Hawaiian *Blackburnia* beetles (Coleoptera, Carabidae, Platynini): Patterns of specialization with implications for conservation

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Abstract: Hawaiianische Käfer der Gattung *Blackburnia* (Coleoptera, Carabidae, Platynini): ökologische Spezialisierungen und Implikationen für den Artenschutz

Die monophyletische hawaiianische Gattung *Blackburnia* SHARP, 1878 umfasst 132 Arten und kann in vier aufeinander folgende Adelphotaxa unterteilt werden: Untergattung *Protocaccus* LIEBHERR & ZIMMERMAN, 2000 (1 Art, flugfähig); Untergattung *Colpocaccus* SHARP, 1903 (4 Arten, flugfähig); Untergattung *Blackburnia* (52 Arten, viele mit reduzierten Flügeln, Flugfähigkeit aber im Grundmuster); Untergattung *Metromenus* SHARP, 1884 (75 Arten mit reduzierten Flügeln). Die phylogenetischen Beziehungen der Gattung zu anderen Taxa der Platynini beweisen, dass *Blackburnia* die hawaiianischen Inseln im Miozän kolonisiert hat, wobei Kauai die zuerst besiedelte Insel darstellt. Die ökologischen Spezialisierungen der einzelnen Arten spiegeln sich in den phylogenetischen Beziehungen der Arten wider. Arten der Untergattung *Blackburnia* besiedeln weniger Habitattypen im Vergleich zu Arten der Untergattungen *Colpocaccus* und *Metromenus*. Die Larven der Untergattungen *Blackburnia* und *Metromenus* entwickeln sich vergleichsweise langsam und einige Weibchen der Untergattung *Blackburnia* legen die größten Eier innerhalb der Platynini. Die größte morphologische und genetische Diversität findet sich innerhalb der Untergattung *Blackburnia*, was auf eine größere Fragmentierung der Populationen der betreffenden Arten hinweist. Die umfassenderen ökologischen Spezialisierungen der Arten der Untergattung *Blackburnia* können auf dramatische historische Populationsschwankungen innerhalb der Arten zurückgeführt werden. Anthropogene Einflüsse, wie die Degradierung spezifischer Habitattypen (mesische *Acacia koa* Wälder) und die Einschleppung von Neozoen (z.B. Formicidae und Isopoda), haben aber die Assoziationen zwischen den phylogenetischen Beziehungen und den ökologischen Spezialisierungen verwischt. Diese Einflüsse machen deshalb eine Voraussage des Gefährdungspotentials der Arten mit Hilfe der Ergebnisse der phylogenetischen Analyse unmöglich. Einige Arten, die noch im 19. Jahrhundert Bestandteil der Koa-Wälder auf Maui waren, sind seit Anfang des 20. Jahrhunderts nicht mehr nachgewiesen worden. Diese nicht mehr nachgewiesenen Arten, welche Bestandteil spezifischer ökologischer Assoziationen waren, können bei genauerer Betrachtung die Gefährdungskriterien der I.U.C.N. erfüllen. Das Fehlen phylogenetisch verwandter Arten macht die Gefährdung der Arten selbst, als auch die Gefährdung der Koa-Wälder als Ökosysteme deutlich.

Key words: *Blackburnia*; phylogenetic analysis; adaptive radiation; endangered species

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The Hawaiian Islands have arisen in isolation in the middle of the Pacific Ocean due to volcanism unleashed by interaction of mantle-deep thermal plumes with the overlying Pacific Plate (MONTELLI et al. 2004, ABOUCHAMI et al. 2005). This volcano "factory" has produced a consistently present string of islands increasing in age from the current Big Island of Hawaii (500,000 years old) northwestwardly to the island of Kure, estimated to be 28-30 million years old (CARSON & CLAGUE 1995). Successively colonizing and proliferating on these islands since Miocene time (LIEBHERR 2005), are beetles classified in the carabid beetle genus *Blackburnia* SHARP, 1878 (LIEBHERR & ZIMMERMAN 2000). The 132 known *Blackburnia* species are arrayed in four successive adelphotaxa. The monotypic subgenus *Protocaccus* LIEBHERR & ZIMMERMAN, 2000, adelphotaxon to the rest of the radiation, is represented by *B. mandibularis* LIEBHERR, 2000 of Kauai. The next-diverging clade is classified as subgenus *Colpocaccus* SHARP, 1903, and is composed of four flight-capable species. The last two adelphotaxa are the nominate subgenus *Blackburnia* and subgenus *Metromenus* SHARP, 1884. The former includes 52 species, and is based on a ground-plan ancestor that was capable of dispersal by winged flight. This clade exhibits the greatest anagenetic diversification of all four clades, with various subgroups exhibiting extensive modifications of the external cuticle, including thickened, ridged, and variously shaped pronota and elytra, as well as elongate legs, and extensive specializations of the male and female genitalia (LIEBHERR & ZIMMERMAN 1998, 2000). Taxa exhibiting cuticular modifications are all brachypterous, suggesting that loss of metathoracic wings was a requisite precursor to modification of body armature. All 75 species of subgenus *Metromenus* are characterized by brachyptery. These also exhibit various body forms however the member taxa are never characterized by the thickened cuticle and associated modifications seen among taxa of sg. *Blackburnia*. Monophyly of the latter three subgenera was corroborated using molecular sequence data (CRYAN et al. 2001), though basal relationships of the three clades were resolved so that *Colpocaccus* and *Metromenus* were construed as adelphotaxa.

In this study, morphological characters, and ecological and genetic characteristics of the various clades are compared. These comparisons illustrate the coordinated diversification of ecological and genetic traits, and how these are associated with different levels of speciation. These traits are then put in the context of species endangerment, assessed using biotic survey data started in the 19th Century, and continuing during present-day efforts to completely describe and characterize the *Blackburnia* fauna.

Materials and Methods

Phylogenetic analytic methods are presented in LIEBHERR & ZIMMERMAN (1998, 2000), LIEBHERR (2003), and CRYAN et al. (2001). Ecological data were derived from primary examination of specimens forming the basis for taxonomic revisionary research. These include historical specimens from BLACKBURN (1885), FINSCH (1879a, 1879b; KARSCH 1881), and PERKINS (MANNING 1986), plus all subsequently collected specimens (LIEBHERR 2000a, unpubl. data). Larval rearing and adult egg-size data were presented in LIEBHERR (2000b) and KRUSHELNYCKY et al. (2004). Methods for assessing species endangerment based on clustering historically collected species using collecting lot information was presented in LIEBHERR (2004).

Comparative Analysis of Specialization

Hawaiian *Blackburnia* beetles can be found in three major habitat types. Beetles occur along the margins of streams, more commonly on the older islands such as Kauai, Oahu, and Molokai which have well-developed, lower-gradient stream systems. Where soil can develop in more mesic forests, beetles can be found in the ground-level leaf litter and underlying humus. In such situations, as well as wetter forests with extensive runoff due to heavy rains, beetles occupy arboreal mossmats adhering to tree trunks and lower branches. These situations serve as daytime refugia for beetles that move at night onto outlying branches.

Comparing species in the four adelphotaxa indicates occupation of riparian situations within the single species clade represented by *B.* (*Protocaccus*) *mandibularis*, to occupation of all three habitats in species of all other clades (Tab. 1). At the archipelagic level, this pattern may represent the taxon cycle (DARLINGTON 1943, WILSON 1961), though we lack outgroup information required to unambiguously optimize the root of *Blackburnia*. At present we know that *B. mandibularis* lives and breeds along streams in riparian moss on Kauai. However, three of four species of *Colpocaccus* occupy all three habitat types, optimizing the base of that clade to the generalized three-habitat state. The roots of the other two clades – *Blackburnia* s.str. and *Metromenus* – both optimize basally to occupation of two microhabitats, terrestrial and arboreal. Better knowledge of the nearest outgroup is required to unambiguously determine how these conditions may be historically related. Of the two diverse subgroups, sg. *Blackburnia* is more ecologically specialized overall, with more than half of the 52 species restricted to a single habitat. Modally, *Metromenus* spp. occupy two habitats (terrestrial and arboreal), with slightly more specialist species than generalist members of this clade.

Of the three habitat types, riparian situations afford the greatest elevational range as riparian corridors extend into the lowlands. Conversely, montane rain forests supporting extensive mossmat development are almost always found above 900 m elevation, though they may occur at elevations as low as 700 m in the

Koolau Mountains of Oahu. Three of four *Colpocaccus* spp. are found in riparian situations, and all four species have geographic ranges that extend to low elevations (Tab. 2). Species within sg. *Blackburnia*, modally occupying arboreal situations, tend to occur in the highest elevational zones. The considerable diversity of *Metromenus* includes nearly as many species that extend to low elevations as those restricted to habitats above 700 m.

Tab. 1: Frequencies (and percentages) of species in each clade of *Blackburnia* inhabiting 1, 2 or 3 habitat types (riparian, terrestrial, arboreal), and ratio of sympatric to allopatric terminal sister species based on the 3 resolved, best-fitting cladograms for all described species (LIEBHERR 2003, Fig. 8).

Blackburnia subgenus	1 habitat	2 habitats	3 habitats	sympatric/allopatric sister species
Protocaccus	1 (100)	0	0	-
Colpocaccus	0	1 (25)	3 (75)	0/ 1
Blackburnia	32 (61)	16 (31)	4 (8)	3/13
Metromenus	25 (33)	31 (41)	19 (25)	6-7/12

Tab. 2: Frequencies of species in each of three clades of Hawaiian *Blackburnia* whose distributions exhibit selected lower elevational limits (m). Elevational range for *B.* (*B.*) *koebelei* (SHARP), 1903 is not known.

Blackburnia subgenus	0-700	701-1000	1001-1300	1301-1800	1801-2100	>2100
Protocaccus	0	1	0	0	0	0
Colpocaccus	3	1	0	0	0	0
Blackburnia	13	10	21	5	1	1
Metromenus	30	26	12	4	3	0

Life history evolution parallels levels of ecological specialization observed in the various clades. Species of sg. *Blackburnia* exhibit the longest larval developmental periods, with first instars averaging 9.4 d versus first instar periods of 5.7 d and 7.6 d in *Colpocaccus* and *Metromenus,* respectively (LIEBHERR 2000). Second and third instar larvae of sg. *Blackburnia* species also exhibit significantly longer developmental periods. Associated with this lengthened larval period is an increase in egg size in species of sg. *Blackburnia* (LIEBHERR 2000 b, KRUSHELNYCKY et al. 2004). Though sg. *Blackburnia* adults are larger than those of the other clades, the increase in egg size exhibits positive allometry in relation to body size. Increased egg size relative to adult body size indicates a greater maternal investment in the initial larval stage. This larger egg size is associated with larger body size of hatchlings. It is hypothesized that larger egg size enhances first instar larval survival in situations where food is limited, though this hypothesis has yet to be tested.

The deployment of molecular sequence data in the phylogenetic analysis of *Blackburnia* permits comparison of genetic diversification within each of the clades. Based on dense taxon sampling (69 of the 132 species) and sequence data from four genes (cytochrome oxidae II, cytochrome b, 28S rDNA, wingless) and morphology (206 unit-coded characters), genetic diversification proceeded in very different manners within sg. *Blackburnia* compared to the other two clades (CRYAN et al. 2001). Total Bremer support values are much higher within *Blackburnia*, indicating congruent phylogenetic characters within the molecular and morphological data sets. As a consequence, the phylogenetic hypothesis for these species is highly resolved. Conversely, character support is much lower within *Metromenus*, with the strict consensus unresolved. Additionally, character conflict is much greater within *Metromenus*, with partitioned Bremer values showing great disparities among the data partitions. As these two clades are adelphotaxa, the disparate levels of congruence cannot be explained by different ages of origin. If sg. *Blackburnia* species, both extant and ancestral, have undergone intermittent and pronounced population declines then repeated bouts of gene fixation would have resulted. *Metromenus* species may not have undergone such population declines, or species in this clade may have undergone gene exchange through intermittent hybridization. Both situations would reduce fixation, especially for mitochondrial genes, leading to a confused phylogenetic signal.

The disparate diversity of the two major clades is best explained by differential evolution of brachyptery. The subgenus *Metromenus* is most diverse, and is most specialized with regard to dispersal ability as all species are brachypterous. This level of specialization is achieved among species that occupy a greater diversity of lower elevational habitats than do species of sg. *Blackburnia* (Tab. 1, 2). Taxa comprising the subgenus *Metromenus* exhibit a paradoxically greater tendency to undergo taxic dispersal subsequent to speciation, as evidenced by the greater proportion of sympatric sister species (Tab. 1). These sympatric *Metromenus* sister species are concentrated on the Koolau Mountains of Oahu; 4 of the 6-7 instances of sympatry within *Metromenus* based on the different cladogram resolutions (LIEBHERR 2003). One of the 3 sympatric sister species within sg. *Blackburnia* also occurs in the Koolau Mountains, suggesting that this very long range has been strongly associated with recently established secondary sympatry. This association may be based on a singular geological event. If ancestral or extant species included populations on the northwestern and southeastern rift zones along the broad windward rim of the primeval Koolau Volcano, they would have been dramatically isolated by the prodigious landslide (MOORE et al. 1989) that sent the northeastern half of the volcano to the ocean bottom. After this geologically instantaneous cataclysm, the previously dry, leeward southwestern face of the mountain was transformed into the present moist windward crest. Subsequent taxic dispersal from the ends toward the center of this newly hospitable corridor would have established secondary sympatry among previously isolated species and populations. Continued survival and diversification of *Metromenus* species on this now highly eroded, low-elevation mountain range is consistent with their aggregate occupation of lower elevation habitats. Much of the summit ridge of the Koolau Mountains lies within the 700-1000 m range that represents the modal elevations of habitats occupied by *Metromenus* species (Tab. 2). Species of sg. *Blackburnia*, on the other hand, are generally restricted today to habitats above 1000 m elevation. Their sparse representation in the Koolaus suggests that prehistoric diminution of diversity within sg. *Blackburnia* may have been an integral consequence of Oahu's geomorphological evolution.

Is Degree of Specialization Related to Endangerment Risk?

Each of the polytypic subgenera exhibits different levels of specialization with regard to dispersal ability and habitat preference. The subgenus *Colpocaccus* includes the most generalized taxa, with all four species characterized by dispersal undertaken by winged flight, groundplan occupation of riparian, terrestrial and arboreal microhabitats, occurrence from low to higher elevations, and relatively rapid larval development. The subgenus *Metromenus* retains the generalized rapid larval period and modal occupation of low elevation habitats. But all representative taxa are composed of brachypterous individuals, taxa occur modally in only two of the three habitat types, and there are more single microhabitat specialist taxa than three-microhabitat generalists. The nominate subgenus *Blackburnia* is the most specialized overall as a clade, with more protracted larval development than the other two clades (LIEBHERR 2000 b). These taxa also tend to occur in higher elevation habitats, with the modal lower limit of 1000 m elevation, and species occur predominantly within one microhabitat. There is disparity in dispersal abilities across the clade however, with the ground plan of the clade characterized by fully developed metathoracic wings. Flight wings have been independently reduced four times (LIEBHERR & ZIMMERMAN 2000), leading to 47 brachypterous taxa (LIEBHERR 2003).
When the numbers of species not observed for significant periods (i.e. 50 years for Oahu, and 100 years for all other islands, LIEBHERR 2004) are tallied for the three subgenera (Table 3), it is clear that species of all levels of specialization have been lost. Strong evidence suggests that the generalized, flight-capable and very abundant lowland species, *B.* (*Colpocaccus*) *tantalus* (BLACKBURN), 1877 of Oahu, was extirpated by ants (LIEBHERR & POLHEMUS 1997). Conversely, even though the subgenus *Metromenus* is composed entirely of brachypterous taxa, this clade has the highest present-day representation of continuously observed species.

Of the three clades, *Blackburnia* s.s. has the highest fraction of long-missing species. This high total is compounded by one 3-species clade for which all species are missing; *B. perkinsi* (SHARP), 1903 of Molokai, *B. koebelei* of West Maui, and *B.* sharpi (BLACKBURN), 1878 of East Maui. Phylogenetically compounded loss has also implicated the adelphotaxa *B. blaptoides* BLACKBURN, 1878 and *B. insignis* SHARP, 1878 of Oahu. In both of these instances it can be argued that underlying ecological characteristics based on common phylogenetic history predisposed these taxa to undergo parallel population declines due to habitat destruction

– principally deforestation and introduction of alien species – that accelerated during the late 19th Century (CUDDIHY & STONE 1990). For the Oahu pair *B. blaptoides* and *B. insignis* – similar to the sympatric *B. tantalus* – ant predation may have led to reductions of populations occupying habitats that historically ranged from 450-900 m elevation (LIEBHERR & ZIMMERMAN 2000).

Tab. 3: Numbers and fraction of *Blackburnia* species within each subgenus not observed in nature for 50-years (Oahu) or 100-years (all other islands); from LIEBHERR (2004), but *B.* (*Metromenus*) *debilis* (PERKINS), 1917 collected on Molokai in 2005.

Subgenus	No. of species	No. species not observed	Fraction species not observed
Colpocaccus	4	1	0.25
Blackburnia	52	9	0.17
Metromenus	75	4	0.05

Tab. 4: Numbers of specimens (exx.) of three Koa-associated *Blackburnia* species and all other sympatric *Blackburnia* specimens by collecting period. Early collectors are listed with year of collecting activity. Difference between the sum of collections from 1902 and before versus all later collections is highly significant (Chi-squared = 71.67, d. f. = 3, $p < 0.005$).

Collector (Year)	*Blackburnia octoocellata*	*Blackburnia sharpi*	*Blackburnia terebrata*	No. other sympatric exx.
Blackburn (1878, 1880)	9	4	5	17
Finsch (1879)	2	1	2	14
Perkins (1894)	12	5	1	903
Perkins (1896)	10	8	4	645
Perkins (1897)	0	2	0	0
Perkins (1900, 1902)	1	3	0	12
All >1902	0	0	0	1656

Cluster analysis (LIEBHERR 2004) of specimens treated in the Fauna Hawaiiensis (SHARP 1913) elucidated the ecological situations common to particular groups of long-missing species. One very strong ecological factor leading to species endangerment involved habitat loss, most dramatically the diminution of *Acacia koa* (Fabaceae) forest caused by logging and conversion of forest to cattle pasture. On Maui, this diminution has been compounded by invasion of portions of the remaining Koa habitat by alien Isopoda (TAITI & HOWARTH 1996, LIEBHERR unpubl. data). Three clustered species historically observed on Koa – *B. octoocellata* KARSCH, 1881, *B. sharpi*, and *B. terebrata* (BLACKBURN), 1881 – have all remained absent from post-1902 samples (Table 4). In this case, simultaneous disappearance of ecological associates lends credence to their mutual, severe diminution, thereby satisfying I.U.C.N. (2001) criteria as critically endangered species. Apparently, specialization for Koa habitation led directly to endangerment through a variety of human-directed activities.

Given the available specimen association data incorporated into the Fauna Hawaiiensis, the I.U.C.N. (2001) criteria for critically endangered species could be expanded to incorporate the simultaneous loss of ecologically associated species. Such a criterion would tie the listing of endangered species to the desirable end of identifying endangered habitats for it is habitats that house species, and without special attention to habitat conservation, resident endangered species lose their chances for survival.

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