dimensions

Measured on the ventral side of the pronotum (Fig. 5*A*), the occipital foramen is 1.15 mm, compatible with the basal widths of the cladistically associated heads; 1.05–1.15 mm (Fig. 5*B*). The pronotal mesothoracic foramen, again estimated by measuring the pronotal underside, is 0.90 mm; slightly larger than twice the 0.40 mm width across the basal articulatory base of the elytron (Fig. 5*C*).

Distribution

The single pronotum representing this species was found at the 390 cm level.

Etymology

The species epithet cryptipes, cryptic feet, is technically correct as no legs are known for this species. However, the name is meant to signify the cryptic similarity of this species to *B. curtipes*. The name is to be treated as a noun in apposition.

Cladistically Associated Head

(Fig. 5*B*)

Material examined

BAC-Makauwahi Cave, NW Pit, HH-75, 340–350 cm (one with clypeus and gula and associated mandibles, CUIC; one with clypeus and gula, NMNH).

Identification

Very similar to *B. curtipes* in the broad frons and small eyes, and well developed isodiametric microsculpture on the frons and vertex, but smaller, frons width 0.90–0.97 mm versus 1.15 mm in *B. curtipes* (Waialeale summit, CUIC). Also, the eyes are relatively larger, covering ~0.50 of the ocular lobe measured from antennal insertion to neck (Fig. 5*B*), versus only 0.40 coverage on the ocular lobe of *B. curtipes*. The frons also has a more distinct median impression in this new species versus the flat, only slightly impressed median frontal area in *B. curtipes*. Mandibles stout, distance from dorsal condyle to apex of left mandible 1.6 × basal width from ventral condyle to molar surface; dorsal surfaces of mandibles impressed basally, scrobes well developed.

Distribution

The two heads associated with this species were both found in the same grid sample taken at 340–350 cm depth.

Cladistically Associated Elytron

(Fig. 5*C*)

Material examined

BAC-Makauwahi Cave, NW Pit, MC-07, 330 cm (left elytra, basal 5/6, humeral fragment, CUIC); HH75, 340–350 cm (right elytron, apex rubbed, NMNH); 2007, 350–350 cm (left elytron, basal 2/3, CUIC); HH76, 370 cm (left elytron, apex rubbed, BPBM); MC-07, 370 cm (right elytron, apex broken, NMNH); HH-76, 380 cm (left elytron, basal half, BPBM); HH-75, 380–390 cm (right elytron, basal 5/6, CUIC); HH-76, 390 cm (left elytron, basal 1/4, NMNH).

Identification

Similar to *B. curtipes* in the slightly costate elytral intervals 1, 3, 5 and 7, those costae rounded, and in the absence of the parascutellar seta (Fig. 5*C*), but with elytral striae indistinctly punctate to smooth basally, versus the much more basally punctate striae of *B. curtipes*; elytron width 1.1–1.3 mm; humerus rounded; three dorsal elytral setae present; 4–5 lateral elytral setae in the anterior series, a medial seta present or absent, and up to four more setae observed in the posterior series on the available elytral fragments; microsculpture transverse, better developed in lower reaches of intervals. Of *Blackburnia* species in the Kauai fauna, only this species, *B. curtipes* and *B. menehune* lack a parascutellar seta.

Distribution

Elytra associated with this species are broadly distributed in the Makauwahi Cave sediments, being found at 330 cm, 350 cm, 370 cm, 390 cm and 400–450 cm depths.

Phylogenetic placement

This species is placed as the sister species to *B. curtipes* in the combined analysis, with elytral configuration providing substantial grouping information: i.e. parascutellar seta absent but three dorsal elytral setae present; rounded costae on intervals 1, 3, 5 and 7; 12 or less lateral elytral setae. The transverse pronotal shape and pronotal setation are also consistent with this placement, as the posterior seta is placed well before the obtuse-rounded hind angle. Thus all three somites presently assigned to this species can group together in one class of most parsimonious trees when all subfossil fragments are cladistically analysed independently. However, the absence of a pronotal median basal bead supports an alternate grouping of the *B. cryptipes* pronotum with *B. rugosa* plus *B. aaae* in another class of most parsimonious trees when somites are analysed independently. Finally, the placement of *B. rugosa* is unstable in the independent analysis, with this subfossil placed as part of the triplet described above, and alternately placed as the adelphotaxon to the entire *B. aterrima* clade figured in the strict consensus (Fig. 2*A*). As it costs no extra steps to fuse the three somites – elytron, head and pronotum – into a single terminal, they are cladistically associated as *B. cryptipes*.

Blackburnia (s. s.) aterrima (Sharp)

(Fig. 5*D*)

Material examined

Head capsule. BAC-Makauwahi Cave, NW Pit, GG-74 sump, 400–450 cm (one with gula, lacking clypeus, CUIC).

Identification

Frons width 1.4 mm (1.15–1.45 mm in extant specimens); paired lateral depressions on frons with very shallow elongate median impression (Fig. 5*D*); sinuate frontal grooves that extend through position of anterior supraorbital seta to adjoin a broad intraocular groove, the inner margin of the eye socket broadly elevated at midlength of eye; gena gently protruded behind eye; posterior supraorbital seta mesad hind margin of eye; microsculpture reduced, transversely stretched, surface with sparsely distributed though evident micropunctures.

Distribution

Presently this species is recorded from the Alakai Plateau, including the upper reaches of the Makaweli River, north-west to the headlands of Kalalau Valley (Liebherr and Zimmerman 2000). These localities span 600–1320 m elevation. The single attributable head capsule was found at 400–450 cm depth in Makauwahi Cave sediments.

Blackburnia (s. s.) bryophila Liebherr

(Fig. 5*E*)

Material examined

Elytron. BAC-Makauwahi Cave, East Pit, concentrate, 310 cm (one left basal half, BPBM); BAC-Makauwahi Cave, NW Pit, MC-07, 330 cm (left and right matching, one left basal half, CUIC); 2007, 330 cm (one left basal half, one left median fragment, NMNH); HH-75, 340–350 cm (one left, NMNH); HH-75, 380 cm (one right basal 3/4, BPBM); HH-76, 390 cm (one left, one left median fragment, one right basal 1/4, CUIC); HH-76, 390 cm (one right basal 3/4, NMMH).

Identification

Elytron width 1.2–1.5 mm; elytral intervals evenly convex, striae coarsely punctate basally, smooth in apical fifth (Fig. 5*E*); basal groove continuous laterally from parascutellar striole, the latter irregular and interrupted in some instances; humerus rounded, narrow, the elytron widest just apicad midlength; parascutellar seta present, three dorsal elytral setae present, subapical and apical elytral setae present; elytral intervals glossy, microsculpture reduced, transverse sculpticells intermittently visible in strial depressions.

Distribution

Extant records of this species include localities on the Alakai Plateau from Mt Waialeale to the Kalalau Valley, the isolated Namolokama Mountain, and Mt Kahili towards the south (Liebherr and Zimmerman 2000). These localities range in elevation from 850 to 1570 m. Mount Kahili represents the most proximate locality to Makauwahi Cave. The species is represented in the following Makauwahi Cave strata; 310 cm, 330 cm, 340–350 cm, 380 cm and 390 cm.

Blackburnia (s. s.) ovata, sp. nov.

(Fig. 5*F*)

urn:lsid:zoobank.org:act:3117DB0A-29A7-48E1-BBA0-C122C393AC66

Material examined

Holotype. BAC-Makauwahi Cave, NW Pit, MC-07, 330 cm (pronotum, CUIC) (Fig. 5*F*).

Paratypes. HH-76, 370 cm (pronotum, NMNH); HH-76, 390 cm (cracked pronotum, BPBM).

Diagnosis

This species is much like *B. bryophila* in the orbicular pronotum with glossy disc, narrow lateral marginal depression with beaded edge, obtuse-rounded hind angles, and pronotal seta placed within the marginal bead, well before the hind angle (Fig. 5*F*). However, this species is characterised by a smaller pronotum – maximum pronotal width 1.50 mm versus 1.7–2.0 mm in *B. bryophila* – that is much more transverse; maximum pronotal width/pronotal length 1.24 versus 1.07 in the other species. The pronotal base is also much less distinctly punctured than in *B. bryophila*.

Description

Pronotal disc glossy, lined laterally with fine transverse wrinkles; basal margin completely beaded, median base smooth with only indistinct punctures; median longitudinal impression finely impressed, crossed by irregular transverse wrinkles; anterior transverse impression broad and very shallow, nearly obsolete; front margin beaded, a convex roll visible even medially; front angles only slightly protruded, tightly rounded; lateral marginal bead lined mesally by a narrow depression, the bead widened basally, especially at articulatory socket of basal pronotal seta; basal seta placed 0.17× pronotal length anterad hind angle; disc with reduced transverse mesh sculpticells evident in wrinkles, otherwise surface glossy.

Physical dimensions

The prothoracic occipital foramen as estimated by measuring the ventral surface of the pronota is 0.95 mm, though no head somite is yet attributable to this species. The mesothoracic foramen similarly estimated is of 0.9 mm diameter, compatible with twice the 0.45 mm width of the basal extension of the single known elytron.

Distribution

This species is based on three pronota, one each collected at 330 cm, 370 cm and 390 in the Makauwahi Cave sediments.

Etymology

The adjectival species epithet ovata refers to the broadly ovate pronotum with obtuse-rounded hind angles.

Cladistically Associated Elytron

(Fig. 5*G*)

Material examined

Non-type material. BAC-Makauwahi Cave, NW Pit, MC-07, 330 cm (left elytron, basal 3/4, CUIC).

Identification

The single elytron assigned to *B. ovata* is very similar to those assigned to *B. bryophila*, though the distinctly smaller size allows it to be diagnosed; elytron width 1.15 mm versus 1.3–1.5 mm in *B. bryophila*. Correspondingly, the discal elytral intervals are narrower – 0.15 mm – compared with those observed in *B. bryophila* individuals; 0.20–0.22 mm. This species can also be diagnosed from *B. bryophila*, based on the lone specimen, by the more deeply impressed basal portions of striae 3 and 4, (Fig. 5*G*), compared to the basally shallow striae observed in *B. bryophila* (Fig. 5*E*). The humerus is narrow, consistent with a brachypterous individual; striae punctate in basal 2/3 of length, the punctures expanding strial breadth; strial punctation equally developed across basal half, reduced apically; elytral disc convex, entire elytral pair therefore producing a convex, hull-like shell; parascutellar seta present; three dorsal elytral setae, anterior in third stria, posterior two in second stria; 10 lateral elytral setae observed, six in the anterior series posterad humerus, one medial, and three present to end of elytral fragment (consistent with the 13 setae present in individuals of *B. bryophila*); colouration piceous, surface glossy, elytral microsculpture transverse mesh, a mixture of shallow isodiametric sculpticells and transverse lines, traceable over some areas with other areas totally glossy, without microsculpture. The pronotal and elytral lateral dimensions are consistent between *B. bryophila* and *B. ovata*; ratio of pronotal width/maximal elytral width (both elytra) ~2/3.

Distribution

The lone elytron was extracted from the sample taken from grid cell MC-07 at 330 cm; one of the two samples that produced a *B. ovata* pronotum.

Phylogenetic placement

The pronotum used to typify this species is always cladistically associated with *B. bryophila* in the analysis including independent subfossil fragments, based on: (1) the presence of the basal pronotal seta in the marginal bead; (2) the very narrow marginal depression with beaded edge; (3) the obtuse-rounded pronotal hind angles with the lateral margin convex anterad the angles; and (4) the reduced discal microsculpture leading to a glossy surface. The elytron can be scored for many of the same characters as that of *B. bryophila* – parascutellar seta present, three dorsal elytral setae present, striae punctate basally and laterally, humeri narrow, intervals rounded – and one cladistic position is at an unresolved trichotomy with *B. bryophila* and the *B. ovata* pronotum. But as many of the same elytral characters are also seen in species of the *B. agilis* (Sharp) + *B. blaptoides* Blackburn clade, an alternate placement of the *B. ovata* pronotum is as adelphotaxon to the *B. agilis* + *B. blaptoides* clade. These two positions alone collapse numerous nodes in the strict consensus, contributing to the massive polytomy headed by *B. aterrima* (Fig. 2*A*). Nonetheless, because placement of both pronotum and elytra in a trichotomy with *B. bryophila* costs no more steps when the somites are treated as a single terminal, these two somites can be cladistically associated as *B. ovata*.

Blackburnia (s. s.) menehune, sp. nov.

(Fig. 5*H*)

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Material examined

Holotype and paratype. BAC-Makauwahi Cave, NW Pit, HH-75, 390–400 cm (left elytron holotype, CUIC; matching right elytron paratype, CUIC) (Fig. 5*H*).

Paratypes. BAC-Makauwahi Cave, East Pit, FF-40, 290–330 cm (right elytron, NMNH); BAC-Makauwahi Cave, NW Pit, MC-07, 330 cm (two left, three right elytra, CUIC); 2007, 330 cm (left humeral fragment, CUIC); S wall, 330–360 cm (left elytron, BPBM); HH-75, 340–350 cm (two left elytra, basal halves, NMNH, CUIC); HH-75, 360–370 cm (right elytron, CUIC); HH-76, 370 cm (two left elytra, CUIC); 2007, 370 cm (left and right elytra, NMNH); HH-75, 380 cm (right elytron, BPBM); HH-76, 380 cm (right elytron, BPBM); GG-75, 390 cm (left elytron, CUIC); HH-76, 390 cm (three left elytra, BPBM, CUIC, NMNH; right scutellar fragment, CUIC).

Diagnosis

This species is unique among the Hawaiian *Blackburnia* due to the deep pits at the bases of elytral striae 3 and 5, coupled with the distinctly raised base of the sutural interval that continues laterally as a raised basal carina, that carina terminated at the narrow humerus (Fig. 5*H*). The internal surface of the elytron bears upraised tubercles at the positions of the deep pits. Elytral striae 2–7 are distinctly raised in crenulate carinae, interval 8 somewhat less upraised but still with a crenulate median ridge. The subapical sinuation is lacking, with the convex apicolateral margin evenly convex. There is no evidence of a plica on the internal elytral surface.

Description

Elytron width 1.85 mm, length 5.8 mm, and basal width across lateral margins of basal articulatory extensions 1.5 mm; parascutellar seta absent, the dorsal surface at base of sutural interval broadly convex (Fig. 5*H*); three dorsal elytral setae, all associated with crenulate carina of third interval; lateral elytral setae distributed as five setae in the anterior series, a single median seta, and seven setae in the posterior series; microsculpture an upraised isodiametric mesh, appearing granulate in deeper portions of the striae.

Physical dimensions

This species is currently known from heads and elytra, with their dimensions defining any future association with a prothoracic somite. The basal diameters of three intact head capsules range from 1.40 to 1.50 mm, whereas the width across the basal articulatory extensions of the nearly intact holotype and associated paratype (Fig. 5*H*) is 1.50 mm. Both of these dimensions preclude physical compatibility of the somites representing this species versus the smaller-bodied *B. rugosa*; a finding in keeping with the rejection of any cladistic affinity between these species based on discrete characters (Fig. 2*C*).

Distribution

Elytra of this species are well represented in the Makauwahi Cave deposit, being found in all strata from 290 to 390 cm.

Etymology

This species is named for the Menehune, the ancient race of Kauaians, who though very small in stature were extremely strong. The Menehune built fish ponds, roads and temples under cover of night (Pukui *et al*. 1975). The epithet is to be used as a noun in apposition.

Cladistically Associated Head

(Fig. 5*I*)

Material examined

Non-type material. BAC-Makauwahi Cave, NW Pit, HH-75, 340–350 cm (frons and genae, NMNH); HH-76, 370 cm (two head capsules, one frons, CUIC); 2007, 370 cm (head capsule minus gula, BPBM); HH-76, 380 cm (two head capsules, NMNH); GG-74 sump, 400–450 cm (head capsule, CUIC).

Identification

Frons width 1.2–1.35 mm, width across cervical collar 1.4–1.5 mm; cuticle thick, colouration piceous; eyes small, ocular lobe moderately expanded posterad eye, lobe without postocular groove, ocular ratio estimated to be ~1.3; narrow intraocular impression continued anteriorly to antennal articulation; frons with frontal grooves mesad intraocular impression that are subparallel mesad eye, convergent near frontoclypeal suture, plus three median sulci, two paramedial sulci laterally embracing a triangular median sulcus, all sulci terminated anteriorly by convexity near frontoclypeal suture (Fig. 5*I*); two supraorbital setae each side, the posterior mesad posterior margin of eye; neck with evident dorsal impression; submentum with two setae each side; frons microsculpture reduced isodiametric and transversely stretched isodiametric mesh.

Distribution

Heads cladistically associated with this species have been found in Makauwahi Cave at 340–350 cm, 370 cm, 380 cm and 400–450 cm depths.

Phylogenetic placement

In the analysis with all subfossil types analysed independently, the head and elytron assigned to this species are grouped as a trichotomy with *B. waialeale*. The head is placed based on the small eyes and the trisulcate frons, both synapomorphies shared with *B. micantipennis* and *B. waialeale*. The elytra share numerous characters with those two species, including costate elytral intervals 1, 3, 5, 6, 7 and 8, and the sutural interval upraised basally where it is continued onto the upraised anterior margin of the elytral basal groove. The very deep pits observed at the bases of elytral striae 3 and 5 in *B. menehune* are present in less extreme form in the species of the *B. blaptoides* + *B. elegans* clade, excepting *B. kipahulu*. This phylogenetic placement predicts a pronotum for this taxon that has sinuate lateral margins anterad the hind angles, moderately expanded marginal depressions, and a punctate disc (Liebherr and Zimmerman 2000; figs 111C, D).

Blackburnia (Metromenus) pavida (Sharp)

(Fig. 5*J*)

Material examined

Head capsule. BAC-Makauwahi Cave, NW Pit, HH-76, 370 cm (one with gula and clypeus, crack extended from posterior margin to left side of frons, CUIC).

Identification

Frons width 0.95 mm (0.8–1.0 mm in extant specimens); cuticle thin, translucent rufobrunneous; eyes moderately sized, gena gently expanded from neck to hind margin of eye socket; inner dorsal margin of eye narrowly upraised; frontal grooves shallow and broad, extended from anterior supraorbital seta to frontoclypeal suture; posterior supraorbital seta mesad and slightly anterad hind margin of eye (Fig. 5*J*); frons and vertex with reduced microsculpture consisting of transverse meshes, the surface glossy. The subfossil exhibits irregular depressions on the frons – one medial and two paramedial – that are inconsistent with extant specimens of *B. pavida*, but the overall size, thin cuticle, eye configuration, and position of the posterior supraorbital seta all place the subfossil as this species to the exclusion of all other extant species. Thus the irregular, asymmetrical depressions are interpreted as artifactual effects associated with compression within the stratigraphic column.

Distribution

The presently known distribution of this species includes the Alakai Plateau, from Waialeale to the headlands of Kalalau Valley, as well as the isolated Namolokama Mountain. These localities range from 900 to 1570 m elevation. The single subfossil was found near the middle of sampled strata at Makauwahi Cave; i.e. 370 cm depth.

Tribe BEMBIDIINI

Genus **Bembidion** Latreille, 1802

Bembidion ignicola Blackburn

(Fig. 6*A–D*)

Material examined

Head capsule. BAC-Makauwahi Cave, NW Pit, 2007, 370 cm (one with gula and clypeus, CUIC). Pronotum: BAC-Makauwahi Cave, NW Pit, 2007, 330 cm; (one, CUIC); GG-74 sump, 400–450 cm (one, CUIC; one, NMNH).

Elytron. BAC-Makauwahi Cave, NW Pit, MC-07, 330 cm (one paired right and left, surface uneven, pebbled, CUIC); 2007, 370 cm (one right, NMNH); HH-76, 390 cm (BPBM); GG-74 sump, 400–450 cm (one left and one right CUIC; one right, NMNH).

Identification

Head with frons width 0.35 mm (0.35 mm in extant specimens); frontal grooves deep, narrow, continued around posterior of eye demarking gena and protruded ocular lobe (Fig. 6*A*); two supraorbital setae each side in convex frontal costa (Blaisdell 1902); frons surface glossy without evident microsculpture but with evident sparsely distributed micropunctures; dorsal surface of neck with evident transverse mesh microsculpture. Pronotum maximum width 0.7–0.8 mm (0.7–0.85 in extant specimens); lateral margin distinctly sinuate basally anterad obtuse-angulate hind angle, the angle set into convex base well anterad lateral terminus of median basal margin (Fig. 6*B*); median base obscurely punctate; median longitudinal impression narrow, well defined; anterior transverse impression broad, shallow, smooth; lateral marginal depression broadest at and immediately posterad lateral pronotal seta, margin little upraised; disc glossy with very reduced microsculpture, micropunctures sparsely distributed across surface. Prosternal process smooth ventrally, unmargined (Fig. 6*C*). Elytron 0.60–0.65 mm wide (0.55–0.62 mm in extant specimens); elytral striae 1–7 punctate basally, length of punctate portions progressively shorter laterally, seventh stria with only five to nine distinct punctures (Fig. 6*D*); two dorsal elytral setae in third interval, the posterior seta free of third stria, near middle of interval; both humerus and more so the apex, pale, flavous, contrasted to piceous disc.

Distribution

In present-day Kauai, this species is known from the upper reaches of water sources feeding the Waimea River: Kokee Stream, Waiakoali Stream, Mohihi River and Koaie Stream (Liebherr 2008). Collecting localities range from 1000 to 1525 m elevation. Subfossils are represented in the following strata of Makauwahi Cave sediments: 330 cm, 370 cm, 390 cm and 400–450 cm.

Bembidion pacificum Blackburn

(Fig. 6*E*, *F*)

Material examined

Pronotum. BAC-Makauwahi Cave, NW Pit, HH-75, 320–330 cm (one, NMNH); GG-74 sump, 400–450 cm (one, CUIC).

Elytron. BAC-Makauwahi Cave, NW Pit, MC-07, 330 cm (one left and two right, NMNH); 2007 (one left and nine right, CUIC); 2007, 350 cm (one left, BPBM); MC-07, 370 cm (two right, BPBM); 2007, 370 cm (one right, CUIC); GG-75, 390 cm (one left, CUIC); HH-76, 390 cm (one left fragment, CUIC); GG-74 sump, 400–450 cm (one left, one left fragment, one right, CUIC).

Identification

Pronotum maximum width 0.95–1.03 mm (1.1–1.15 in extant specimens); lateral margin broadly sinuate anterad obtuse hind angle; median basal margin moderately convex, nearly straight medially (Fig. 6*E*); median base diffusely punctate to rugose laterally each side to arcuate laterobasal depression; median longitudinal impression and anterior transverse impression obscure; lateral marginal depression moderately broad throughout length, lined with isodiametric microsculpture, the margin obscurely upraised; disc medially smooth with sparsely distributed micropunctures, laterally covered with well developed, transversely stretched isodiametric microsculpture. Elytron width 0.80–0.85 mm (0.85–0.90 mm in extant specimens); elytral striae 1–7 punctate in basal 3/4 of length, punctures similarly extended towards apex across width (Fig. 6*F*); two dorsal elytral setae, the posterior seta closer to third stria than to second; apex with flavous lunule extended subparallel to the convex margin, no paler area near humerus; elytral intervals glossy, microsculpture obsolete.

Distribution

This species was recorded in Kauai only from Kaholuamano, a major collecting locality of R. C. L. Perkins (Sharp 1903) south of Waialae Stream (Liebherr 2008). The species was collected in 1894 at an elevation of ~1200 m, and it has never been seen since on Kauai, though there is a 1920 record from Oahu. The species is relatively well represented in Makauwahi Cave samples, being recorded from 320, 330, 350, 370, 390 and 400–450 cm horizons.

Genus **Tachys** Dejean, 1821

Tachys oahuensis Blackburn

(Fig. 6*G–I*)

Material examined

Head capsule including gula and clypeus. BAC-Makauwahi Cave, NW Pit, HH-75, 320–330 cm (one, NMNH); GG-74 sump (four, CUIC).

Pronotum. BAC-Makauwahi Cave, NW Pit, GG-74 (two, CUIC).

Elytron. BAC-Makauwahi Cave, NW Pit, HH-75, 320–330 cm (one left, NMNH); 2007, 330 cm (one left, one right, CUIC); HH-75, 340–350 cm (one left, BPBM); MC-07, 370 cm (one right, NMNH); GG-74 sump, 400–450 cm (six left, three right, CUIC).

Identification

Head capsule with frons width 0.35 mm (0.32–0.35 mm in extant specimens); frontal grooves moderately convergent, extended posteriorly beyond posterior supraorbital seta to join juncture of gena and ocular lobe; ocular lobe protruded from gena; vertex with scale-like, transversely stretched microsculpture, the sculpticell margins distinct (Fig. 6*G*), sculpticells more

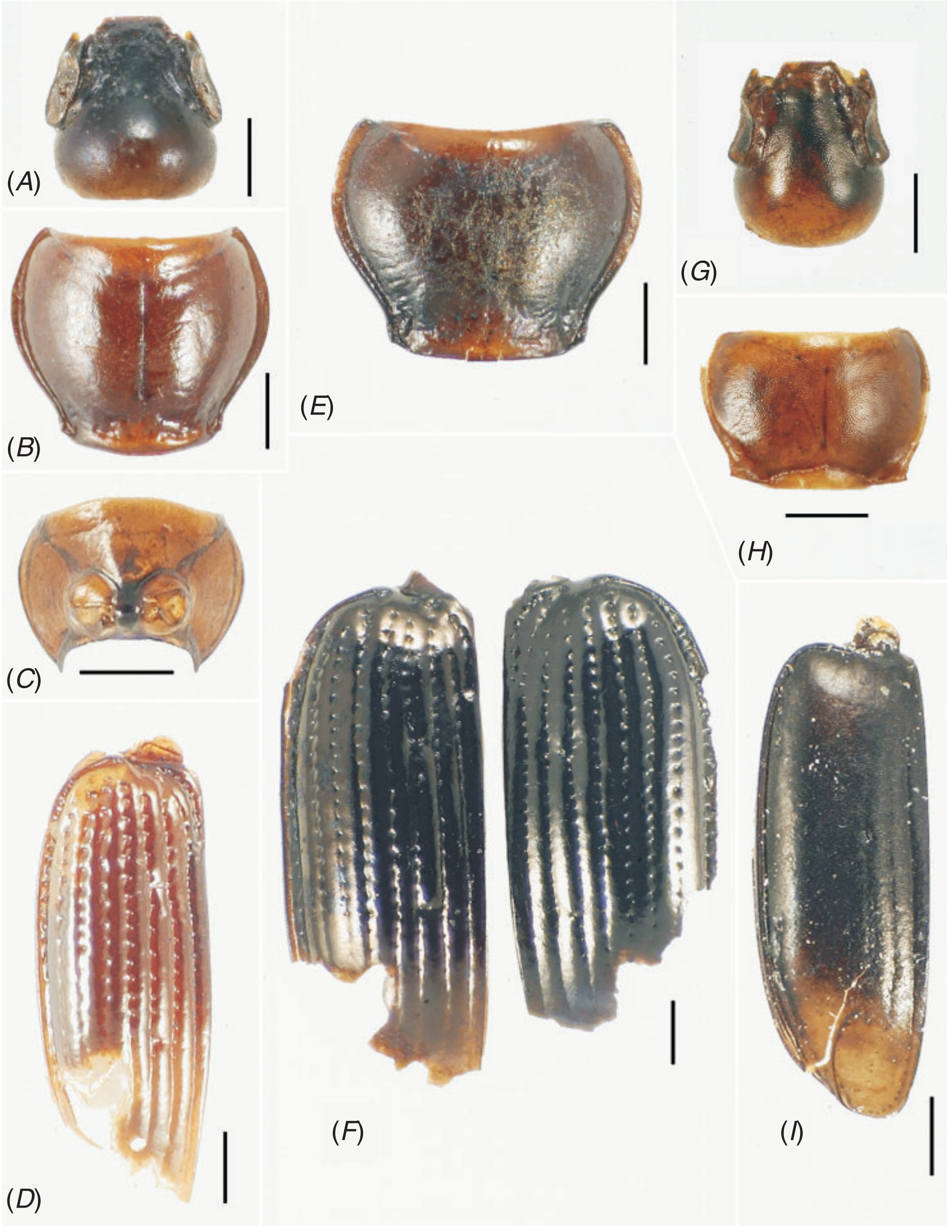

Fig. 6. Subfossil fragments of Bembidiini from Makauwahi Cave, Kauai: (*A*) *Bembidion ignicola* head capsule, dorsal view; (*B*) *B. ignicola* pronotum, dorsal view; (*C*) *B. ignicola* prothoracic ventrites (prosternum, proepisterna and proepimera) and procoxae, ventral view; (*D*) *B. ignicola* left elytron, dorsal view; (*E*) *Bembidion pacificum* pronotum, dorsal view; (*F*) Paired elytra of *B. pacificum* derived from the same sample, dorsal view; (*G*) *Tachys oahuensis* head capsule, dorsal view; (*H*) *T. oahuensis* pronotum, dorsal view; (*I*) *T. oahuensis* left elytron, dorsal view. Scale bars = 0.50 mm.

transverse on neck. Pronotum transverse, maximum pronotal width 0.70 mm (0.55–0.70 mm in extant specimens); lateral margin sinuate before acute hind angle (Fig. 6*H*), basolateral seta expanding lateral margin at point of insertion; median base bordered anteriorly by deep, punctate groove; median longitudinal depression shallow, indicated by melanic stripe; anterior transverse impression broad, shallow; lateral marginal depression narrow in apical 4/5, edge narrowly upturned; disc with well developed transverse mesh microsculpture, some isodiametric sculpticells intermixed. Elytron width 0.55 mm (0.40–0.50 mm in extant specimens); parascutellar seta present; two dorsal elytral setae in third stria, apical seta immediately mesad base of recurrent stria, the stria evenly curved to its base (Fig. 6*I*); transverse mesh microsculpture on disc, apex with reduced microsculpture mesad recurrent stria; apex flavous, paler than remainder of disc and base.

Distribution

This species has been recorded from Laysan, Kauai, Oahu and Molokai during the historical era (Britton 1948; J. K. Liebherr unpubl. data). All specimens have been collected from low elevation habitats, often in salty back beach habitats. Specimens have also been collected in light traps at low elevation sites such as Hickam Field, Oahu and the Public Health Building, downtown Honolulu. This species has been found throughout most of the sequence of Makauwahi Cave deposits, at depths of 320–330 cm, 340–350 cm, 370 cm and 400–450 cm.

Discussion

The coastal location of Makauwahi Cave, within the south trending drainage of the Haupu ridgeline, establishes the geographic boundaries within which non-motile organic remains might have originated in the cave deposits. The occurrence there of subfossil fragments hypothesised to represent seven newly described *Blackburnia* species supports recognition of a lowland area of endemism including the Makauwahi Cave site. The closest upland area to Haupu comprises the southern spur of the Waialeale massif; Mt Kahili (Fig. 1*A*). At 700 m elevation, Haupu's summit is 240 m lower than the 940 m Mt Kahili. Four of the seven endemic Makauwahi *Blackburnia* have closest relatives on Kauai. In three instances, those relatives presently occur in habitats at much higher elevations. *Blackburnia mothra* is sister species to *B. lata*, a species described from the Alakai Plateau at 1160 m elevation (Liebherr 2003). *Blackburnia cryptipes* is sister to *B. curtipes*, a species that occurs in habitats ranging from 1210 m elevation to the summit of Mt Waialeale at over 1500 m elevation (Liebherr and Zimmerman 2000). The third allopatric sister-species pair, *B. waialeale* and *B. menehune*, are maximally separated elevationally, with the former known only from Waialeale's summit bog area, 1530–1545 m elevation (Liebherr and Zimmerman 2000), and the latter from near sea level at Makauwahi Cave. The fourth pair of Kauai sister species pair are sympatric, with *B. ovata* and its sister, *B. bryophila*, known from Makauwahi Cave. The latter is currently resident in the uplands, where it is known from habitats ranging from 850 to 1570 m elevation on Mt Kahili, Waialeale summit, Namolokama Mountain, and the Alakai Plateau north-west to Kalalau Valley (Liebherr and Zimmerman 2000; J. K. Liebherr, unpubl. data). That *B. ovata* was derived as a peripheral isolate of *B. bryophila*, with the more wide-ranging species subsequently expanding its range, is one possible hypothesis regarding the biogeographic history of these sister species. The distributions of all four species pairs would have been influenced by Pleistocene climatic changes associated with glacial periods; those changes including increased rainfall at low elevations, and a lowering of the trade wind inversion – which determines tree line – to ~1500 m versus the present-day 2000 m level (Loope 1995).

Of the extant species represented in the Makauwahi Cave fauna, only *Blackburnia posticata* occurs on the geographically proximate Mt Kahili. The macropterous *B. posticata* is the most commonly encountered and ecological catholic *Blackburnia* on Kauai, and its range includes localities at 600 m elevation in the Makaleha Mountains, north-east Kauai (Liebherr and Zimmerman 2000). Its absence from lowland sites near Makauwahi Cave and the bordering ridge Haupu – supported by fieldwork that resulted in other taxa being sampled in those situations (Stone 1957; Asquith and Messing 1993; Otte 1994; Gillespie and Rivera 2007) – implies a present-day lack of any supporting habitat for this species in this area. The continued absence from Haupu of the ecologically most generalised, flight-dispersive Kauai *Blackburnia* species casts a pall on any hopes that the locally extirpated or globally extinct Makauwahi Cave species presented above remain resident there.

The three newly described Makauwahi Cave *Blackburnia* with closest off-island relatives are in all instances hypothesised to be members of clades including species resident on Maui Nui or Hawaii Island. *Blackburnia godzilla* joins a clade of two Hawaii Island species and a third from Haleakala, Maui (Fig. 2*C*). All are flightless species of large stature (Liebherr and Zimmerman 2000). The sister species *Blackburnia rupicola* and *B. incendiaria* (Fig. 2*C*) inhabit terrestrial microhabitats in upland scrub vegetative communities, where they can be found in leaf litter associated with plants such as *Sophora* (Fabaceae). They also climb vegetation at night, and have been beaten from scrubland plants and found under bark flaps on *Acacia koa* (Fabaceae). The fourth member of this clade, *B. ewingi*, has been found under the bark of a downed *Metrosideros* log (Myrtaceae). Thus we may postdict that *B. godzilla* predominantly foraged near the ground, though they may have also climbed plant stems. These habits would have put these large, flightless individuals into direct contact with the climbing, omnivorous Pacific rat (Shiels *et al*. 2013).

The flight-capable *B. burneyi* is ambiguously related to both *B. kukui* and *B. lucipetens*, both arboreal species encountered on Hawaii Island. *Blackburnia lucipetens* is the more geographically widespread of the two, being recorded also from Maui Nui and even Oahu; a rare summer flight record at a store window in downtown Honolulu (Liebherr and Zimmerman 2000). We hypothesise that the thin cuticle and subparallel elytra of *B. burneyi* also supported such flight capacity, suggesting that *B. burneyi* was a fully arboreal species. That such a dispersive species became extinct seems counterintuitive. Yet such was also the case for the presently extinct, though historically most-commonly encountered Oahuan species, *B. tantalus* (Blackburn) (Liebherr and Polhemus 1997). *Blackburnia rugosa* represents the third and last species with off-island relatives, in this instance a cave species, *B. aaae* of Haleakala, Maui. *Blackburnia rugosa* is represented only by the prothorax, that somite sharing a rugose notal surface with its closest Kauai relative, *B. curtipes*. This latter species has been collected under prostrate stems of tree ferns or under logs (Perkins 1913), suggesting that *B. rugosa* also spent much time at ground level. Though we lack elytra, the heavy cuticle supports a brachypterous condition in this species, meaning that individuals would have been in contact with ground foraging rats while also dependent on forest tree cover.

The addition of extinct Kauai species to clades previously known only from extant species on Maui Nui and Hawaii Island reinforces the biogeographic pattern of progressive colonisation by *Blackburnia* beetles from older Hawaiian islands to younger (Liebherr and Zimmerman 2000). Among the species in the clade bracketed by *B. burneyi* and *B. tibialis* (Sharp) (Fig. 2*C*), the addition of *B. burneyi* demonstrates broad representation on Kauai for two lineages that have colonised downstream islands. And though *B. octoocellata* is the adelphotaxon to the clade subtended by *B. godzilla*, that clade previously lacked any Kauai representative. *Blackburnia godzilla*'s presence on Kauai demonstrates that large-bodied, flightless, terrestrially adapted *Blackburnia* were able to colonise islands downstream. This species' occurrence on Kauai also predicts subfossil occurrence of a related large-bodied taxon on Oahu, now likely also extinct.

The temporal persistence of carabid beetle species near the Makauwahi Cave site is not at all associated with their probability of subsequent extinction (Table 1). If anything, the opposite appears better supported, as the extant species *B. aterrima* and *B. pavida* occur over only small portions of the strata. This would suggest that these particular species were not abundant at this site, perhaps because these presently more upland species were never abundant in lowland habitats. All other species, whether extinct globally, extirpated locally on Kauai, or presently extant on Kauai, occur throughout most of the sampled strata. Thus it appears that a carabid beetle community of consistent membership occurred at this site below ~300 cm depth – i.e. the estimated time of Polynesian colonisation based on presence of *Rattus exulans* and other archaeological evidence – to 450 cm depth, that stratum estimated to have been deposited ~4500–5000 years ago (Burney *et al*. 2001). Below this we have yet to sample and would expect that a similar fauna would be found throughout the earlier, unsampled part of the Makauwahi Cave sequence. Only two species, *B. rugosa* and *B. menehune*, occur in sediments datable to post-human colonisation, although radiocarbon dating of two *B. menehune* somites (N. Porch, unpubl. data) from these levels demonstrated these specimens were reworked by the putative tsunami into the Polynesian-aged sediments. The overall pattern of extinction points to the complete and simultaneous decimation of a natural lowland assemblage of endemic species concomitant with occupation of the area by humans.

One of the three species of Bembidiini illustrates a pattern of localised extirpation observable only in geographically widespread species. *Bembidion pacificum* has not been observed on Kauai since R. C. L. Perkins' 1894 collection, and it was last collected on Oahu in 1920 (Liebherr 2008). Blackburn (1878) recorded it as 'rare but widely distributed' below 810 m elevation on Oahu. The occurrence of this species in Makauwahi Cave points to its ability to occupy such lowland sites, in accordance with Blackburn's 19th century observations. That it has been gone from both islands for nearly 100 years points to its probable extinction in historical time, with the Makauwahi Cave samples providing evidence of its membership in a primordial lowland carabid community.

The lowland carabid beetle assemblage near Makauwahi Cave comprises a diverse representation of clades across Division 1; i.e. the nominate subgenus *Blackburnia* (Fig. 2*C*). Though the species in this fauna occupy lowland habitats, they are in many instances highly nested cladistically within the phylogenetic hypothesis. Under the assumptions of the taxon cycle, wherein generalised colonists occupy lowland strand-like habitats and more highly derived phylogenetic relatives occupy montane habitats (Wilson 1959, 1961), only the most generalised *B. posticata* would be predicted to occupy lowland habitats. The other species at this site – including the large-bodied *B. godzilla* (Fig. 3*C–I*), and the brachypterous, armoured *B. menehune* (Fig. 5*H*) – are highly specialised derivatives of Kauai's *Blackburnia* evolutionary radiation that would not be predicted to be occupants of marginal, coastal habitats under the assumptions of the taxon cycle. Given that lowland-inhabiting *Blackburnia* spp. represented on Kauai were associated with riparian or forest habitats (Burney *et al*. 2001), it may be argued that the Kauai Carabidae are not appropriate as a test of the taxon cycle, because the Kauai *Blackburnia* fauna lacks any strand species. Conversely, interpretation of primordial coastal Kauai as ecologically marginal may be inappropriate, as this area supported an extinct avian fauna including large Nene-like brants, a small duck with reduced eyes, a flightless rail and a long-legged owl (Olson and James 1982*b*, 1991; Burney *et al*. 2001; Iwaniuk *et al*. 2009). The subsequent derivation and specification of the taxon cycle as the taxon pulse (Erwin 1979, 1981, 1985) posits that lowland, streamside carabid taxa form the foundation of adaptive radiations, with forest floor and upland-adapted taxa irreversibly diversifying during adaptive radiation. That pattern is definitely not in place for this radiation, as several of the lowland taxa – *B. mothra*, *B. cryptipes* and *B. menehune* – are all sister species to taxa presently restricted to montane habitats. Thus both hypotheses must be rejected when biogeographic patterns of Kauai *Blackburnia* are analysed in a cladogenetic context (Liebherr and Hajek 1990). Adding the newly described extinct taxa to the previous phylogenetic hypothesis of Hawaiian *Blackburnia* (Liebherr and Zimmerman 1998, 2000) demonstrates that extinction must be taken into account in any generalised attempt to explain phylogenetic patterns in an ecological context.

The newly described fossil taxa also enhance our understanding of body size evolution in *Blackburnia*, as three of the extinct species represent the largest-bodied congeners known from Kauai. *Blackburnia godzilla* is the largest *Blackburnia* known, with a body length of 18 mm: head capsule length 3.1 mm (Fig. 3*E*), pronotal length 4.1 mm (Fig. 3*C*) and elytral length 10.8 mm (Fig. 3*G*). The largest extant *Blackburnia* beetles are individuals of East Maui's *B. rupicola* measuring 15.9 mm body length (Liebherr and Zimmerman 2000). Although Liebherr (1988) proposed that phyletic size increase evolves predominantly in brachypterous carabid taxa, body size appears to be based also on additional factors, as individuals of *B. godzilla* are more than 10% longer than individuals of the other three brachypterous species in its clade (Fig. 2*C*). Of all the species in this clade, *B. godzilla* lived at the lowest elevations, presumably experiencing a warmer temperature regime more favourable to its development compared with temperatures in the montane scrublands and forests currently occupied by its clade-mates (Liebherr and Zimmerman 2000). *Blackburnia mothra*, with an estimated body length of 12.0 mm – head capsule length 2.3 mm (Fig. 4*E*), pronotal length 2.9 mm (Fig. 4*C*) and estimated elytral length 6.8 mm (Fig. 4*F*) – exhibits the second largest body size of any Kauai *Blackburnia*. This species is characterised by larger body size than the other three Kauai species in its clade (Fig. 2*C*): (1) the semi-aquatic *Blackburnia riparia* from Waialeale summit (9.7 mm maximum length; Liebherr and Short 2006); (2) *B. atra* from 895 m on Mt Kahili (11.6 mm; Liebherr and Zimmerman 2000); and (3) *B. lata* from the Alakai Plateau (11.1 mm; Liebherr 2003). Within this clade, the two species occurring at the lowest elevations, *B. mothra* and *B. atra*, exhibit the largest body sizes, consistent with warmer temperature regimes favouring the development of larger bodied *Blackburnia* adults. The extinct, macropterous *B. burneyi* ranks third in body size among Kauai *Blackburnia* using elytral width – the most reliable proxy for body size based on elytral fragments (Fig. 4*A*, *B*) – though its elytral width of 2.45 mm is slightly smaller than that of its cladistic relatives *B. lucipetens* (2.55 mm) and *B. kukui* (2.92 mm) (Fig. 2). The latter two species exhibit maximal body lengths of 12.7 mm and 13.5 mm respectively (Liebherr and Zimmerman 2000). In all three of these Division 1 species larger adult body size would have been associated ontogenetically with larger-bodied larvae. Based on controlled laboratory rearing of extant *Blackburnia* larvae (Liebherr 2000), larval instars are of maximal duration among Division 1 species (Fig. 2*C*); larval development through the three instars averaged 59 days for Division 1 species versus 36 days for Division 0, and 47 days for Division 2. Thus occupation of lowland habitats by the large-bodied extinct Division 1 taxa would have provided the maximally favourable thermal conditions available for attaining larger larval body size within the temporal limitations of the springtime (i.e. increasing day length) breeding season observed for *Blackburnia* spp. (Liebherr 2000).

The phylogenetic distribution of subfossil, extirpated and extinct taxa in the Makauwahi Cave deposits is heavily skewed towards representation of species in the subgenera *Colpocaccus* and *Blackburnia* (Divisions 0 and 1; Fig. 2*C*) versus species of subgenus *Metromenus* (Division 2; Fig. 2*B*). Of 21 Kauai species in the former two subgenera, there are subfossil representatives of 10, versus only one species represented among 12 Kauai species in subgenus *Metromenus*. We believe it is possible this disparity is an artifact of preservation, as the cuticle of many of the large-bodied brachypterous taxa in subgenus *Blackburnia* is very thick and well sclerotized. Therefore this type of cuticle may have withstood the grinding actions during initial deposition in the sand and peat mixture characterising the stratigraphic column (Burney *et al*. 2001) better than the thinner, less melanised cuticle characterising species in subgenus *Metromenus*. This enhanced destruction of lightly melanised cuticle is demonstrated by the eroded elytral apices of the *Bembidion* spp. (Fig. 6*D, F*), whereby the areas of pale maculae characteristic of each species have been abraded and lost, while the harder, more melanised cuticle remains. Alternatively, the rarity of subgenus *Metromenus* may reflect real differences in the relative contribution of the subgenera of *Blackburnia* to the highland and lowland carabid fauna rather than taphonomic differences in preservation potential. With current data it is difficult to determine between either of these hypotheses. Thus we do not claim to have an accurate representation of the lowland carabid fauna of Kauai that was destroyed through the agencies of man. But now that there are fossils, there are some interesting tales to tell.

Acknowledgements

David Burney and Lida Pigott Burney are thanked for their immense ongoing practical and intellectual support of Porch's work at Makauwahi Cave Reserve. Initial sampling was supported by a National Geographic Society research grant to Porch and Burney (Grant #8348–07), and subsequently by Porch's Australian Research Council DECRA Fellowship (DE130101453), exploring the nature and extent of human impacts on Indo-Pacific insect biodiversity. Extensive field surveys of the extant Kauai Carabidae have been supported by awards to Liebherr from the National Geographic Society (#4431–90, #5929–97) and the National Science Foundation (DEB-9208269, DEB-9806349, DEB-0315504).

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