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Author(s): Rebecca J. Rundell

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Snails on an evolutionary tree: Gulick, speciation, and isolation*

Rebecca J. Rundell

Biodiversity Research Centre and Departments of Zoology and Botany, University of British Columbia, Canadian Institute for Advanced Research, Program in Integrated Microbial Biodiversity, Vancouver, British Columbia V6T 1Z4, Canada

Correspondence, R. J. Rundell: rrundell@interchange.ubc.ca

Abstract: Geographical separation is arguably fundamental to speciation. John Thomas Gulick (13 March 1832 – 14 April 1923), a missionary from the Hawaiian Islands and one of the earliest evolutionary biologists, was among the first to recognize the critical role for geographical separation in the diversification of ecologically similar Hawaiian land snails. Although Gulick's work is not well-known today, his ideas were discussed by Darwin and Wallace as well as leaders in the Modern Evolutionary Synthesis (e.g., Wright and Mayr) who saw an important role for geographical isolation in speciation. It was perhaps no accident that organisms with low vagility, such as land snails of the Hawaiian Islands (i.e., achatinelline tree snails and ground-dwelling amastrid snails) exemplified the importance of geographical separation in speciation. Here I provide context for Gulick's snail research, showing that the natural setting of the Hawaiian Islands, combined with Gulick's development as a naturalist and evolutionary thinker lead to important insights on speciation, resulting from observations of substantial species richness in achatinelline and amastrid land snails, among the ridges and valleys of the Hawaiian Islands. Gulick's research on lesser-known organisms, island land snails, illustrates key areas for future inquiry, particularly in understanding "nonadaptive" contributions to evolutionary radiations.

Key words: nonadaptive radiation, geographical, allopatric speciation, Hawaii

Many island land snail faunas exhibit high species richness in a very small land area (Crampton 1916, 1925, 1932, Solem 1990, Cowie *et al.* 1995, Cook 1996, 2008, Cowie 1996, Chiba 2004, Holland and Hadfield 2004, Parent and Crespi 2006, Rundell 2008, 2010). Examples of species with striking ecological differences can provide explanations for such diversity, but species with subtle or nonexistent ecological differences have been, and are, less well understood. Many closely related and morphologically similar species in other taxa (e.g., birds) once suspected to be ecologically similar, were later found to be ecologically distinct (MacArthur 1958). Still species remain for which ecological differences are elusive (e.g., snails; Gulick 1873a, 1889a). John Thomas Gulick (13 March 1832 – 14 April 1923), an evolutionist and missionary, was the discoverer of intra-island endemism among Hawaiian land snails (Gulick 1853, Reif 1985). He was unable to find ecological causes for the substantial species richness he observed in the Pacific endemic hermaphroditic pulmonate land snail families Amastridae and Achatinellidae (particularly subfamily Achatinellinae) within the Hawaiian Islands. Gulick used observations of these snails to develop theories on the role of geographical isolation in speciation, which were revolutionary in Darwin's time (Carson 1987, Hall 2006a).

Darwin's contemporaries, in the face of the new theory of natural selection, were perplexed by the vast array of morphological differences among species with no apparent adaptive significance; indeed, even much later such species-level variation proved confusing (Provine 1986: 453). Some argued for a critical role of natural selection, even for such unexplained differences (Wallace 1888, 1889), whereas other evolutionists sought explanations beyond natural selection (e.g., "physiological selection" of Romanes; Provine 1986: 216). Those in the latter camp were criticized, particularly by naturalists, who eventually not only faced assault by Lamarckian views but also from the growing contingent of experimental biologists, whose work proliferated following the revelation of Mendel's genetic research in 1900. In its historical context (e.g., given the widespread acceptance of Lamarckism, even into the early to mid 1900s; Gulick 1916, Mayr and Provine 1980), it is perhaps understandable that defense of natural selection was so heated, in response to any apparent exception or perceived replacement to the theory (e.g., Wallace's 1888 disagreement with Gulick). Now, we accept the important role of natural selection in the production of new species (Coyne and Orr 2004) and, generally, the idea that seemingly inconsequential characters might have selective

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value (e.g., intraspecific differences: conspicuous polymorphisms in *Cepaea nemoralis* Linnaeus, 1758 of England, Cain and Sheppard 1950, Provine 1986: 437-456, Brush 2009; interspecific differences: *Mandarina* Pilsbry, 1894 land snails on the Bonin Islands, Japan, Chiba 2004).

However, particularly in the land snail world, we find ample evidence of species that are ecologically similar and exhibit subtle morphological differences. Such species are frequently allopatric, because presumably ecologically similar species cannot remain distinct in the same place at the same time. Clades that have diversified under such conditions can be defined as “nonadaptive radiations,” i.e., collections of related ecologically similar species that are allopatric or parapatric replacements of one another (Gittenberger 1991, Rundell and Price 2009). Such radiations include e.g. some groups of salamanders (Wake 2006) and island land snails (Cameron *et al.* 1996, Cook 2008). Note that ecological similarity alone is insufficient for identifying nonadaptive radiation, and the criterion of allopatry (recognized as “isolation” by Gulick) is important.

Gulick, a naturalist, evolutionist, missionary, and malacologist from the Hawaiian Islands, was among the first to describe such patterns of allopatric ecologically similar species, and he used them to assert a potential role for geographical isolation in speciation (Carson 1987). Gulick’s contributions to evolutionary theory (A. Gulick 1932, Lesch 1975, Kottler 1976, Reif 1985, Hall 2006a, 2006b) and his life as a missionary and evolutionist (A. Gulick 1932, Amundson 1994) are reviewed elsewhere, as are the general geology and biota of the Hawaiian Islands (Wagner and Funk 1995). Gulick also has been cited for his research on both Polynesian land snails (Cowie 1992, Holland and Hadfield 2004, 2007) and speciation (Mayr 1963a, 1976, 1982, Wright 1978, Price 2008) although his work is still relatively unknown to most biologists. Regarding geology, it should be noted that the utility of the hot spot island chain of the Hawaiian Islands as a potential natural laboratory for the study of evolution and biogeography (i.e., a sequence of islands from youngest to oldest), was not clearly understood in Gulick’s time. While early in his career Gulick emphasized that the Hawaiian Islands were distinct from the mainland, each separated by deep channels, and each island contained hundreds of endemic species that had evolved on those islands (Gulick 1853), the theory of hot spot island chain formation was unknown until 1963 (Wilson 1963). Fossils that allowed more accurate dating of islands had only recently been discovered (in the early 1960s; Wilson 1963) and before this, it was assumed that the main Hawaiian Islands were very close in age. It was perhaps extraordinary, then, that Gulick would suggest that Hawaiian snail species might have evolved *in situ* and existed on these isolated islands for “one thousand or ten thousand years” (Gulick 1853: 10).

Given Gulick’s careful explication of a pattern that might be common among land snails, I suggest that his research warrants a closer look from a malacological perspective. I also suggest that such insight is necessary for a full understanding of his thinking on geographical isolation. In this paper, I briefly discuss Gulick’s early development as a naturalist. I then describe the patterns he saw among the land snails of the Hawaiian Islands. I do not aim to ground-truth each of Gulick’s data points, which would require an extensive review of land snail collections in light of the complicated taxonomy of his focal taxa (Cowie *et al.* 1995), some of which is underway (e.g., using Welch’s data on *Achatinella mustelina* Mighels, 1845: Holland and Hadfield 2007) although complicated in part by widespread extinction, particularly among the achatinellids and amastrids (Hadfield 1986, Solem 1990, Hadfield *et al.* 1993, Cowie *et al.* 1995, Holland and Hadfield 2007). Instead, I provide a historical framework for understanding Gulick’s contributions to our understanding of land snail evolution and the role of geographical isolation. I also suggest that distinctions between diversification patterns in the Hawaiian land snail fauna and other species-rich island land snails illustrate the fortuitous nature of discovery: Gulick’s unique position in the Hawaiian Islands and chosen study organisms allowed him a clearer understanding of geography’s potential role in speciation than might have been obtained in another study system. Furthermore, by collecting most of what has been written by and about Gulick here, I hope to stimulate future exploration of his work.

Gulick is usually associated with *Achatinella* Swainson, 1828 Hawaiian tree snails (subfamily Achatinellinae, family Achatinellidae) from the island of Oahu (Wright 1978, Carson 1987, Hadfield *et al.* 1993, Cowie *et al.* 1995, Stearns and Stearns 1999, Holland and Hadfield 2004, Hall 2006a), and he frequently referred to other land snails, e.g., small-bodied achatinellids such as *Auriculella* Pfeiffer, 1855, but also the Amastridae, most of which are (or were, before most of the family went extinct; Solem 1990, Cowie *et al.* 1995) ground-dwelling. Gulick placed amastrid species within Achatinellidae. Although it was then clear (Baldwin 1887) as it is now, that Amastridae represent a unique family distinct from the Achatinellidae (Cowie *et al.* 1995; this is also supported by molecular evidence: Holland and Hadfield 2004). Therefore, for clarity, amastrids will be referred to as such throughout, rather than as ground-dwelling members of the Achatinellidae, as they are in Gulick’s writings (e.g., Gulick 1872). Hereafter, the ecological categories of “tree” and “ground-dwelling” snails are collectively referred to as “land snails.” Tree snails (as defined here) are found on the leaves and bark of live trees, shrubs, and emergent vegetation, whereas ground dwelling snails are found predominantly in or on the leaf litter or rotting logs.

DEVELOPMENT OF A NATURALIST

John Thomas Gulick was born in 1832 on the Hawaiian Island of Kauai (A. Gulick 1932), a few months into the voyage of the *Beagle* (Darwin 1845). His parents were missionaries from the third of twelve companies of missionary ships (the first ship arriving in 1820; Kay 1970) sent to the Hawaiian Islands by the American Board of Commissioners for Foreign Missions to promote Christianity, agriculture, and formal education. Education, which was particularly valued by the missionaries, many of whom had received formal training at northeast American institutions (Kay 1997), spread quickly among Hawaiians, once the missionaries translated Hawaiian language to written form (A. Gulick 1932, Tate 1961). Although it is now clear that missionaries and other westerners had far-reaching negative impacts on the Hawaiian people and environment (Daws 1968), the missionary families' inquisitive minds and adventurous spirit combined with the advantage of settling within the largely unexplored Hawaiian environment, also contributed to important advances in the western discovery and understanding of the biota. They gradually acquired material such as reference books, cabinets, and the occasional microscope to aid in the growing natural history obsession, and sent material abroad for identification, quickly realizing that most of the species surrounding them were unique to the Islands (A. Gulick 1932, Kay 1970, 1997).

Land snail collecting, especially of the multi-colored *Achatinella* tree snails, was a particular passion among Oahu boys and girls alike (Gulick 1853, Kay 1970, 1997). Therefore, Gulick's enrollment in 1842 in the newly founded (1841) Punahou boarding school for missionary children (near what was then considered Honolulu, Island of Oahu), placed him firmly in the midst of "land shell fever" (Baldwin 1887: 2, Kay 1970, 1997), at the age of 10. Subsequently, between visits to Kilauea volcano (Island of Hawaii; Kay 1997), school, religious and agricultural pursuits, Gulick read Darwin's *Voyage of the Beagle* (1845; Carson 1987) and received taxonomic training from Dr. Wesley Newcomb (Gulick Papers 1841-1916, Kottler 1976), a physician who was in residence at Queen's Hospital (Honolulu) from 1850 to 1855 (Abbott and Young 1973, Kay 1997). Newcomb happened to be one of the premier conchologists in North America and maintained correspondence and relationships with leading malacologists such as Gould, Cuming, Sowerby, Ancey, Tryon, and Pfeiffer (Clarke 1960). He traveled broadly and amassed the third most complete shell collection on the continent, which he sold to Cornell University in 1868 for \$15,000 (Clarke 1960). These collections included one of the finest sets of Achatinellidae known at the time, which represented years of field work and captive rearing of species in the Hawaiian Islands (Clarke 1960). Gulick's relationship with Newcomb thus proved fortuitous.

In 1853 (at age 21), referring specifically to the influence of the *Voyage of the Beagle* and Dr. Newcomb, Gulick gave "A Lecture on the Distribution of Plants and Animals" before the Punahou Debating Society. Gulick's lecture described principles of adaptation, biogeography, the impact of isolation, particularly on islands, and the striking resemblance of the patterns of endemism among Hawaiian land snails with animals of the Galápagos. This effectively set the stage for what was to become a lifetime of research and promotion of Hawaiian land snails, and the Hawaiian biota in general, as ideal subjects for illustrating evolution and the role of geographical isolation (Gulick 1853, excerpted in A. Gulick 1932: 114-119).

In the years that followed, Gulick studied at Williams College in Massachusetts (graduating in 1859; Parsons 1884), where he continued to present his findings on Hawaiian land snails (A. Gulick 1932: 145) and gained a reputation among his colleagues as a "deep" and serious student and natural historian (A. Gulick 1932: 147). Gulick met Louis Agassiz (famed zoologist, whose work Gulick had read only a few years prior; Kay 1997), who enlisted him to collect in South America, though the trip was cut short due to political unrest in Panama (Hall 2006a). Gulick also read *On the Origin of Species* in the year of its publication (Darwin 1859; A. Gulick 1932, Carson 1987). He studied at Union Theological Seminary and received a Sc.D. from Oberlin (Ohio) and an honorary Ph.D. from Adelbert College (Western Reserve University, now Case Western) in Ohio (Williams College, Class of 1859, Class Letters: Hawaiian Mission Children's Society Library Journal Collection 1819-1900; A. Gulick 1932: 278). Gulick worked as a missionary in Japan and China for about 20 years (during which time he once received severe censure for extreme delay in reaching his post, as a result of evolution (see Kottler 1976: 331-332), personal and snail-related stops abroad; A. Gulick 1932, Carson 1987), interrupted by breaks in the United States, England (where he attended scientific meetings and visited prominent biologists Romanes, Darwin (1872), and others) and elsewhere (A. Gulick 1932: 230). Although Gulick's occupation as a missionary kept him away from the Hawaiian Islands for many years, there is little evidence to suggest that Hawaiian land snail evolution was ever far from his mind (Gulick Papers 1841-1916, Gulick 1885, A. Gulick 1932, Hall 2006a). Although for much of his life, correspondence was Gulick's only lifeline to intellectual peers who shared his passion for evolutionary biology. Nevertheless, Gulick was prolific in writing and speaking on the subject of evolution, and kept sets of snail shells with him for study and discussion. During trans-oceanic travels, he kept many of his collections in New York, and later, on the 1872 trip to England where he met with Darwin, Gulick unsuccessfully attempted to sell his collection to the British Museum (Gulick Papers 1841-1916, A. Gulick 1932, Hall 2006a).

Gulick was married twice and had three children, including a Chinese daughter his first wife (who died in 1875) had saved from a wrecked ship (Parsons 1884). Gulick eventually returned to his beloved Hawaii, participating sporadically in religious, scientific, and educational pursuits as health permitted until his death in 1923 at the age of 91 (A. Gulick 1932). This was an impressive lifespan, given poor health, eyesight, and exhaustion and that frequently plagued him in his early years (A. Gulick 1932: 22, Gulick Papers 1841-1916). The letters, journal entries (Gulick Papers 1841-1916), and publications (including species descriptions: Gulick 1858, Gulick 1873b, Gulick and Smith 1873) left behind now illustrate the development of his theory.

A ROLE FOR GEOGRAPHICAL ISOLATION IN EVOLUTION

The best-known land snail radiation exhibiting little, if any, ecological differences among species is that of the achatinelline tree snails of the Hawaiian Islands, first widely discussed by Gulick (*e.g.*, Gulick 1872, 1873a, 1873b, 1883, 1887, 1889a, 1889b, 1904, 1905). He demonstrated that particularly in the genus *Achatinella* of Oahu, species diversification was promoted by, for example, isolation among geographically distinct valleys, separated by ridges (valley and ridge names illustrated in Fig. 1), and that there was little, if any, difference in the habitat of each species. Gulick also observed differences in individuals' shell characteristics as distance increased from a "source" population.

However, an obvious mechanism by which such prolific diversification of species exhibiting no obvious ecological differences might occur, was initially unclear to Gulick (Gulick 1872). He believed that natural selection could explain adaptive changes within lineages, but it could not explain speciation (Kottler 1976, Reif 1985), particularly when species lived in seemingly identical environments (Gulick 1887, 1889, 1905). Natural selection had strong adherents (*e.g.*, Wallace 1889), and apparent alternatives, such as the one proposed by Gulick that focused on isolation, were sometimes interpreted as claims that natural selection was not the primary mechanism for evolution (Carson 1987), and thus presented a threat to Darwinism itself (Provine 1986: 219-220). Gulick suggested that populations might not only be geographically isolated (*i.e.*, experience "indiscriminate isolation" Gulick 1890e, Reif 1985), but could become "segregated" or experience a reduction in gene flow (Gulick 1905, Reif 1985). "Intensive segregation" (*i.e.*, divergence by natural selection; Gulick 1905, Reif 1985) could occur, but it was ultimately a succession of isolations over long intervals that could lead the way to a new habit in dealing with the environment and formation of divergent species ("cumulative

segregation": Gulick 1905; *i.e.*, speciation by divergent evolution, Reif 1985). Unique varieties (*i.e.*, groups within species, showing unique differences in form and color) were considered incipient species (Gulick 1905), which could become species (*i.e.*, strongly pronounced varieties; Gulick 1905). Gulick noted an "inherent tendency to variation" (Gulick 1873a: 499) that we now recognize as genetic variation (Carson 1987). In the absence of a genetic basis for his explanations, Gulick's claim was hard to justify, but attempts to define mutations in the early 1900s eventually supported some of his ideas (Gulick 1905, 1908, Reif 1985). For example, Gulick described a scenario in which a "mutation" of shell coiling direction (chirality) might arise and eventually lead to a new species (Gulick 1905, 1908). We now accept that both isolation and selection operate in the formation of new species (Carson 1987), but Gulick was on the wrong side of the debate when the bulk of his research was published.

One observation that might have lead Gulick to seek an alternative explanation for his observations was that some land snail species occurred on ridges that were connected to one another, rather than just in more geographically isolated valleys. It therefore was unclear to Gulick how such species could differentiate, particularly if they lived on the same plants and had the same predators. Gulick accepted that adaptation could occur (Reif 1985), but he did not find substantive evidence of it in his snails. In Gulick's mind, natural selection could only operate in cases such as the Darwin's finches, where obvious ecological differences and "survival of the fittest" was involved (Gulick 1872, 1873a). Gulick's observations, in contrast, lead him to support nonadaptive explanations (Provine 1986: 216-220).

Although Gulick's speciation mechanism received substantive criticism (*e.g.*, Wallace 1888), it was clear that his novel observations showing the production of many ecologically similar snail species among the ridges and valleys of the Hawaiian Islands might have broader implications for evolutionary theory. By the turn of the century, it was more widely accepted that natural selection alone might be insufficient to explain speciation (Provine 1986: 220). Indeed, Gulick supposed at one point that Wallace did not actually disagree with many of his main propositions (Kottler 1976: 406). Gulick used distribution patterns of achatinellids and amastrids as evidence for a primary role of geographical isolation (Gulick 1887, Reif 1985) in evolution (Gulick 1872, 1873a, 1883, 1889a, 1889b, 1904, 1905). Although his first publications were largely ignored by early Darwinists, Gulick can be partially credited for the eventual acceptance of isolation as an important aspect of speciation (Provine 1986: 220, Carson 1987).

Gulick's data (especially Gulick 1887; Lesch 1975) were identified by George Romanes, a prominent biologist and friend of Darwin, as potential support of Romanes's own

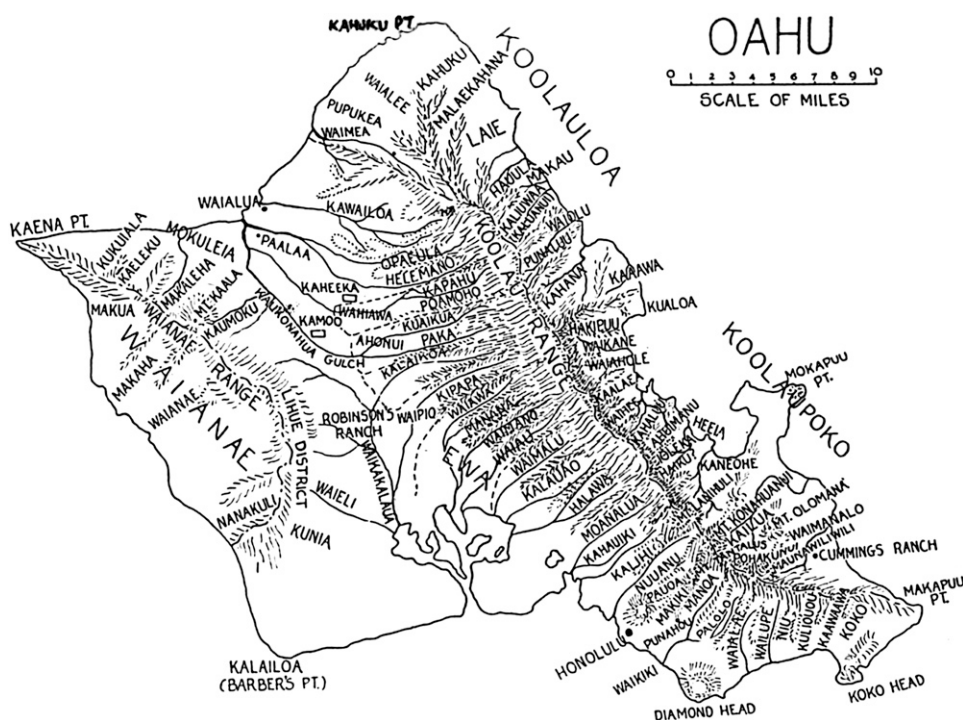


Figure 1. Map of the island of Oahu (Hawaiian Islands). Gulick assembled this map to illustrate his localities in 1873, in response to Wallace's urging in 1872, so that Wallace could include it with Gulick's paper. The process of fruitlessly trying to find a map, and then finally having to assemble it himself using his own memories and checks of Hawaiian oral historic lore, meant that Gulick's paper went before the Linnean Society of London without the map (A. Gulick 1932: 235). Gulick used this map in later years.

ideas on the role of isolation in speciation. These data seemed to provide support for Romanes's theory of physiological selection (Gulick 1906, Lesch 1975, Kottler 1976), which was an unfortunately misleading description for what eventually was known as "reproductive isolation" (Mayr 1982: 565; Kottler 1976; and alluded to in Gulick 1890c, 1908). The close relationship between Gulick's work and Romanes initially increased the visibility of Gulick's work among prominent biologists (Gulick Papers 1841-1916), but also exposed it to criticism by defenders of natural selection, particularly Wallace (e.g., Wallace 1888; Gulick 1890d, 1890f). Romanes, however, finally had empirical data to support his claims, and he eventually blended his own views with Gulick's such that physiological selection was subsumed within the general principle of isolation. He was planning experiments to support these ideas (with Darwin's encouragement) until his premature death in 1894 (Lesch 1975). Romanes's substantial correspondence with Gulick, which was maintained between 1887 and 1894 (Gulick Papers 1841-1916, A. Gulick 1932, Kottler 1976) indicates a richly rewarding scientific relationship that otherwise had been mostly absent from

Gulick's adult life, given his isolation as a missionary stationed in the Far East (A. Gulick 1932). However, Gulick's lack of direct assistance in analyzing his own data ultimately might have been a setback in better understanding and promoting his findings.

Despite widespread discussion of ideas on geographical isolation, Gulick's research was not broadly incorporated into evolutionary thought. Among the reasons for this are: Gulick's publication of his largest work (1905) years after Darwin but pre-dating wider acceptance of genetics (Mayr and Provine 1981 Reif 1985) as well as complicated terminology of his papers (Hall 2006a), lack of experimental evidence (Reif 1985), and perhaps his association with the maligned Romanes (Lesch 1975, Kottler 1976). Gulick's ideas were used in support of early Mendelians' theories of saltational/mutational change (perhaps ironically, because Gulick himself was a naturalist, rather than an experimental biologist), as opposed to the

majority of naturalists (e.g., Wallace, Hooker, David Starr Jordan, Poulton) whose data supported the idea of gradual evolution by natural selection (Mayr 1980). However, the importance of isolation was gradually gaining acceptance, and geographical isolation's key role in speciation was eventually accepted by naturalists such as Grinnell and D. S. Jordan (Lesch 1975). This provoked a re-examination of past work by, e.g., Moritz Wagner, who was technically the first to describe isolation as critical in species formation (in 1868; Mayr 1963a: 484, Mayr 1982: 562-565) although Gulick came to similar conclusions on isolation independently (Gulick 1890a, 1908).

Despite falling out of favor as a result of new studies by "mutationists" in the early 1900s, the important role for geographical isolation in speciation was largely acknowledged by 1942 (Mayr 1982). Coining of the term "isolating mechanisms" (the barriers maintaining reproductive isolation of species; Dobzhansky 1937: 405) was important in this endeavor. This and other work around that time lead to a gradual acceptance of geographical modes of speciation (Mayr 1980: 131). Following the Modern Synthesis, Gulick

was cited by Mayr (1963, 1976, 1980, 1982) and Wright (1978), who recognized the importance of geographical isolation in speciation (e.g., genetic drift; Provine 1986). Gulick's work also laid a foundation for the idea of isolation and random drift leading to nonadaptive differentiation (Provine 1986: 408). Indeed, with the substitution of a few words and phrases, Wright suggested that Gulick's work might describe one of the leading views on how genetic shifts might turn natural selection toward speciation (Carson 1987). Isolation was not emphasized by Darwin, who instead favored pure selectionist explanations for evolution (Carson 1987), but Darwin did discuss the significance of isolation (e.g., Darwin 1872: 81). Darwin's renewed interest in the subject of isolation was indicated in a long meeting with Gulick in 1872 (A. Gulick 1932: 234, Gulick Papers 1841-1916).

WHAT GULICK SAW: PATTERNS OF LAND SNAIL EVOLUTION IN THE HAWAIIAN ISLANDS

Snail diversity and ecology

Gulick focused on two Pacific-endemic land snail families, the Amastridae (326 species) and the Achatinellidae (212 species; Cowie *et al.* 1995), both of which are (or were, prior to the extinction of many species; Solem 1990, Cowie *et al.* 1995) major components of the land snail fauna on the island of Oahu (Fig. 1), where he spent most of his time. These families, which contain some of the largest-bodied, or at least conspicuous, snail species in the Hawaiian Islands, also happen to comprise 70% of described Hawaiian land snail species. (There are 763 nomenclaturally valid species described from the Hawaiian Islands, and almost all of these are endemic, and many are single-island endemics (Cowie *et al.* 1995, Cowie 1996).) The fact that Gulick studied amastrids and achatinellids is not surprising, especially given their beauty and popularity at the time (especially of achatinelline tree snails). Gulick documented about 200 species of amastrids and achatinellids (Gulick 1872, 1883). However, had Gulick lived permanently on the island of Hawaii (the "Big Island") he might have had dramatically different impressions of how evolution proceeded. Here, the Succineidae are (were) most diverse, and exhibit patterns indicative of adaptive radiation, with species' shell shape fitting habitat preferences including waterfalls, tree ferns, leaf litter, and dry scrub areas on the leeward side of Mauna Kea (Rundell *et al.* 2004, Holland and Cowie 2009).

Amastridae

Only a few extant amastrid species remain (Solem 1990, Cowie *et al.* 1995, Holland and Hadfield 2004)—remnants of perhaps the most spectacular, yet least well-known, Pacific

land snail radiation. Amastrids are leaf litter or ground dwellers with brownish shell color although much of their ecology remains unknown. They include two subfamilies (genera in parentheses indicate nomenclaturally valid genera *sensu* Cowie *et al.* 1995): Amastrinae (*Amastra* Adams and Adams, 1855, *Carelia* Adams and Adams, 1855, *Laminella* Pfeiffer, 1854, *Planamastra* Pilsbry, 1911, *Tropidoptera* Ancey, 1889) and Leptachatininae (*Armsia* Pilsbry, 1911, *Leptachatina* Gould, 1847, *Pauahia* Cooke, 1911). The genus *Carelia*, restricted to the oldest Hawaiian main islands of Kauai and Niihau, comprises species with the longest shells of any Hawaiian land snail, some species reaching 80 mm (Cowie *et al.* 1995). Gulick's inclusion of amastrids in his papers might be overlooked by non-malacologists because his taxonomy lumped these species together with the achatinellids (e.g., Gulick 1872). Although it appears from his explanations of evolution in the two groups that he did not see a ground-dwelling amastrid species as potentially sister to an achatinellid species (e.g., due to shell chirality differences, Gulick 1872, 1883); certainly this would have significantly changed his conclusions, which were distinct from any notions of adaptive shifts into different habitats.

Nonetheless, Gulick noted potential differences between the ecology of amastrids and achatinellids (Gulick 1872, 1883). He suggested that the ground habitats of amastrids would lead to larger species ranges among these snails, and therefore he categorized them as having a "medium" level of geographical restriction, in contrast to achatinellids, which were highly restricted, and "field" species (possibly invasive species, but this is unclear), which were widespread (Gulick 1872). There has been insufficient research on amastrids to evaluate this hypothesis, but work on other ground-dwelling Pacific land snails suggests that such species can have highly restricted ranges, often more so than tree snails from the same region (Rundell 2010). It is possible that the drab colors of the amastrids, relative to the colorful achatinelline tree snails especially, impacted Gulick's assessment of species, *i.e.*, the more colors, the more "species bins" can be found for those colors. However, Gulick also had the enviable advantage of viewing and collecting amastrids in the wild, and therefore had the opportunity to directly observe interspecific differences. Perhaps Gulick simply possessed less expertise in amastrid taxonomy. Certainly it would be worthwhile to examine his observations in light of significant amastrid museum collections (e.g., Bishop Museum Malacology Collections, Honolulu).

Achatinellidae

Achatinellids are some of the best-known land snails in the world. Most museums have at least one drawer full of these colorful banded or jewel-like tree snails (*i.e.*,

achatinellines), yet these are but a subset of the diversity contained within the group. There are five subfamilies: Achatinellinae (including *Achatinella*, *Newcombia* Pfeiffer, 1854, *Partulina* Pfeiffer, 1854, and *Perdicella* Pease, 1870, but subgenera such as *Bulimella* Pfeiffer, 1854 are also discussed by Gulick (1872, 1889b)); these species reach the largest body sizes of any Pacific achatinellids), Auriculellinae (*Auriculella*, *Gulickia* Cooke, 1915), Pacificellinae (*Lamellidea* Pilsbry, 1910, *Pacificella* Odhner, 1922), Tornatellinae (*Philopoa* Cooke and Kondo, 1961, *Tornatellaria* Pilsbry, 1910, *Tornatellides* Pilsbry, 1910), and Tornatellininae (*Elasmias* Pilsbry, 1910). The number of synonymies in this family (e.g., summarized by Cowie *et al.* 1995) suggests that the family Achatinellidae has been subjected to over-splitting; however, some experts have suggested that species richness in Hawaiian land snails, even achatinellids, has been underestimated (Solem 1990).

The observations on which Gulick based his theory of evolution through nonadaptive means and isolation, and then spent most of his life defending, were largely of the *Achatinella* of Oahu, which were some of the most brilliantly and variably colored achatinellids (e.g., Hall 2006a). Gulick also frequently referred to “*Helicteres*” (*sensu* Gulick 1873b), which was a subgenus of achatinellines (e.g., as is *Bulimella*). “*Helices*” are also mentioned, and depending on the context, are usually simply other species of amastrids or achatinellids (Gulick 1889b) although “*Helix*” likely refers to planispiral snails such as helicarionids (e.g., Gulick 1872).

Among the most critical facts regarding the natural history of most achatinellines, was the snails’ fidelity to trees, which they were unlikely to leave for their entire life history, as well as the preference of achatinellines for shady groves within valleys, that were separated from other shady groves by drier areas (Gulick 1905: 220). For some species, per-tree population densities were estimated to be 500 individual adult snails per tree or 2000 adults and juveniles per tree (i.e., *Partulina confusa* Sykes, 1900; Hadfield 1986). An individual snail’s fidelity to the same tree, sometimes throughout much of an individual snail’s life (Solem 1990, Hadfield *et al.* 1993), could have important consequences for restriction of gene flow. This extremely low-dispersal lifestyle might dramatically impact speciation in this group, contributing to subdivision of populations that could remain intact for long periods of time, perhaps slowly accumulating mutations (e.g., Price 2008) or, as Gulick suggested at the time (though little evidence existed for the his idea) “spontaneous variations” could arise (Gulick 1872), e.g., in a new direction of shell chirality in two mating individuals from a single tree (Gulick 1905: 68-70, 1908). However, Gulick did not expect that this was the predominant means of species formation (Gulick 1905: 70).

It could be argued that the ground-dwelling amastrids would have less restricted species ranges, because individuals

might be free to roam the seemingly endless, interconnected ground-scape (as Gulick inferred; Gulick 1872), in contrast to the individual trees inhabited by achatinelline tree snails. I think this outlook neglects the inherent patchiness of leaf litter and logs, and perhaps the preferences for different amastrid species to prefer some dead leaves to others; however, the ecology of most amastrids will never be well known, because the majority of species are now extinct. Thus, it is possible that both amastrids and achatinellids had equally restricted ranges, which, although suggested by the large species numbers in both families, did not seem immediately clear to Gulick. However, he was quite interested in exploring this idea among Kauai *Carelia* (Gulick 1872), which would have been isolated between steep ridges in some areas, such as the Na Pali coast (Solem 1990).

Island geology, isolation, and similar environments

Beginning in his 1872 paper and re-stated in other papers (Gulick 1873a, 1883, 1905), Gulick established the following patterns illustrating the impact of geographical isolation (at different scales) and island size on speciation. Islands tend to have unique faunas (e.g., land snails of Cuba; Gulick 1872) and the achatinelline tree snails are completely unique to the Hawaiian Islands. Within this island group there are different achatinelline genera and these are distributed throughout the valleys of the Hawaiian Islands. Species on Kauai are more distinct from species of Oahu and Maui, for example, than those islands’ species are from each other and might have dispersed, for example, by being carried by birds (Gulick 1873a, 1910). There are no Recent *Achatinella sensu stricto* Cowie *et al.* 1995 on Kauai; there is a putative subfossil achatinelline, *Newcombia* (Gage 1996) although data suggest it represents a back-colonization from younger islands (Holland and Hadfield 2004). However, there are Amastridae (i.e., *Carelia* (Cowie *et al.* 1995) unique to Kauai and Niihau), which might indeed be considered quite distinct from amastrids of other main Hawaiian Islands.

Gulick also remarked that substantial speciation has taken place in a very small area, particularly among achatinellids and amastrids, so that most species are single-island endemics and within Oahu most species are restricted to one mountain range, the Koolaus, an area 40 miles (64.4 km) long by 5 to 6 miles (8.0 to 9.7 km) wide (Gulick 1872), each species having a range of only 1 to 5 miles (1.6 to 8.0 km; Gulick 1872). Both the ideas of isolation of island archipelagos and isolation within those archipelagos have been cited as potentially important drivers of speciation, but in the mid to late 1800s, these ideas were still relatively new. What made Gulick’s perspective unique was its emphasis on the impact of subdivision of isolated areas (e.g., within mountain ranges such as the Koolau Mountains of Oahu) on species diversification within a relatively small area. Among the achatinellids

and amastrids, but *Achatinella* in particular, sometimes unique species were found in neighboring valleys (Gulick 1872).

The orientation of the main mountain range that Gulick studied and that was home to many species of *Achatinella*, the Koolau Mountains of northwestern Oahu (Fig. 1), turned out to be instrumental in showing a clear role for geographical isolation of populations and speciation. These mountains have an elongate “spine” with parallel valleys arranged along their length (A. Gulick 1932). In contrast, Gulick noted that varieties were less distinct on Maui, and it was therefore more difficult to connect species using the gradations in color or pattern of different varieties. He attributed this problem to the concentric arrangement of valleys on Maui (Gulick 1872). This geological pattern might have presented a similar challenge for studies of *Partula* Férussac, 1821 tree snails in French Polynesia (Crampton 1916, 1932); although the arrangement of some valleys, e.g., on Moorea, resembles that of valleys in the Koolaus, and there is greater potential for contact at either end of the mountain range (Clarke and Murray 1969, Murray and Clarke 1980). Notably, Crampton (1932: 188; Provine 1986: 437) found support for nonadaptive differences in size, shape, and color of *Partula* snails, whereas later study demonstrated adaptive habitat partitioning among coexisting *Partula* species (Murray and Clarke 1980, Cowie 1992). Ecological and biogeographical distinctions between the Hawaiian achatinellines and French Polynesian partulid tree snails that apparently resulted in such dissimilar radiation patterns still warrant further investigation (e.g., as was suggested by Cain and Sheppard 1950; Provine 1986: 442-443).

The most controversial part of Gulick’s hypothesis on diversification through “nonadaptive” means (Hall 2006a) was his insistence that habitats on either side of a ridge, for example, were identical (Gulick 1872, 1889a). Gulick gave careful descriptions of snail habitats that supported this view (Gulick 1872, 1889a). He could find no clear adaptations to specific environmental conditions or enemies on either side, despite Wallace’s insistence that all environments are different (Wallace 1889: 149). Gulick did note that some species preferred certain trees (e.g., *Bulimella*’s preference for kukui trees (*Aleurites moluccana*; Gulick 1872)), and he acknowledged the role of selection for certain species, yet his observations of most other snail species lead him to nonadaptive explanations (Gulick 1885, 1897, 1904, Kottler 1976: 330, Hall 2006a). Plant species were sufficiently widespread on the islands that there seemed to be no difference from valley to valley. It is difficult today to clearly understand potential habitat preferences of snail species because a large proportion of the indigenous Hawaiian forest has been destroyed. Thus, it is not evident whether current plant preferences (which indicate the setting in which snails can glean fungus from leaves or bark) accurately represent the breadth of species on which the snails once lived (Gulick 1905). Modern populations of

Achatinella mustelina are known to occur on several indigenous plant species (Hadfield *et al.* 1993), and several *Achatinella* species can survive on the common indigenous forest tree *Metrosideros polymorpha* (ohia-lehua) supplemented by cultured fungus (Rundell 2000, pers. obs.; Stearns and Stearns 1999: 33). It is possible different plant species might have historically harbored different fungal species on their leaves and bark, which the snails consumed, but this is unknown. It is also possible that this fungal diversity might have declined, with the extinction or reduction of indigenous plants.

It was unclear to Gulick why species would not “pass over their narrow bounds and become mingled” (Gulick 1872: 223). After all, species occurred not just in the valleys, but on the ridges; indeed ridgetops are all that remain of some species’ distributions (e.g., Hadfield *et al.* 1993). Slow dispersal and fidelity to the tree habitat, as noted by Gulick (indeed, fidelity to individual trees might be common, as in *Achatinella mustelina*: Hadfield *et al.* 1993), in combination with gradual acquisition of mutations might help to account for this (Gulick 1905, 1908), but obviously Gulick posed a very interesting question. It might have been the observation of ridgetop snail species and varieties that lead him to believe that geographical isolation alone was insufficient for speciation to occur (e.g., Gulick 1872, 1873a: 500, 1905: 221). Gulick also explored the possibility that ridge-dwelling species might have a higher dispersal capacity than valley-dwelling species (Gulick 1905: 221). He later indicated that these separate populations would “develop different types of variation” and would eventually be “liable to subject themselves to different forms of selection” (Gulick 1914: 63).

Populations, varieties, and change with distance

The fact that subtle gradations of shell phenotypes could be found linking species, and as distance increased, the difference in phenotypes also increased, also seemed to support Gulick’s notion that the process of speciation was largely driven by degrees of geographic isolation. Such data were acquired by careful collection of the many different shell phenotypes Gulick observed in each land snail population (A. Gulick 1932). Given the current extinction crises, particularly among Pacific island land snails (Solem 1990, Gould 1991, Cowie 1996), but especially among achatinelline species with low reproductive rates (Hadfield *et al.* 1993), the collection of the great number of individuals that this method required now seems outrageous (*i.e.*, Gulick collected and procured at least 44,500 shells in three years; Hadfield 1986, Stearns and Stearns 1999). It is difficult to imagine that Gulick and his contemporaries did not directly contribute to the decline of some achatinelline snail species since literally thousands of slow-to-reproduce adult snails were commonly collected or procured from indigenous Hawaiian collectors in a single day

(Hadfield 1986). Although at some localities, there were signs that species might have been already in decline (e.g., in 1853: A. Gulick 1932: 123), in some cases as a result of overgrazing (Gulick 1873a: 504, Baldwin 1887), particularly in the 30 years following the release of cattle by Captain George Vancouver in 1804 (Kay 1997). The tragedy of snail “deserts” where once there were literally tens of thousands of individuals (Hadfield 1986, Stearns and Stearns 1999) cannot be disputed.

However, when viewed within a historical context, Gulick’s desire to collect each potential phenotype within a population reflected progressive, non-typological thinking (e.g., Reif 1985). Certainly some taxonomic divisions below the species level might have no genetic significance, when analyzed using modern techniques (e.g., Waianae Mountains, Oahu *Achatinella mustelina* subspecies named by Welch (1938); Holland and Hadfield 2007), but there is likely some information contained within the many subspecies, varieties, and variations identified by Gulick and others. For example, in a preliminary study, Pelep and Hadfield (2010) found that some genetic differences corresponded with differences in shell shape. Gulick identified *ca.* 800 to 900 varieties of Oahu snails from his focal taxa (Gulick 1872), which he supposed to be “segregated” from other varieties (Gulick 1905: 222).

Regardless of the ultimate status of these different phenotypes, Gulick seemed to intend them as evolutionary works in progress and raw material for understanding variation, rather than immovable types (Gulick 1872, 1883). Some variations were well-known to him to be varieties of the same species, but others were not (Gulick 1889b: 348). Gulick also knew that there was not a new species in every valley—some species spanned multiple valleys (Gulick 1872, 1883). But within these wide-ranged species there were varieties (*i.e.*, groups within species, showing unique differences in form and color) and these showed population diversity (Gulick 1889a). Varieties would grade into one another over distances across the range of a species (Gulick 1872, 1889a). Collection of a “series” within populations and species (Gulick 1872; *i.e.*, collecting all potential varieties or color morphs of a species, for which achatinellines possessed many: Gulick 1889b) was not uncommon among systematists, even before Darwin (1859), because these early biologists recognized that individuals of a species are not identical (Mayr 1980). Gulick suggested that understanding the patterns of minute gradations (*i.e.*, differences in form and color) would help him understand the evolution of species in the context of the geography of an area and distance from the “home of the type” (*i.e.*, a typical form of the species selected by Gulick: 1889b: 347; Gulick 1858, 1872, 1889a; also see Mayr 1980: 130). The different banding patterns and colors among the achatinellines was of great interest, but Gulick could not understand how these differences correlated with plant preference (Gulick 1872). In other land snails (e.g., *Cepaea*)

such differences have been shown to have adaptive significance (Cain and Sheppard 1950, Provine 1986); however, no adaptive significance has been found for color or banding variation in achatinelline tree snails.

Wallace did find exception with some of Gulick’s explanation of diversity within populations. He argued that some of the forms described by Gulick (e.g., his explanation of “varieties”; Gulick 1889b) should only be considered “variations” which could not be counted as “taxonomically significant varieties” that arose when natural selection had acted upon them. Wallace observed that “variations” would spring up without dependence on the environment (Gulick 1890b, A. Gulick 1932: 462). In fact, this criticism seemed to reiterate Gulick’s observations (Kottler 1976), and Gulick emphasized that Wallace had not demonstrated the environmental differences of which he spoke (Kottler 1976: 330). Criticism notwithstanding, Gulick was also concerned with careful documentation of each locality from which he gathered or purchased his populations of snails (Gulick 1872, A. Gulick 1932, Gulick Papers 1841-1916). He stated that “Each valley, with its area two to three miles in length, and but one or two miles in width, needs to be separately explored, and all the shells labeled with the name of the valley” (Gulick 1872: 224). This was a novel approach in an age when “Sandwich Islands” was considered sufficient data (Cooke 1941) although some of the localities in Gulick’s descriptions (e.g., Gulick 1873b) report “Sandwich Islands” for the locality. It is possible that Gulick did not recognize the importance of recording exact localities in his early field work and shell procurement activities with his Hawaiian collectors. Given the lack of detailed locality information in many of Newcomb’s (Gulick’s first mentor) collections (Clarke 1960), it is doubtful this was a lesson Gulick learned early on, before he was conversant in evolutionary theory. It is perhaps worth remembering that Darwin himself was not always careful to label *e.g.*, finch species, even according to their island of collection (Carson 1987).

However, Gulick’s data were sufficient to demonstrate the effects of isolation on evolution. He noted that in one genus from one mountain range, species were connected by varieties with minute gradation in form (*i.e.*, shell shape) and color (Gulick 1889a), whereas species of the same genus on different islands were not so completely connected by intermediate forms. Gulick observed that the degree of difference between several species in the same group was in proportion to the species’ separation in space (Gulick 1872, 1883, 1905).

CONCLUSIONS

Comparisons with other island land snail studies

Modern studies have found that geographical isolation likely plays an important role in island land snail evolution

(Solem 1984), for example among land snails of the Atlantic Madeiran archipelago (Cook 1996, Cook 2008), and Lord Howe Island and Rapa (Solem 1984). Ecological differences have been suggested to place a strong role in completion of the speciation process (e.g., different hill habitats of Cook 1996), and it has also been suggested that neutral processes might account for high species richness at any one site (Cook 2008). Solem (1984) refers to the latter as a “mosaic assemblage” in which species are added to an assemblage with little or no competitive exclusion. Here, scattered clusters of different species can be associated with specialization on particular plant communities. The two ideas seem to run counter to one another: at the beginning of the process not only isolation, but adaptation to unique habitats was required for speciation, but individual local land snail communities comprised “weakly interacting” species (Chiba 2007).

Gulick demonstrated that species diverged in nearly identical environments on either side of a barrier, and very few adaptations to local environments could be found. Wallace’s criticism that we do not know enough about these snail species to assume that ecological differences do not exist (e.g., Wallace 1889: 148), remains largely unanswered, except by Gulick himself (e.g., Gulick 1905), and modern observations that several species can survive on one indigenous tree species, *Metrosideros polymorpha* (ohia-lehua; Stearns and Stearns 1999, Rundell 2000, pers. obs.), and some species can survive on more than one indigenous plant species (Hadfield *et al.* 1993).

The resulting communities of more distantly related species in the valleys and on ridges were also species-rich, but Gulick was less concerned with community-level patterns (but see e.g., Gulick 1889a), which have led to the more recent ideas of “nonadaptive” influences on land snail diversification, as in studies mentioned above. Furthermore, there are differences in habitat types and the distribution of those habitats, between the Hawaiian Islands, and for example, the Madeiran Islands. Whereas Gulick noted patches of landscape (e.g., “meadows”) distinct from the rainforest, generally the amastrids and achatinellines were not present there, and so these patches only served to further isolate his species (Gulick 1872). The rainforest where most of Gulick’s species lived was relatively uniform. In contrast, in the Madeiran Islands, the variety of landscapes augments species diversity within a clade and provide unique microhabitats to which species adapt. Within each habitat, convergence in shell shape may occur (e.g., as with Bonin Islands *Mandarina*; Chiba 2004).

These brief examples demonstrate the variety of ecological and evolutionary processes that may contribute to land snail diversification. Investigation of the intersection between radiations of species (nonadaptive or adaptive) and subsequent community assembly involving those species, is

clearly important for a better understanding of land snail evolution on islands. In some sense, Gulick’s study system choice was fortuitous in providing the most straightforward example of geographical isolation and the effects of distance on species differentiation.

Future directions

A few great malacologists followed, and were coincident with Gulick in documenting Hawaiian land snails, including Cooke, Welch, and Kondo (Cooke 1941, Cooke and Kondo 1960; reviewed by Solem 1990), and it is on their collections that we must now base a large part of our research on diversification in these spectacular snails. Unfortunately, these pioneers of Hawaiian malacology did not produce enough students or intense interest in the snail fauna when these species were still extant, and so it may be too late to ask some of the important evolutionary and ecological questions of these snails (Solem 1990). Certainly, malacology has rarely been part of the “bandwagon effect” lamented by Simpson and Mayr, where most of the attention, resources, and bright students flock to fields that are technologically or conceptually advancing at a rapid rate, promising fame and fortune (Mayr 1963b: 1, Simpson 1964: 113-114, Beatty 1994: 348).

But magnificent museum collections remain, and combined with populations surviving in the wild and in captivity, we can learn a great deal (Hadfield *et al.* 1993, Holland and Hadfield 2004, 2007). Focus on the less charismatic, non-achatinelid achatinellid families (although many species are also likely extinct; Solem 1990) might also reveal fascinating patterns based on molecular data, that could be compared with Gulick’s ideas (e.g., R. H. Cowie, unpubl. data on tornatelline snails). Collections-based studies of shell shape and internal morphology, particularly of the amastrids, could also provide important insights. In this sense, amastrid collections are the best-preserved “fossils” in the world; indeed, there are also fossil and sub-fossil amastrids that could be included in analyses of Recent amastrid taxa.

Perhaps we could approach museum collections with the same spirit of Gulick, in the largely unexplored (by western eyes, at least) Hawaiian Islands. “Here we are, by fortune or by providence, placed in the midst of an unexplored field, which promises to the student of nature the richest rewards: and what boy, what girl—we may rejoice that we are boys and girls when we see what there is yet for us to learn—but who is here amongst us that cannot do something to advance the cause of science, if he will only commence now...” (Gulick 1853: 10).

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