R. C. L. Perkins: 100 Years of Hawaiian Entomology¹

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ABSTRACT: R. C. L. Perkins comprehensively surveyed the insect fauna of the Hawaiian Islands one century ago, initially as the collector for the *Fauna Hawaiiensis* survey project and subsequently as an entomologist with the Hawaiian Sugar Planters' Association. The Hawai'i he observed was in a period of rapid transformation. Thus, he has the unique distinction of being the first and last person to record the habits of many native Hawaiian species. The islands on which he collected were already heavily impacted by exotic herbivores—including goats, cattle, sheep, and pigs—yet he was able to sample remnant pockets of native vegetation that are now lost in a jungle of exotic introductions. His broad understanding of insect natural history allowed him to document ably the habits of insect groups that we are only beginning to understand 100 yr later. Moreover, his collections and extensive taxonomic contributions afford us a firm foundation for future taxonomic and evolutionary studies of the uniquely rich and highly endemic Hawaiian insect biota.

R. C. L. PERKINS EXHIBITED a combination of traits that led him to a broad understanding of the natural history of the rapidly developing Hawaiian Islands of the late nineteenth century. He was an extremely able naturalist who traveled much of the Islands alone or in company with native guides. He spent long periods under extremely adverse conditions collecting insects, birds, and other natural history specimens. He saw to the preparation of these specimens at Cambridge University where the faunal survey leading to publication of the Fauna Hawaiiensis had its headquarters under the leadership of Dr. David Sharp. And he ably revised numerous groups of the Hawaiian insect fauna in the Fauna Hawaiiensis project. That a single person could study and understand a biota at so many levels is remarkable.

The following contributions form the proceedings of a symposium, "The Legacy of R. C.

L. Perkins: 100 Years of Hawaiian Entomology," convened on 27 August 1996 at the 20th International Congress of Entomology held at Florence, Italy. The participants addressed the current status of understanding in a variety of insect groups, some well known to Perkins and others only casually observed by him. These contributions seek to illuminate the importance and suitability of the Hawaiian insect fauna for the study of a variety of biological phenomena, including phylogenetic diversification, the interactions of morphological and behavioral evolution, biogeographic patterns and the importance of dispersal and vicariance, molecular evolution, hostplant insect evolution, and conservation biology. Perkins' broadly based expertise invariably shed light on most of these areas of biological inquiry, and we dedicate these papers to his immense achievements both in the field and in the laboratory.

R. C. L. Perkins

Robert Cyril Layton Perkins was born in Gloucestershire, England, on 15 November 1866 and died in Devon on 29 September 1955. Even as a boy he exhibited prodigious natural history talents, collecting insects before the age of seven (H. Scott 1956). He attended Jesus College, Oxford, on an open Classical Scholarship, but

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switched to zoology as an upperclassman. While at Oxford he joined the Oxford Natural History Society, concentrating on the study of the bees and wasps of Oxford under the guidance of Edward B. Poulton.

In 1891, 2 yr after graduating from Oxford, he was chosen by The Sandwich Islands Committee (a joint committee of the British Association for the Advancement of Science and The Royal Society) to serve as the collector for a biological survey of the Hawaiian Islands. This biological survey aimed to build on knowledge of the Hawaiian Islands fauna first provided by the efforts of Reverend Thomas Blackburn, who had served as chaplain to the Bishop of Hawaii in Honolulu from 1876 to 1882 (Lea 1912). Blackburn collected on O'ahu, Maui, Lana'i, and Hawai'i, described 76 native Hawaiian insect species in the orders Coleoptera, Neuroptera, Hemiptera, and Hymenoptera (Nishida 1992), and also sent specimens to Dr. David Sharp, then a practicing medical doctor in Dumfries, Scotland (Walker 1922). Sharp went on to coauthor a memoir on the Hawaiian Coleoptera in collaboration with Blackburn (Blackburn and Sharp 1885). In 1890, Sharp accepted an invitation to serve as curator at the University Museum of Zoology at Cambridge. That same year he was elected a Fellow of The Royal Society. Sharp served as secretary of The Sandwich Islands Committee under four different chairmen throughout its 22-yr existence, arguably providing the continuity required for such a large and varied undertaking. He served as Perkins' mentor during the project, writing early on: "Be sure in the different islands not to miss taking a thing because you have got it previously in another island, for we want very much such information as to what occurs in each island. I have no doubt you are now learning the special ways of catching the things. Don't forget my sifting dodge, also try under big stones in semishady places, also sunset sweeping and beating, and don't forget to try light in suitable places especially if you can set it on a white sheet in a nice open place out of doors. From what H. H. Smith said, he found evening sweeping and beating very productive" (Sharp 1892).

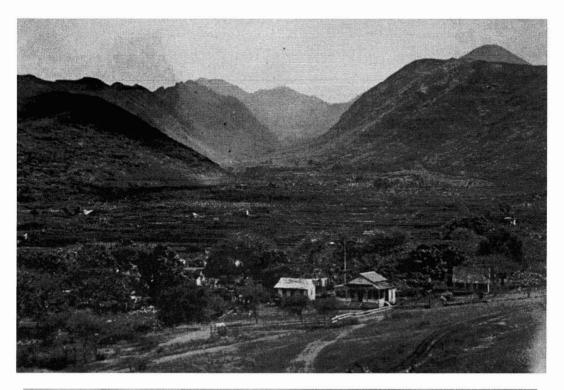
Perkins arrived in Honolulu in March 1892 to begin collecting birds, insects, and mollusks (Manning 1986). He collected in the Islands until

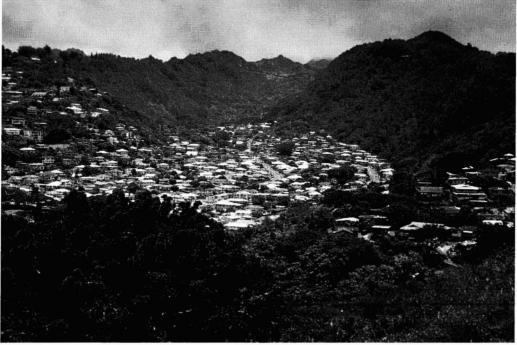
September 1894 and then returned to England to oversee the preparation of specimens. He returned to Hawai'i from March 1895 to March 1897 to continue collecting for the *Fauna Hawaiiensis* project. A third period of collecting from May 1900 until December 1901 completed his activities with the *Fauna Hawaiiensis* project. A complete itinerary of his Hawaiian collecting for the *Fauna Hawaiiensis* project was presented by Manning (1986).

After the end of collecting for Fauna Hawaiiensis, he worked as an economic entomologist in the Islands, first with the Territorial Board of Agriculture and Forestry, and then as the director of the Entomology Division of the Hawaiian Sugar Planters' Association (HSPA) Experiment Station. Early on he appreciated the great benefits of importing exotic natural enemies for biological control of introduced pests, at the same time noting the great risk to the native fauna brought about by this activity (Perkins 1897b). He worked closely with Albert Koebele, a pioneer of biological control, to release and introduce natural control agents to Hawai'i, including those specific to the tropical American noxious plant, Lantana. This release program resulted in substantial reduction of Lantana populations and was considered a highly successful example of biological control (Perkins and Swezey 1924).

Perkins' Hawai'i

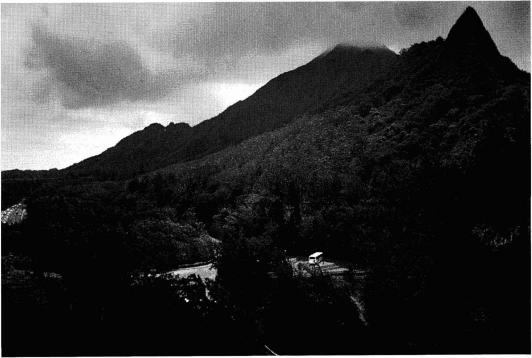
When R. C. L. Perkins arrived in Honolulu in 1892, the soon-to-be overthrown Hawaiian kingdom contained fewer than 100,000 inhabitants; the modern state of Hawai'i now supports over 1.1 million. The slopes behind the city (Figure 1), and in fact the lower elevations on the leeward sides of all the Islands, had been grazed down to a bleak, dusty wasteland by goats and cattle, leaving native forest only at high elevations on the ridges and mountaintops (Figure 3). Adventive exotic insect pests, such as the bigheaded ant, Pheidole megacephala (F.), recently had been introduced accidentally and were quite common in lower-elevation disturbed habitats (Perkins 1892a). The reforestation projects that produced the large groves of introduced Eucalyptus, ironwood, fig, and Norfolk Island pine seen today had not yet been initiated. The places where Perkins walked would be biotically





FIGURES 1–2. Pauoa Valley from north slope of Punchbowl Crater. 1, (top) 1889 (William Tufts Brigham [E. B. Scott 1968]). Mount Tantalus, a favorite collecting site of Perkins, is visible in background of upper right side of picture. 2, (bottom) 1996 (Dan A. Polhemus). Note the progressive encroachment of Honolulu urban neighborhoods on valley and surrounding ridges. Many native insect species familiar to Perkins are now extirpated from Mount Tantalus (Perkins 1906a).





FIGURES 3-4. Upper Nu'uanu Valley from Mount Kōnāhuanui ridge spur above the Pali lookout. 3 (top) 1908 (Ray Jerome Baker [Ronck 1984]). The valley at this time was extensively overgrazed by introduced cattle and goats, thus allowing Perkins to move freely among pockets of native vegetation and to discover ground-dwelling native insects. 4 (bottom) 1996 (Dan A. Polhemus). Reforestation efforts have resulted in extensive and dense secondary growth forest of Casuarina, Eucalyptus, and Ficus.

unrecognizable to him today because of the extensive intentional and unintentional afforestation and urbanization that has taken place in the intervening 100 yr (Figures 2, 4).

Despite the ecological disturbance of the nineteenth century, Perkins found many native lowland insect species. On O'ahu, Perkins' collecting efforts were concentrated in the mountains behind Honolulu and at Wai'anae, the Helemano Plantation, and the Anahulu River valley of the north shore (Figure 5), where he spent parts of 36 months collecting for Fauna Hawaiiensis (Perkins 1892a, 1896a, 1897a, 1900-1901). In 1892, the valleys behind Honolulu were open ranch and farmland, and much more easily traversed than now (Figures 1, 3); many have since become urban neighborhoods (Figure 2) and the remainder are now heavily forested with tangles of introduced secondary growth vegetation (Figure 4). In the first presidential address to the newly formed Hawaiian Entomological Society, Perkins predicted vast losses to the fauna on Mount Tantalus because of impending development (Perkins 1906a). Similarly, on the Wai'anae coast where Perkins collected extensively (Perkins 1896a, 1897a), houses now extend far up Wai'anae Valley. Perkins might recognize the dry forest remaining near the valley headwall, but the lower valley is currently plagued by chronic brush fires that eradicated any vestige of native vegetation years ago. By contrast, Mount Ka'ala summit plateau is a State Natural Area Reserve and retains much of its original character. In central O'ahu, the Helemano Plantation is now studded with military radio antennas, and the lower and middle sections of the Anahulu River are degraded from a century of sugarcane growing and no longer support most of the unusual aquatic insects that Perkins collected there. The reaches of the Ko'olau Range northwest of Honolulu, known as the Ko'olauloa or "long Ko'olau," were marked by Perkins as "unsurveyed and inaccessible" (Figure 5). They remain an anomalous pocket of poorly collected wilderness in the midst of Hawai'i's most densely inhabited island.

Perkins concentrated his collections on Kaua'i around the port town of Līhu'e (Perkins 1896e) and in the mountains rimming the spectacular Waimea Canyon (Perkins 1894c, 1895a). The Līhu'e area has long ago gone to sugarcane

and urbanization, but Perkins might still recognize the Waimea slopes and the Alaka'i Swamp, except perhaps the vast stands of introduced *Eucalyptus* and ironwood at lower elevations. Mount Wai'ale'ale, the wettest spot on earth, remains a remote and rarely visited summit. Perkins did not walk there. Instead he concentrated his Alaka'i Swamp collecting efforts on what he called the "High Plateau" along the Mōhihi-Alaka'i Trail in the vicinity of "1st Camp" (Figure 6) (Perkins 1895c).

During two short visits to Lāna'i, Perkins stayed at the Kō'ele Ranch (Perkins 1894a), which has now become a posh international resort. The mountain behind the ranch, Lāna'ihale (Figure 7), still retains patches of the original forest at its summit where remnants of the native upland insect fauna can be found. Lāna'i has been devastated by a succession of introduced grazing animals (Hobdy 1993), cultivation, and reforestation with *Eucalyptus* and *Casuarina*. Nevertheless this island, with its post-Perkins pineapple-based economy, has been spared the massive introductions of alien insect species observed on O'ahu. Perkins might still feel at home here, at least on Lāna'ihale.

On Moloka'i (Figure 7), the high forests where Perkins collected along the Pelekunu rim are still extant. These, along with Pelekunu Valley, form the centerpiece in a network of state, federal, and Nature Conservancy preserves. Of all the places in Hawai'i, this area has probably changed the least since Perkins' time, except that then he was able to observe and collect a wide variety of native birds (Perkins 1893a,b. 1896d) that have since declined dramatically. His feat of descending into Pelekunu Valley on foot is unlikely to be repeated, at least not by an entomologist: "July 13th-16th. Started about 6.30 a.m. with gun and about 30 cartridges in case I should see any good birds. Got to the Pali fairly dry, only one heavy shower. . . . It began to rain, when I had gone some way down and the ridge was running with wet and slippery. I heard the Oo, but could not get to them.... About one-third of the way down I was walking along an apparently good piece, not steep, with bushes on my left and a pali (or nearly) on the right. My gun was in my left hand, the axe in my right. The ridge here was overgrown with fern and I suddenly stepped on nothing, where

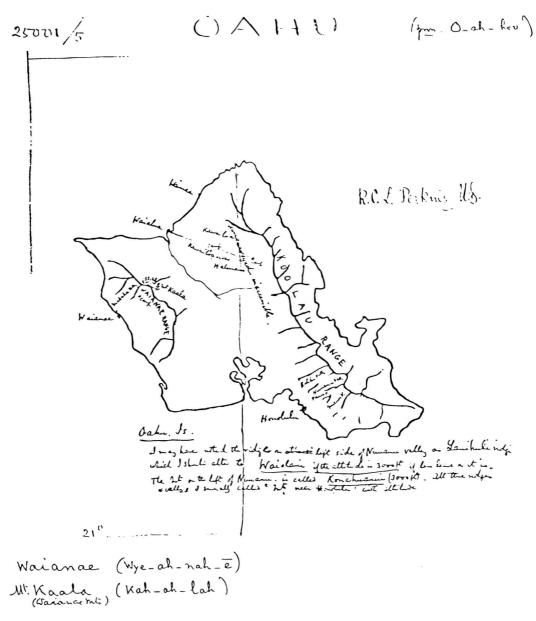


FIGURE 5. A sketch map of O'ahu drawn by R. C. L. Perkins, obtained as photocopy from Frank Howarth via Klaus Sattler via Elwood C. Zimmerman. Notation at bottom reads: "Oahu Is. I may have noted the ridge on left side of Nuuanu Valley as Lanihuli ridge which I should alter to Waiolani if the altitude is 3000 ft if less leave as is. The mt on the left [sic right] of Nuuanu is called Konahuanui (3000 ft.). All these ridges & valleys I generally called 'Mts near Honolulu' with altitude." Labeled localities running clockwise from due north are "KOOLAU RANGE; Camp; unsurveyed and inaccessible; Manoa Valley; Pauoa Valley; Nuuanu Pali; Kalihi Valley; Honolulu; WAIANAE RANGE; Mt. Kaala; Camp; Waianae; Makaha Valley; Waialua; Waimea; Kawailoa; Camp; Kawailoa river; Halemano."

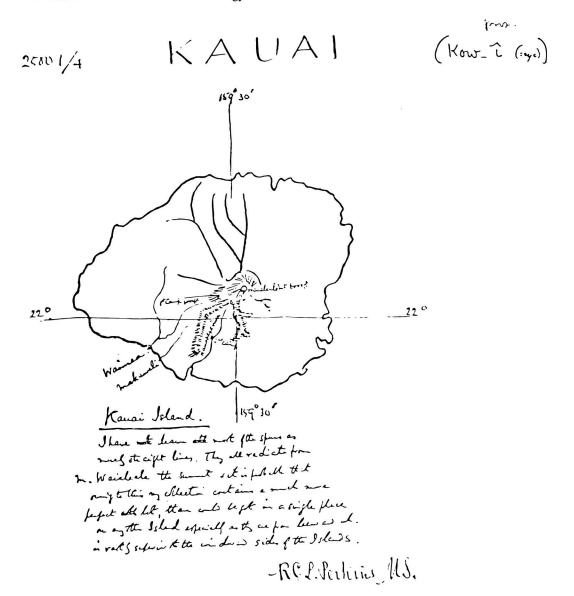


FIGURE 6. Perkins' sketch map of Kaua'i, as per Figure 5. Notation at bottom reads: "Kauai Island. I have drawn most of the spurs as merely straight lines. They all radiate from Mt. Waialeale the summit & it is probable that owing to this my collection contains a more perfect lot, than could be got in a single place on any other Island especially as they are from leeward which is vastly superior to the windward sides of the Islands." Labeled localities running clockwise from due north are "Waialeale Mt 6000 ft; 2nd Camp; Hanapepe river; Makaweli; Waimea; 1st Camp 4000 ft."

a landslide had taken place on the right side, unnoticed by me. I naturally dropped both gun and axe and the former rested in the bushes, but the latter fell over the edge and I heard it ... striking the bed of the stream below. The ferns I grabbed hold of were stag-horn and tough and

I pulled myself up carefully till my chest was well on top and all was well, except for my axe, which I made no attempt to recover. I went slower and more carefully after this" (Perkins 1893b).

The West Maui Mountains are a rugged, rain-

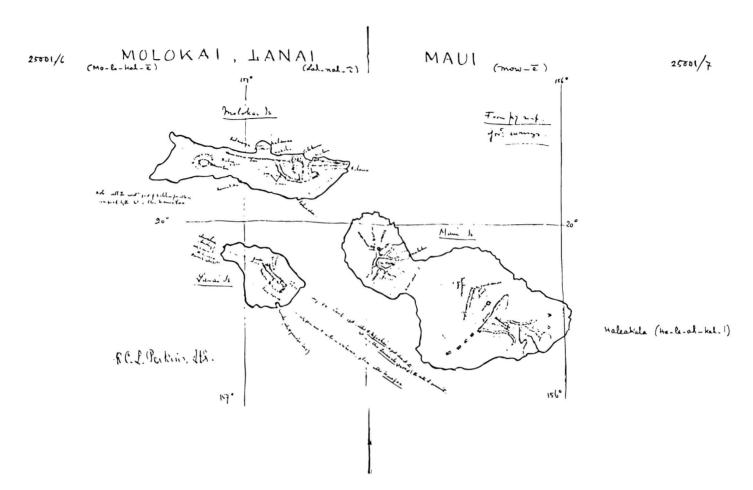


FIGURE 7. Perkins' sketch map of islands composing Maui Nui, as per Figure 5. Labeled localities for Moloka'i, running clockwise from due north: "Kalaupapa; Leper settlement; Kalawao; Waikolu; Pelekunu; Wailau; Halawa; Kaluaaha; 2 Camps 3000 4000; Kaunakakai; Mauna Loa; Kalae." For "2 Camps," the 4000-ft camp is Pēpē'ōpae Bog, the 3000-ft camp is Kūpā'ia on the south rim of Kaunakaki Gulch. Labeled localities for Lāna'i, as above: "Koele; 1st Camp; Camp Aug. 94; Aug. 94 Camp, spot called <u>Halepaakai</u>, & just above it the Mt is called <u>Lanaihale</u> (3400 ft) the actual summit; only permanent water in 6 holes here, place called Waiapaa; Manela (only Hymenops here); Camp Febr. 94; Awalua (landing) only micros I think here & Hymenops. Coleops. . . ." Labeled West Maui localities, as above: "Wailuku; Iao Valley; Eke Crater." Labeled East Maui localities, as above: "Makawao 2000; Blackburn's stopping place; Olinda 4000; My camp 5000 ft; 5000 ft; 6000 ft; Haleakala Crater."

shrouded bastion that repelled most of Perkins' collecting efforts (Perkins 1894b). He relied on Albert Koebele for the few specimens obtained from the western flanks around 1000 m elevation and on Brother Matthias Newell for specimens from 'Īao Valley (Perkins 1896c). It has taken 100 yr of technological innovation, in the form of helicopters, nylon tents, and light camping gear, along with dry favorable weather conditions associated with El Niño events in the Pacific Ocean, finally to allow entomologists complete access to the towering peaks and plunging valleys, many of which still retain a predominantly native character.

On East Maui, the subdivisions of Kula, Makawao, and Olinda now spread far up the flanks of Haleakalā, through country that in Perkins' day was ranch land and forest. Most of his old collecting sites (Perkins 1894b, 1896c, 1896g) are now irrevocably altered by development, except in the Waikamoi drainage, which is preserved as a Nature Conservancy Preserve at higher elevations and is a protected watershed of the East Maui Irrigation Company at lower elevations. The higher elevations of the mountain lie in Haleakalā National Park and were severely degraded by grazing in the decades after Perkins collected there, but under current national park management are slowly returning to the way that Perkins might have seen them. In the 1890s, during the "mini-ice age" that ruined crops in mainland North America, substantial snowfall occurred on the summit of Haleakalā (Perkins 1894b). Several high-elevation endemic carabid beetles have not been seen since, possibly eliminated by the development of observatories, or surviving only at low population levels because of recent drier climate. The timberline on the mountain has also been altered extensively by the planting of exotic conifers at Hosmer's Grove. Perkins noted the distinct fauna of the native forest versus open scrub above the timberline, with different species showing total fidelity to either habitat type (Perkins 1894b, 6-11 April). This ecotone is still evident to the east of the Ko'olau Gap.

On Hawai'i, Perkins had the opportunity to observe bird populations repeatedly (Perkins 1892b, 1894d, 1896b), allowing him to discern the vast ecological changes that were occurring in the Kona District during the 1890s. The vege-

tation of that area has been fragmented in the last hundred years, and its native biota is much diminished. The Ka'ū District (Figure 8) to the south has fared better (Perkins 1895b); Kīlauea Volcano is the core of Hawai'i Volcanoes National Park (Perkins 1896f, 1906b), and the slopes and summits of the Nīnole Hills still retain good native forest cover in spots. On the Hilo side of the island, the perpetually wet windward flanks of Mauna Kea remain an entomologically unexplored wilderness above 700 m elevation where the cane fields end. Perkins collected there in 1894 (Perkins 1894e), concentrating on birds. Subsequent collections by Otto Swezey and F. X. Williams form the basis for most of what we know about the insect fauna of that district. Only recently have entomologists started surveying the Kohala Mountains, where Perkins relied on collections by the ornithologist G. C. Munro for his knowledge of the fauna (Perkins 1937).

Perkins' trips to the field in the Hawaiian Islands were made on foot, or on horseback where the trails permitted. Modern entomologists in Hawai'i still find that a tremendous amount of walking is required to reach relatively undisturbed habitats, but they can at least drive to the trailheads in automobiles. For the current generation of entomologists it has been the helicopter, more than any other single innovation, that has opened up the last surviving Hawaiian wildernesses, allowing quick access to even the most remote peaks. The accurate entomological survey of these remaining montane areas, and the realization of their richness and distinctive endemicity, has been offset by the loss of the native insect biota in lower elevations since Perkins' time. He collected from much that is now lost to us, whereas we have started to sample those areas he wanted to reach but could not. Through all of these efforts, a more balanced picture has emerged of the Hawaiian biota.

Collections

Perkins collected on all the high islands except Kaho'olawe. He arranged his collections in lots, collecting 643 lots during the period 1892–1897 (Anonymous n.d.). Brief descriptions were associated with lot numbers usually indicating locality and dates. Later lot numbers

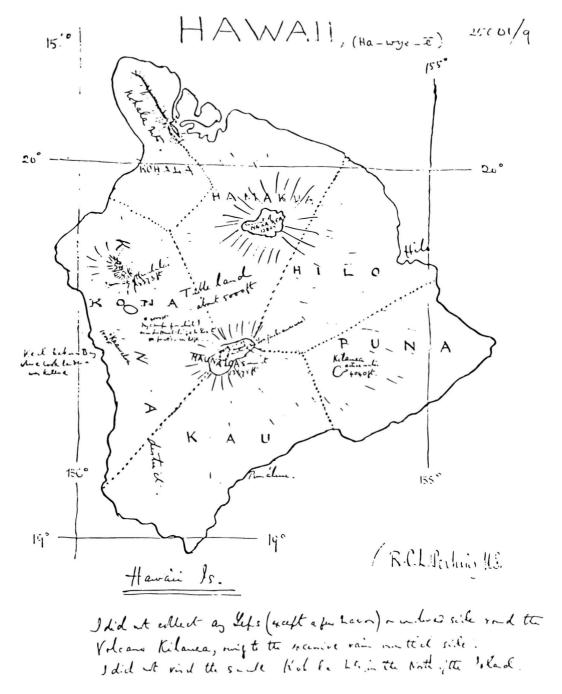


FIGURE 8. Perkins' sketch map of Hawai'i, as per Figure 5. Notation at bottom of map reads "Hawaii Is. I did not collect any Leps (except a few Macros) on windward side round the Volcano Kilauea, owing to the excessive rain over that side. I did not visit the small Kohala Mts in the North of the Island." Labeled localities clockwise from Kohala District: "Kohala Mts.; HAMAKUA; Summit of Mauna Kea 13805; Table land about 5000 ft; Hilo; HILO; PUNA; Kilauea active crater 4040 ft.; KAU; Punaluu; Mauna Loa Summit 13673 ft; Active summit crater of M Loa (Mokuaweoweo); KONA District; 4000 ft My camp from which I ascended Hualalai, & M. Loa to the forest's upper edge; Kaawaloa 1500 ft; Kealakekua Bay where Cook landed & was killed; Summit of Hualalai 3273 ft."

above 705 were concentrated on O'ahu (Perkins 1900-1901). Material was sent to Dr. David Sharp at Cambridge University, and some of the earlier lots were prepared under the supervision of Perkins during his return to England in late 1894 to early 1895. For material of some orders (e.g., Coleoptera) lot numbers were handwritten on the bottoms of each specimen mounting card, whereas printed labels indicating locality and date were glued to the upper surface. This was not done for collections made after 1900: "My object on this my last period of collecting for the Committee was not so much the acquisition of new species as to make some special investigation of the habits and variation of species especially some of the very difficult genera of Coleoptera. . . . The material that I had collected very carefully had been nearly all mounted up fresh and was sent to England. Batches of Proterhinus and of different species from special trees, and batches of such beetles of one species collected from different trees for the study of variation were specially numbered by myself as well as labelled with the usual data. Unfortunately when I returned for a trip to England in the summer of 1907 the cards had been cut up and the individuals separated without the preservation of my own numbers, these having been made to follow on from the numbers used for previous collections. Consequently only the usual data were generally available, and my own notes which I had retained were largely useless" (Perkins 1900-1901). Although some Carabidae, for example, bear specific lot numbers above 705, Perkins, perhaps due to frustration, did not retain notes associated with these later lot numbers, leaving current-day revisers to ponder on the information lost.

The material forming the basis for Fauna Hawaiiensis was subsequently divided among three principal repositories: The Natural History Museum, London; the B. P. Bishop Museum, Honolulu; and the describing author's institution if that differed (Sharp 1913, Manning 1986). The Natural History Museum retained a full complement of taxa described from Perkins' material. Other representative lots were sent to major institutions, whereas other smaller lots came up for sale; for example, a lot of Carabidae was not claimed by The Natural History Museum and was sold to René Oberthür (E.

C. Zimmerman, pers. comm.), whose collection now resides in the Paris Museum. Most of Perkins' later collections made during and after his time as an HSPA entomologist (e.g., resulting in Perkins 1917, 1936, 1937) are now deposited in the Bishop Museum.

Taxonomic Contributions

Perkins contributed extensively to the revisionary taxonomy that composed Fauna Hawaiiensis, revising the Odonata (Perkins 1899c. 1910a), Orthoptera (Perkins 1899b, 1910a), the beetle families Curculionidae, Aglycyderidae, Ciidae, Anobiidae, Bostrichidae, as well as groups of heteromerous beetles (Perkins 1900, 1910b), and Hymenoptera (1899a, 1910a). He also wrote an extensive introduction to Fauna Hawaiiensis (Perkins 1913), which provides a comprehensive overview of the endemic insect groups. He described 897 endemic Hawaiian insect species, including 17 damselflies (Odonata), 37 crickets (Orthoptera: Gryllidae), 22 barklice (Psocoptera), 38 lacewings (Neuroptera), 496 beetles (Coleoptera), and 268 bees and wasps (Hymenoptera). Based on recent taxonomic revisions of native Megalagrion damselflies (D.A.P., unpubl. data), crickets (Otte 1994), barklice (Thornton 1984), colletid bees of the genus Nesoprosopis (Hymenoptera) (Fullaway 1918; H. V. Daly, pers. comm.), and carabid beetles (Britton 1948; J.K.L. and E. C. Zimmerman, unpubl. data), Perkins' synonymy ratio is about 7% (eight synonymous names among 117 Perkins names in these groups). He had the benefit of priority with regard to describing the groups he did, but suffered from the necessity of describing species based on limited numbers of specimens. His understanding of natural biological entities stemmed from his field observations, ensuring that the species-level taxa he recognized have almost always remained valid after the addition of new taxonomic material. His 897 descriptions of endemic taxa constitute about 15% of the currently described Hawaiian insect fauna. That his work was done with such accuracy ensures a solid classification of species-level taxa upon which new workers may base their studies.

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