Molecular phylogeny and biogeography of the endemic Hawaiian Succineidae (Gastropoda: Pulmonata)

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Abstract

The endemic Hawaiian Succineidae represent an important component of the exceptionally diverse land snail fauna of the Hawaiian Islands, yet they remain largely unstudied. We employed 663-bp fragments of the cytochrome oxidase I (COI) mitochondrial gene to investigate the evolution and biogeography of 13 Hawaiian succineid land snail species, six succineid species from other Pacific islands and Japan, and various outgroup taxa. Results suggest that: (1) species from the island of Hawaii are paraphyletic with species from Tahiti, and this clade may have had a Japanese (or eastern Asian) origin; (2) species from five of the remaining main Hawaiian islands form a monophyletic group, and the progression rule, which states that species from older islands are basal to those from younger islands, is partially supported; no geographic origin could be inferred for this clade; (3) succineids from Samoa are basal to all other succineids sampled (maximum likelihood) or unresolved with respect to the other succineid clades (maximum parsimony); (4) the genera Succinea and Catinella are polyphyletic. These results, while preliminary, represent the first attempt to reconstruct the phylogenetic pattern for this important component of the endemic Hawaiian fauna.

Keywords: COI; Colonization pattern; Conservation; Evolutionary radiation; Islands; Land snails; mtDNA; Phylogeography; Pulmonata; Succineidae

1. Introduction

The Hawaiian islands have long been recognized for the spectacular diversity and endemism of their biota (Simon, 1987). The extreme isolation of the islands (Fig. 1) coupled with their sequential linear origin as the Pacific plate moves across a stationary “hot spot,” with magma periodically breaking through the crust to form volcanic islands, make the islands an ideal model for investigating the relationship between biogeography and phylogeny in an oceanic island system (e.g., Carson, 1987). Phylogenetic and biogeographic study of Hawaiian birds, insects, and several groups of plants has been underway for some time (e.g., Wagner and Funk, 1995) but not until very recently have Hawaiian land snails been approached from such a perspective (Cowie, 1995, 1996; Holland and Hadfield, 2002; Pokryszko, 1997; Thacker and Hadfield, 2000).

There are over 750 nomenclaturally valid land snail species in 15 families in the Hawaiian islands; 99% of these species are endemic (Cowie, 1995; Cowie et al., 1995). It has long been assumed that each endemic group (genus, subfamily, or family) of species within this huge diversity has resulted from in situ speciation from a single ancestral taxon (Zimmerman, 1948). However, this has rarely been rigorously tested. Ascertaining the biogeographic origins of these radiations is essential to understanding their evolution and the fact that multiple origins have been recently demonstrated in some Hawaiian terrestrial invertebrate groups (Gillespie et al., 1994; Robinson and Sattler, 2001) suggests that
other taxa may have similarly complex evolutionary histories.

At least 65–75% (Solem, 1990) or perhaps as many as 90% (Cowie, 2001) of the Hawaiian land snail species are currently extinct, rendering complete molecular phylogenetic study impossible for most taxa, including the Hawaiian Succineidae. Although the number of extant succineid species is unknown, during field sampling it became apparent that many taxa were either rare or possibly extinct. Nevertheless, as a family, proportionately more species are probably extant than is the case for any other family of Hawaiian land snails, so the Succineidae offer the best opportunity to address evolutionary questions of Hawaiian land snail diversification. The Hawaiian succineids are not formally protected under US federal or state law, but the group is of conservation concern.

Succineidae are found worldwide (Patterson, 1971; Pilsbry, 1948), reaching their highest diversity in Pacific islands, India, and the Americas (Barker, 2001). Though often associated with riparian areas (e.g., Kerney and Cameron, 1979), the Succineidae are also well-represented in rainforests and dry habitats (Barker, 2001). The Hawaiian succineids comprise 42 recognized species, all endemic, with 35 single-island endemics (Cowie et al., 1995), suggesting that most speciation in this group has occurred within islands (Cowie, 1995), in contrast to the primarily inter-island mode of speciation in the Hawaiian picture winged Drosophila (Carson and Kaneshiro, 1976). The Hawaiian Succineidae have radiated into a diverse array of habitats, from montane rainforests to xeric coastal dunes (Cowie, 1995; Cowie et al., 1995). Succineid shell types reflect these ecological differences, making them candidates for studies of adaptive radiation, convergence, and morphological evolution.

Hawaiian succineids are currently placed in three genera: Succinea Draparnaud, 1801 (34 species, approximately 1/3 of which are known only as fossils or dead shells; Rundell, unpublished data), Catinella Pease, 1870 (six species), and Laxisuccinea Cooke, 1921 (two species, known only as fossils). Placement in Succinea, a genus with a global distribution, reflects the fact that most species were described in Succinea; they will probably only be correctly placed once their internal morphology has been studied. Species determinations are based largely on shell size and shape.

This preliminary phylogenetic reconstruction of Hawaiian Succineidae provides an important starting point for rigorous testing of evolutionary, biogeographic, and ecological hypotheses of geographic origin(s) and subsequent diversification. Mitochondrial DNA markers have proven particularly useful in the elucidation of phylogeographic patterns in Hawaiian terrestrial invertebrate radiations (e.g., DeSalle, 1995; Gillespie et al., 1994; Holland and Hadfield, 2002; Thacker and Hadfield, 2000). However, the Succineidae are only the third Hawaiian land snail group to be studied using modern phylogenetic techniques. Previous studies include a morphological analysis of Lyropupa Pilsbry (Pokryszko, 1997) and molecular analyses of achatinelline tree snails (Holland and Hadfield, 2002; Thacker and Hadfield, 2000).

Here, we test two main hypotheses, using molecular evidence from the cytochrome oxidase I (COI) gene: (1) that the Hawaiian succineids are monophyletic, derived from a single ancestral colonization; and (2) that the colonization pattern follows the progression rule (Funk and Wagner, 1995), which states that species from older islands are basal to those from younger islands, that is, that the sequence of colonization follows the ages of the islands. This work represents the first major
investigation of Hawaiian Succineidae since that of Cooke (1921).

2. Materials and methods

2.1. Sampling

We sampled 13 Hawaiian succineid species from all of the main islands (Fig. 2), three species from Japan (including as representatives of eastern Asia), a single species from Tahiti (Society Islands), and two species from Samoa (Table 1, Fig. 1). Asia is the most likely geographical source area of most Hawaiian land snail groups, as a result of island-hopping through Polynesia (Cowie, 1996). Thus, although few, these additional non-Hawaiian species are representative of the likely source of the Hawaiian taxa. Non-succineid outgroup taxa were included from six different terrestrial gastropod families (Table 1). The family Athoracophoridae was selected because it is generally considered the sister group to Succineidae and together they comprise the Elasmognatha, on the basis of both morphological (Barker, 2001) and molecular (Wade et al., 2001) analyses. Phylogenetic placement of the Succineidae relative to non-elasmognaths is uncertain (Wade et al., 2001), so representatives of four additional stylommatophoran pulmonate families were included: Bulimulidae (putative sister to elasmognaths (Wade et al., 2001)), Bradybaenidae (putative sister to Succineidae (Holland and Hadfield, unpublished data)), Clausiliidae (putative sister to elasmognaths (Dutra-Clarke et al., 2001)) and Partulidae. A Hawaiian basommatophoran pulmonate (Lymnaeidae) was also sampled.

All specimens were collected between February 1999 and May 2001 and either frozen at $-80^\circ$C or preserved in 70–99% ethanol immediately following collection. Species determinations were based on previously identified material, including type material, in the Bishop Museum (Honolulu). Remains of specimens used will be deposited in the Bishop Museum Malacology Collection.

2.2. DNA extraction, PCR amplification, sequencing

Muscle tissue from the foot was used for all DNA extractions. DNA was extracted using a DNeasy kit according to the manufacturer’s instructions (Qiagen, Valencia, CA). DNAs were eluted in deionized autoclaved water and refrigerated.

Universal COI primers (Folmer et al., 1994) were used to amplify the target fragment of mtDNA. Bovine serum albumin (BSA) and DMSO were added to all PCRs (total 25 µl). PCRs were carried out in a PTC-100 thermocycler (MJ Research). Optimal PCR conditions were as follows: 2 min at 92°C, 35 cycles of 94°C for 30 s, 40°C for 30 s, and 72°C for 45 s, with a final 7 min extension at 72°C. Reaction tubes were then kept at 4°C and subsequently frozen at $-20^\circ$C, pending analysis.

Amplification of target DNA yielded a 663-bp fragment. Following agarose (1.5%) gel electrophoresis to verify fragment size, DNA fragments were purified using QIAquick spin columns (Qiagen). Purification followed the manufacturer’s protocol. DNAs were cycle-sequenced using PCR primer and an ABI Prism DYE Terminator Cycle Sequencing Reaction Kit in a Perkin-Elmer 9700 thermal cycler and sequenced using an ABI 377 automated sequencer (PE Biosystems).

2.3. Data analysis

Sequences were edited, aligned by eye, and deposited in GenBank (Table 1). Genetic divergence, minimum evolution (ME), maximum parsimony (MP), and maximum likelihood (ML) analyses were conducted using PAUP* 4.0b10 (Swofford, 2002). For ME analyses, several substitution models were used to produce distance matrices and trees, and the results were compared. Models included the Jukes-Cantor, Kimura 2-parameter, HKY85, and GTR + G + I. In order to reduce runtime for MP and ML bootstrap analyses, four of the outgroup taxa were removed from the dataset (the bulimulid, clausiliid, partulid, and bradybaenid sequences), after tree topologies were tested and proved robust to outgroup sampling differences. For the MP analysis, equal weighting and a heuristic search option with tree bisection reconnection (TBR) branch-swapping and 100 random additions were applied. Bootstrap support (Felsenstein, 1985) for each node was assessed based on 1000 replicates for ME and MP approaches, and 100 replicates for ML trees.
Modeltest v3.06 (Posada and Crandall, 1998) was used to select the optimal substitution model for the ML tree, and settings included a user-defined substitution rate matrix based on the Modeltest results. Modeltest runs through PAUP* using a likelihood ratio test and identifies the optimal model using a $\chi^2$ distribution.

3. Results

3.1. Sequence characteristics and genetic divergence

Out of 663 total base pairs representing 221 codons, 215 nucleotide sites for Hawaiian succineids were variable. Of these 215 variable positions, 38 were first codon position (17.7% of total), 2 were second codon position (0.93% of total), and 175 were third codon position (81.4% of total). Empirical nucleotide frequencies were biased toward A and T ($A + T = 67.4\%$); mean values were: $A = 25.2\%$, $C = 14.2\%$, $G = 18.3\%$, and $T = 42.2\%$. Nucleotide frequencies were nearly identical for all succineids and all succineids plus outgroup taxa. The mean transition to transversion ratio for all succineids was 1.4.

The mean genetic divergence among all succineid taxa was 16.6% ($\pm 4.3\%$). The mean genetic divergence between *Lymnaea aulacospira* and the Succineidae was 27.4% ($\pm 1.2\%$). The mean genetic divergence among Hawaiian succineids was 15.1% ($\pm 4.1\%$), and the mean genetic divergence within clade A was 13.6% ($\pm 3.4\%$) and within clade B was 10.5% ($\pm 4.7\%$).

The minimum between-species genetic divergence for Hawaiian succineids was 2.5% between *Succinea quad- rata* (island of Hawaii) and *Succinea rubella* (Lanai). Within-species genetic diversities were 0.9% between *Succinea lumbalis* individuals, 0.8% between *Succinea lutulenta* individuals, and 3.1% between *Catinella baldwini* individuals. The Samoan species *Succinea manuana* and *Succinea modesta*, from different islands but morphologically indistinguishable, differed by 0.2%.

3.2. Phylogenetic analyses

Gene trees composed of 25 and 21 taxa are shown in Figs. 3 and 4, respectively. Topologies were nearly
identical under ME (not shown), ML (Fig. 3), and MP (Fig. 4) approaches. Although consensus tree topology shows monophyly of the Succineidae, bootstrap support was weak regardless of optimality criterion used (56/52% bootstrap for ME/MP and less than 50% for ML), and data exhibited moderate to strong statistical support for two main clades, labeled A and B (clade A bootstrap ME/MP/ML: 93/90/80%; clade B bootstrap: 98/86/61%). Both clades were identical in terms of both taxonomic composition and topology for ME, MP, and ML approaches. Clade A consisted of Hawaiian taxa only, from Kauai, Oahu, and the Maui Nui complex (Molokai, Maui, Lanai, which were once a single island). Clade B comprised all sampled island of Hawaii species, a species from Tahiti and two of the species from Japan. Clade C consisted of the two Samoan species.

A likelihood ratio test indicated that the optimal model was the general time-reversible model with gamma distribution (G) and number of invariant sites (I) (GTR + G + I), with a likelihood score of $-\ln L = 6838.94$ and parameters $G = 0.5727$ and $I = 0.5091$. In the ML tree produced using this model (Fig. 3), *Oxylosma hirasei* was basal to clades A and B, and clade C was basal to *O. hirasei*. *Athoracophorus bitentaculatus* was basal to the entire succineid ingroup. *L. aulacospira* was basal to a clade containing the remaining four outgroup taxa. In this clade, *Albinaria coerulea* and *Bradybaena similaris* were sister taxa, with *Eua zebrina* basal to this subclade, and *Placostylus ambagiosus* basal to *E. zebrina*.

Two equally parsimonious trees of 1269 steps resulted from the MP analysis (not shown). (CI = 0.4169; RI = 0.4865). Topology of the succineid ingroup clades was identical between the two equally parsimonious trees and also identical to the ML topology shown in Fig. 3. The MP bootstrap tree depicted in Fig. 4 differed from the GTR ML tree (Fig. 3) in that, in the MP tree,
the relationships among *O. hirasei* and clades A–C were unresolved.

A ML bootstrap tree (not shown; ML bootstrap values shown in Fig. 4) produced using an HKY85 model was similar to the MP tree (Fig. 4) in overall topology, including the two distinct main clades, A and B, the unresolved positions of *O. hirasei* and clade C. The ML bootstrap tree (not shown) differed from the MP bootstrap tree (Fig. 4) in three nodes within clade A. In the ML bootstrap tree, there was a polytomy among the Kauai (two species), Oahu/Lanai (two species) and Molokai/Maui (four species) subclades. There was another polytomy within the Molokai/Maui subclade, among the two Maui species and the Molokai subclade.

The ME bootstrap tree (not shown; bootstrap support in Fig. 4) differed only at two nodes from the MP bootstrap tree. In the MP tree (Fig. 4) *A. bitentaculatus* is basal to the monophyletic succineid ingroup. Whereas, in the ME bootstrap tree, *A. bitentaculatus* shared a basal position with clade C. The second difference between the ME and MP topologies was in the relationship between the Kauai taxa *Catinella explanata* and the sister taxa “undescribed species” and *S. lumbaris*. The MP topology showed *C. explanata* basal (77%) to the other two Kauai species, whereas in the ME topology this relationship was unresolved.
4. Discussion

4.1. Phylogeography and origins

The phylogenetic results suggest: (1) succineids from Kauai, Oahu, Molokai, Maui, and Lanai are monophyletic (clade A, Figs. 3 and 4); (2) species from the island of Hawaii are paraphyletic with taxa from Tahiti (clade B; Figs. 3 and 4); (3) clade A shows a colonization sequence roughly conforming to the progression rule; (4) Samoan succineids and a single Japanese succineid are basal to the two main clades (A and B) in the ML analysis (Fig. 3); (5) the succineid genera Succinea and Catinella are polyphyletic; (6) the succineids analyzed form a monophyletic group.

Although there are 42 recognized Hawaiian succineid species, as many as one-third may be extinct (Rundell, unpublished data). In addition, we were unable to find other species despite intensive field work focused near the type localities of these species and in other apparently suitable localities. These species are probably either extinct or extremely rare. Thus our sampling of the fauna was not comprehensive. Nevertheless, as each additional species was included in the study there were no fundamental changes in tree topology. Therefore, despite the acknowledged limitations of our sampling, it is probably the best that is possible, and we feel confident that our basic tree topology is robust. In general, all phylogenetic trees produced in this study, including both topologies shown (Figs. 3 and 4), were congruent. However, the bootstrap analyses produced trees with slightly reduced deeper node resolution. Potential explanations for unresolved nodes include the possibility of third codon position saturation and incomplete sampling because of lineage extinction.

Although a single colonization event was previously assumed for the Hawaiian succineids (Zimmerman, 1948), our data do not support this hypothesis. Instead, at least two colonization events probably resulted in two distinct succineid clades, A and B. Clade B consists of all island of Hawaii taxa sampled, a species from Tahiti, and two species from Japan, which were basal (Figs. 3 and 4). Therefore, succineid species from the island of Hawaii are more closely related to succineid species from Tahiti and Japan than they are to any of the other Hawaiian succineid species sampled. The mean genetic divergences, 13.6% among clade A species, and 10.5% among clade B species, suggest that the clade B radiation may have occurred more recently than the clade A radiation, which is in agreement with the ages of the islands (Fig. 1).

Of particular interest in clade B are two of the island of Hawaii species, S. konaensis and S. quadrata, which are moderately to highly supported (100/95/76% ME/MP/ML) sister taxa (Figs. 3 and 4) with a genetic divergence of 2.5%. They share very similar shell morphology but currently have non-overlapping ranges (though their historical ranges, at least of S. konaensis, were much larger) and live in very different habitats: S. konaensis in dry scrubland on the ground; S. quadrata in rainforest on vegetation. This supports the idea that evolution may occur rapidly under circumstances allowing for segregation of populations into environments presenting different adaptive opportunities (Schluter, 1998). However, both S. konaensis and S. quadrata are in need of more detailed study from both a phylogeographic and ecological perspective before we can fully understand the evolution of these two taxa.

The island of Hawaii is less than 0.5 million years old, and there are 22 succineids (19 endemic) known from this island (Cowie et al., 1995). Additional work on the evolution of succineid species on the island of Hawaii is therefore likely to provide more insights into the complexity and rate of evolutionary change. Unfortunately, many species may be extinct or exceedingly rare (Rundell, unpublished data), which may limit further sampling for molecular work.

An Asian (or Australasian) origin has been thought likely for a number of other Pacific island land snail groups (Cowie, 1996; Pokryszko, 1997). The phylogenetic analyses presented here, with Japanese species basal to Clade B (Fig. 3), are consistent with this suggestion. Since the Tahitian species falls within the island of Hawaii clade (clade B, Fig. 3), it is possible that Tahiti was colonized from Hawaii. However, this seems unlikely since the island of Hawaii is younger than Tahiti. We cannot rule out multiple colonizations of the island of Hawaii, with an ancestor or ancestors from the South Pacific. Future phylogenetic work incorporating a range of succineid species from the Americas, Asia, and elsewhere in the Pacific will be required to elucidate the origin(s) of clade B (as well as clade A; see below).

The general pattern of relationships within clade A (Figs. 3 and 4) provide only weak support for the progression rule (Funk and Wagner, 1995) of successive colonization from the older island (Kauai, 5.1 Ma) to younger islands (W. Maui, 1.3 Ma). Although Kauai species are basal to all other species in clade A, there are several exceptions to a progression rule pattern. Based on the progression rule we would predict species from Oahu (3.7 Ma) to be basal to those from Molokai (1.9 Ma) and Lanai (1.3 Ma), with those of Molokai being more closely related to those of Lanai. However, S. rubella from Lanai is sister to Catinella rotundata from Oahu, rather than the Molokai species, indicating a discontinuous colonization pattern. Increased sampling, if additional extant succineids from Oahu and the Maui Nui complex exist, may improve our understanding of the evolutionary history resulting in this biogeographic pattern. Indeed, incomplete sampling within island faunas, which have often been impacted by
high extinction rates, presents challenges for the interpretation of phylogenetic results (Emerson, 2002).

All Maui and Molokai species sampled form a single clade. The Maui species *S. lutulenta* and *C. baldwini* appear ancestral to the Molokai species *Succinea canella* and an undescribed species, which again violates the progression rule. This suggests that at least one ancestor from Maui (1.3 Ma) may have colonized Molokai (1.9 Ma). In addition, it is initially surprising that from Maui (1.3 Ma) may have colonized Molokai progression rule. This suggests that at least one ancestor appear ancestral to the Molokai species *Succinea canella* clade. The Maui species *S. lutulenta* (Maui endemics), *S. canella* inhabits both Molokai and Maui. Distribution of *S. canella* on Maui only includes West Maui (according to data associated with Bishop Museum collections). Therefore it is possible that West Maui and Molokai succineids are more closely related than are East and West Maui species. More taxa need to be added to test this hypothesis, but the grouping of these three species is consistent with the complex and interrelated geological history of Maui and Molokai, which became conjoined and then separated by ocean during the Pleistocene (Carson and Clague, 1995; Juvik and Juvik, 1998).

Clade A, which includes the species from all of the main islands except the island of Hawaii is probably the result of a separate colonization event. Further work is needed to discover the geographic origin of this clade. However, the idea that an ancestor to clade A came from an older Hawaiian Island (rather than Kauai being the first island to be colonized by a non-Hawaiian ancestor) cannot be ruled out (Carson and Clague, 1995).

The ages of the Hawaiian succineid lineages are still uncertain but an ancestral succineid could have arrived in the Hawaiian archipelago as early as about 29 Ma. Since some Hawaiian succineids inhabit coastal dune-lands and low-elevation forests, which suggests that Hawaiian succineid ancestors could have thrived in similar environments, land of sufficient elevation to provide suitable habitat was consistently available from this time to the present (Carson and Clague, 1995; Clague, 1996; Price and Clague, 2002). Phylogenetic studies of other Hawaiian invertebrate radiations suggest origins far exceeding the age of Kauai, the oldest extant high island (Jordan et al., 2003; Russo et al., 1995).

4.2. Genetic divergence

The large difference (20.6%) between *S. quadrata* (Island of Hawaii) and *S. rubella* (Lanai) can be understood in the context of separate colonization events, which are indicated by our data. The smaller but variable genetic divergences among other species are more difficult to interpret. For example, two *C. baldwini* individuals (from Maui) differed by 3.1%, while the ecologically and geographically distinct island of Hawaii species *S. konaensis* and *S. quadrata* only differed by 2.5%. It could be that these two island of Hawaii species diverged more recently than did the two *C. baldwini* populations, and that *C. baldwini* comprises two or more cryptic species. However, Holland and Hadfield (2002) found a maximum intraspecific divergence of 5.3% among populations of the Hawaiian land snail *Achatinella mustelina* (*Achatinellidae*). In other land snail species, interspecific distances may be quite low (e.g., 3.9–4.5% and 2.1–5.1% for some *Albinaria* species; Douris et al., 1998). Only detailed population-level study will resolve these issues as they relate to the Succineidae.

Other within-species genetic divergences (0.9% for *S. lumbalis* and 0.8% for *S. lutulenta*) suggest that, unlike *C. baldwini*, some Hawaiian succineid species may be genetically uniform. The very small divergence (0.2%) between *S. mahuana* and *S. modesta* (American Samoa) suggests they are the same phylogenetic species; externally they are morphologically indistinguishable. The two species were described from different Samoan islands (see Cowie, 1998) and specimens were assigned to the two species based on collection localities (*S. mahuana* from Olosega; *S. modesta* from Aunuu). These two Samoan species form a clade distinct from clades A and B and in the ML analysis are basal not only to the Hawaiian but also to the Tahitian and Japanese succineids (Fig. 3); in the MP analysis these groups are involved in a polytomy thus shedding no light on their relationships (Fig. 4).

4.3. Taxonomy

The Succineidae examined in this study appear to form a monophyletic group. According to our data (Figs. 3 and 4), if *Catinella* is an evolutionarily meaningful genus, then future morphological investigation should reveal that *S. canella*, *S. lutulenta*, the undescribed species from Kauai, *S. rubella*, and *C. explanata* all belong within the genus *Catinella*. Given the current taxonomic placement of these taxa, however, *Catinella* is polyphyletic with *Succinea*.

Based on COI sequence data, the Hawaiian species currently placed in *Succinea* were polyphyletic. *O. hirasei* and *Neosuccinea kofai* fall between the island of Hawaii *Succinea* species and the Samoan *Succinea* species. This is not surprising, given that *Succinea* has a global distribution, and because species were generally described in and have remained in *Succinea* for lack of adequate taxonomic study. No taxonomic changes are suggested here. However, the Succineidae worldwide, particularly the Pacific taxa, which are severely understudied, require detailed morphological investigation followed by taxonomic revision.
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