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Evolution

Multiple origins of a spider radiation in Hawaii

(*Tetragnatha*/colonization/morphology/molecular phylogeny)

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ABSTRACT **The Hawaiian Islands are renowned for some of the most spectacular species radiations in the world. Most of these radiations have been attributed to single colonization events, although the evidence supporting monophyletic origins is often poorly resolved and/or ambiguous. Without a concrete understanding of the origins of species radiations, it is impossible to understand the phylogenetic pattern of species proliferation or the spectrum of morphological, ecological, and behavioral modifications attributable to a single colonist. In this study we examined the species radiation of the spider genus *Tetragnatha* in Hawaii. Unlike their mainland congeners, the Hawaiian *Tetragnatha* are extremely diverse in morphology, ecology, and behavior. We tested whether this diversity arose from a single or multiple colonization events. We coupled morphological (37 characters) and molecular (sequence from the 12S ribosomal subunit of mitochondrial DNA) approaches to assess the phylogenetic position of the Hawaiian *Tetragnatha* relative to continental congeners and to examine evidence for monophyly. We provide evidence that the Hawaiian *Tetragnatha* emanate from multiple origins. At least two independent species radiations, the "spiny-leg" clade and the web-building species *Tetragnatha stelarobusta* and *Tetragnatha acuta*, have arisen from one or more founder events. Two additional natural colonizations have resulted in the establishment of non-speciose lineages, as represented by *Tetragnatha hawaiensis* and *Doryonychus raptor*.**

Colonization of isolated islands involves both the arrival of viable propagules and their subsequent establishment. MacArthur and Wilson (1) modeled species numbers that would be expected on a given island and hypothesized a strong inverse relationship between species richness and distance from the source of colonists. The Hawaiian archipelago falls at the extreme end of this relationship, being the most isolated archipelago in the world. The chain is separated from the nearest continental land mass by nearly 4000 km of ocean and is noted for its lack of representation by many normally prominent biotic components. Before human occupation, the isolation of the islands proved to be a major barrier to colonization. However, among the small number of colonists that reached the archipelago, speciation has occurred repeatedly, often with such extraordinary magnitude that single colonists have given rise to large numbers of morphologically, ecologically, and behaviorally diverse species. The Hawaiian Islands are therefore characterized by phenomenally high numbers of species representing very few species groups (2) and provide some of the best illustrations of such species swarms, including both animals [e.g., drepaniid honeycreepers (3, 4), land snails (5), crickets (6), and *Drosophila* (7, 8)] and plants [e.g., beggar's ticks and tarweeds (9)].

Studies of these species radiations in the Hawaiian Islands have demonstrated their enormous potential for elucidating patterns and mechanisms of explosive speciation. However, a critical element to a comprehensive interpretation of these extraordinary radiations is whether the radiation is a consequence of a single or multiple introductions. Knowledge of the number of introductions (*i*) establishes the phylogenetic status of the species radiation, (*ii*) shows whether the range of morphological and ecological strategies that exist currently arose from a single source or whether part of this variation was "injected" into the community by multiple introductions, and (*iii*) allows events subsequent to colonization to be studied as replicated systems, in situations where closely related taxa are responsible for multiple colonization events.

However, the problem of identifying the number of colonists responsible for a given radiation has proved enigmatic. Only recently (50) have the appropriate tools been developed to assess the number of separate colonizations within a lineage by using phylogenetic systematics (10). This approach has been employed recently to establish the monophyly of the Hawaiian *Drosophila* (Drosophilidae, ref. 11), *Ptycta* (Psocidae, ref. 12), and silverswords (Asteraceae, ref. 13). Each of these cases provides evidence that a huge amount of morphological variability can arise during species diversification (14). Similar analysis of the Hawaiian *Scaptomyza* (Drosophilidae, ref. 11) suggests that the comparable diversity in this group is of multiple origin, although the evidence is not strong (15). Currently there is no definitive evidence for repeated invasions of a speciose genus in Hawaii.

The spider genus *Tetragnatha* is one of the most recent radiations to have been discovered in the Hawaiian Islands (16, 17). It is one of only four spider genera to be substantially represented in the Hawaiian archipelago (18). The Hawaiian *Tetragnatha* are extraordinarily diverse in morphology, ecology, and behavior, thus presenting a striking contrast to their extremely homogeneous congeners throughout the rest of the world (19). Included among the Hawaiian tetragnathids are groups of species that have relinquished web building and have developed either long leg spines (16) or elongate tarsal claws (20, 21) for raptorial feeding. Other groups build webs in specific habitats uncharacteristic of *Tetragnatha*, including among the foliage and bark of the forest canopy and among roots and moss on the forest floor (ref. 17 and unpublished data). Taken together, these numerous species dominate the niche of exposed vegetation for terrestrial invertebrate predators.

In this study we use the radiation of *Tetragnatha* in Hawaii to test the popular notion that such radiations tend to be monophyletic. A single introduction would provide further evidence of the extraordinary diversification possible after single founder events (14, 22). Multiple introductions of individuals of the same genus would allow comparison of the outcome of repeated founder events. We coupled morphological and molecular approaches to assess the phylogenetic

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Abbreviations: PTP, cladistic permutation tail probability; T-PTP, topology-dependent PTP.

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position of the Hawaiian *Tetragnatha* relative to continental congeners and to examine evidence for monophyly.

MATERIALS AND METHODS

The genus *Tetragnatha* is one of the largest genera of spiders, with ≈290 described species, excluding synonyms. The radiation of *Tetragnatha* in Hawaii comprises a large number of species, only 25 of which have been described (16–18, 23). We examined representatives of the genus from Hawaii and from the continents of Asia, Australia, and North America. The Hawaiian *Doryonychus raptor* is a highly modified species, and the sole representative of the genus is *D. raptor* from Kauai (18, 20, 21). However, the gross body morphology, eyes, and genitalic structure of *D. raptor* are typical of the genus *Tetragnatha* (H. W. Levi, personal communication). Because this species represents extreme specialization and because its relationship to the other Hawaiian spiders is obscure, we included it in our analysis.

Phylogenetic Analysis of Morphological Data. We scored a total of 37 morphological characters relating to the cheliceral armature and shape, leg spination and length, ocular pattern, cephalothoracic shape, and shape of the seminal receptacles in the female and to the cheliceral armature and shape and the palpal morphology of the male. (Data on characters and their states are available from the authors on request.) We used representatives of the two putative sister genera to *Tetragnatha* as outgroups: *Pachygnatha autumnalis* Keyserling and *Glenognatha heleios* Hormiga and Döbel. As representatives of continental *Tetragnatha*, we collected species from Queensland, Australia (*T. rubriventris* Doleschall from coastal vegetation, and *T. macilenta* L. Koch and *T. valida* Keyserling from riverside); Guilin, China (*T. praedonia* L. Koch and *T. maxillosa* Thorell from lakeshore); eastern North America (*T. versicolor* Walckenaer from Tennessee lakeshore); and Puerto Rico [*T. pallescens* F. P. Cambridge and *T. nitens* (Audouin in Savigny) from lakeshore]. We also scored characters from six endemic Hawaiian tetragnathids: three were web-builders, with two (*T. stelarobusta* and *T. acuta*) endemic to the Maui Nui island complex (17) and one (*T. hawaiensis*) that occurs on all the major island groups. Three were non-web-builders, of which two (*T. waikamoi* from Maui and *T. perreirai* from Oahu) behave as active, cursorial predators and have developed long spines on their legs (16) and one (*D. raptor* from Kauai) uses long tarsal claws to impale prey (18, 20, 21). We also included Hawaiian representatives of the circumtropical species *T. mandibulata* Walckenaer, which probably has been recently introduced to the archipelago through human activity (18). Characters were analyzed as unordered states by using Fitch (24) parsimony in PAUP 3.0 (25). The outgroups were used to root the trees.

Phylogenetic Analysis of Mitochondrial DNA (mtDNA) Data. Using PCR, we amplified and sequenced a 207-base section of mtDNA coding for most of the third domain of the 12S ribosomal subunit. Methods are given in detail elsewhere (26). Sequences were aligned by eye to the published *T. mandibulata* sequence. We compared sequences from four species of *Tetragnatha* from outside Hawaii—*T. mandibulata, T. pallescens, T. nitens*, and *T. versicolor*—and six species from Hawaii—*D. raptor, T. hawaiensis, T. stelarobusta, T. acuta, T. waikamoi*, and *T. perreirai*. Using *D. raptor* as the outgroup (based on morphological evidence), we conducted a phylogenetic analysis over all 207 bases, again using PAUP 3.0, without weighting, and with various types of weighting that emphasize transversion differences. Gaps in the alignment were ignored.

RESULTS AND DISCUSSION

Phylogenetic Analysis of Morphological Data. Character changes were weighted equally (compensatory weighting according to number of character states), and a branch and bound search gave three minimum-length (109) trees; consistency index, 0.503, retention index, 0.626 (Fig. 1*A*). The trees differed only in their placement of the two Hawaiian species *T. stelarobusta* and *T. acuta* relative to the *T. waikamoi–T. perreirai* group. Subsequent reweighting by successive approximations (characters weighted by maximum value of the rescaled consistency indices, refs. 30 and 31) gave two minimum-length trees after a single iteration, with a consensus identical to Fig. 1*A*; consistency index, 0.717, retention index, 0.814. Bootstrapping (1000 replications) was used (with all character changes equally weighted) to assess confidence in the analysis.

Tests for Nonmonophyly in Morphological Data. In order to evaluate whether the observed hierarchical structure in the data might represent random character covariation, Faith and Cranston (32) developed tests of cladistic permutation tail probability (PTP) tests. Recent modifications of these tests have allowed specific phylogenetic topologies to be tested, specifically as they relate to monophyly, by using topology-dependent PTP tests (T-PTP test; ref. 33). We used T-PTP tests to investigate nonmonophyly of the Hawaiian tetragnathids. We generated a set of 1000 random data sets (character states chosen at random across taxa without replacement) and determined the phylogenetic length that these data sets would produce under conditions of monophyly and nonmonophyly. For each randomized data set we calculated the length difference under both conditions. We then determined the proportion of all data sets for which the length difference was as large as or larger than that for the original data. We examined three conditions of monophyly of the Hawaiian *Tetragnatha* (Table 1). We constrained the topology so that the following were included in a monophyletic group with *T. perreirai, T. waikamoi, T. stelarobusta*, and *T. acuta*: (*i*) *D. raptor* and *T. hawaiensis* or (*ii*) *T. mandibulata* and *T. hawaiensis*. Both these constraints gave significantly longer trees, providing strong support for nonmonophyly of these taxa. (*iii*) When only *T. hawaiensis* was constrained to be included with the other four Hawaiian *Tetragnatha*, the tree was not significantly longer (P = 0.326). Based on the morphological data set alone, therefore, the nonmonophyly of *T. hawaiensis* and the *T. perreirai–T. waikamoi–T. stelarobusta–T. acuta* group does not have strong support. However, confidence in the nonmonophyly of *T. hawaiensis* and these other Hawaiian *Tetragnatha* could be gained if the phylogenetic pattern were repeatable on the basis of an independent sample of characters (34).

Phylogenetic Analysis of mtDNA Data. There were 95 variable positions (55 informative) among the 10 species (Fig. 2). Parsimony analysis suggested one best tree with a length of 155 steps and a consistency index of 0.813 (Fig. 1*B*). Neighbor-joining trees (35) and a maximum likelihood analysis using PHYLIP (36) gave trees with identical topologies to the PAUP tree. In all three analyses, *T. pallescens* fell within the group of five Hawaiian *Tetragnatha*, and the Hawaiian *D. raptor* was as distant from this group as were the continental species *T. nitens* and *T. mandibulata*. The tree topology is exactly the same if transversions are weighted 5× transitions or if transitions are ignored altogether. The molecular data suggest that there are four major groups of Hawaiian tetragnathid spiders: (*i*) the spiny-leg group (e.g., *T. perreirai* and *T. waikamoi*), (*ii*) a web-building group (e.g., *T. acuta* and *T. stelarobusta*), (*iii*) the single species *T. hawaiensis*, and (*iv*) the divergent species *D. raptor*.

Genetic distances among these four groups were high (Table 2). *D. raptor* showed 25–28% sequence difference

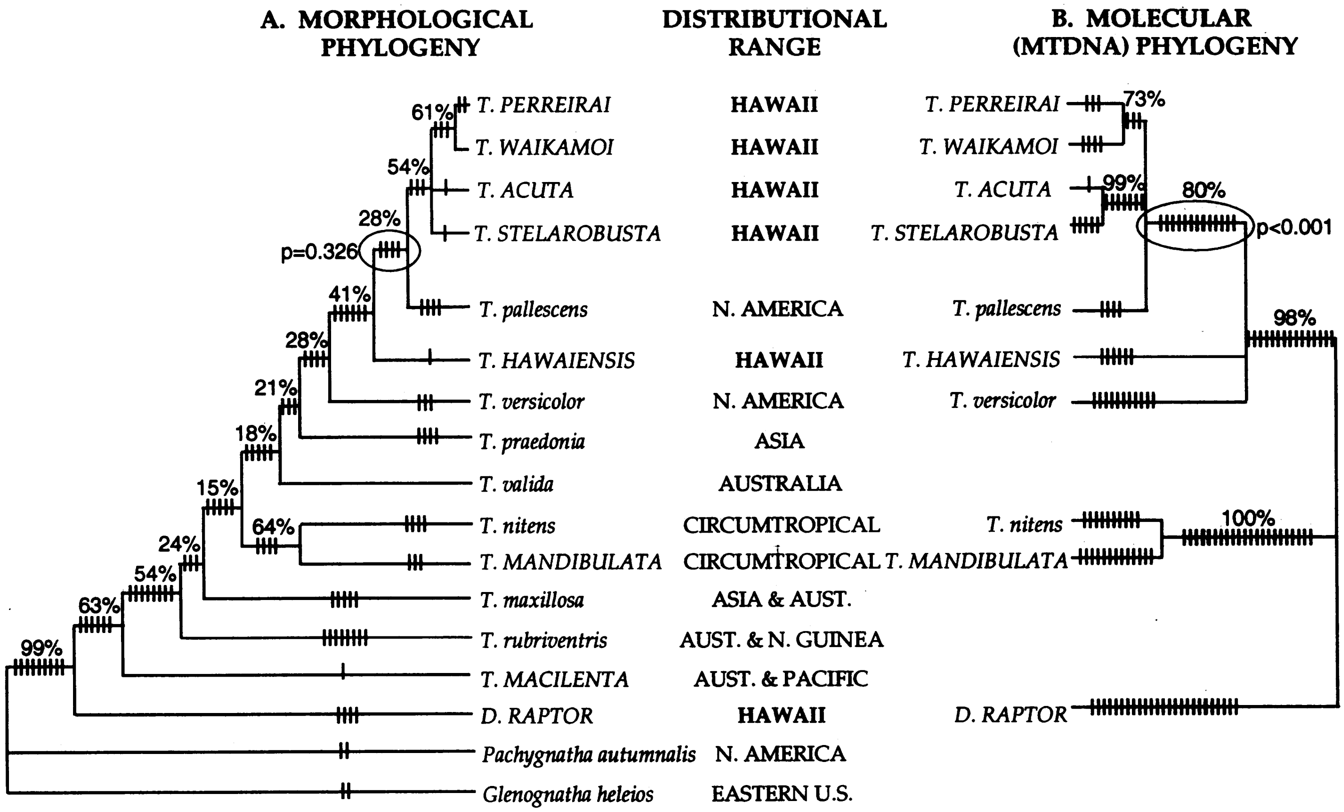

FIG. 1. Phylogeny of representative *Tetragnatha* from continental areas and the Hawaiian Islands, shown by strict consensus trees based on morphological (*A*) and molecular (mtDNA) (*B*) characters. *Pachygnatha autumnalis* and *Glenognatha heleios* are the outgroups. Species found in Hawaii are given in uppercase letters; all of these species except *T. mandibulata* and *T. macilenta* are confined to the Hawaiian Islands. Distributional ranges are given for each species (16, 19, 27–29). Bars indicate single character changes. Percentages are bootstrap values for each node. Topology-dependent cladistic permutation tail probability (T-PTP) values are given for the *T. hawaiensis–T. pallescens* node (circled).

from the other Hawaiian species [distances based on the Kimura two-parameter model using the equations of Li *et al.* (37)]. *T. hawaiensis* was 12–14% different from other Hawaiian *Tetragnatha*, and the spiny-leg clade was 7–9% different from the web builders *T. acuta* and *T. stelarobusta*. The most closely related species were *T. stelarobusta* and *T. acuta*, which differed by only 1.5% of their 12S sequence. By comparison, the maximum sequence diversity (based on the 16S ribosomal subunit) within the Hawaiian *Drosophila* is 4% (38).

Tests for Nonmonophyly in Molecular Data. As for the morphological data above, the molecular results suggest that the Hawaiian tetragnathid spiders are not a monophyletic group and that multiple introductions to the Hawaiian archipelago have occurred. To test the robustness of these conclusions, the DNA data were used to calculate maximum likelihood (39) for a number of phylogenies that force the Hawaiian taxa to be monophyletic. The maximum likelihood value for the best tree (Fig. 1*B*) was −982.1. Significantly lower maximum likelihood values were obtained both when *T. hawaiensis* was forced to be monophyletic with *T. perreirai*, *T. waikamoi*, *T. acuta*, and *T. stelarobusta* (log-likelihood, −1006.7) and when all six Hawaiian species (i.e., including both *T. hawaiensis* and *D. raptor*) were forced together (log-likelihood, −1035.8) (see ref. 39). We tested the significance of the nonmonophyly of the Hawaiian tetragnathid spiders, again using T-PTP tests as outlined above for the morphological data. Each of the tests provided strong support for the nonmonophyly of *T. hawaiensis* and the other Hawaiian *Tetragnatha* (Table 1).

These analyses confirm the close position of the continental species *T. pallescens* to the Hawaiian spiny-leg clade and the *T. acuta–T. stelarobusta* web-building group. The lowland species *T. hawaiensis* falls significantly outside this cluster of species, with the morphologically, ecologically, and behaviorally divergent *D. raptor* as a distant relative.

Comparison of Morphological and mtDNA Data. The implied repeatability of the phylogenetic pattern generated from morphological characters and mtDNA sequences increases confidence in the polyphyly of the Hawaiian tetragnathids.

Table 1. Results of PTP tests to test for nonmonophyly of Hawaiian tetragnathid spiders

Topological constraint (taxa forced into monophyly)*	Data	Observed length under monophyly	Length under constraint for shortest-length trees†	PTP value (significance, *P* value)
T. hawaiensis	Morphological	195	18	<0.001
and *D. raptor*	Molecular‡	169	14	<0.001
T. hawaiensis	Morphological	178	1	0.326
	Molecular‡	160	5	<0.001
T. hawaiensis	Morphological	202	25	<0.001
and *T. mandibulata*	Molecular‡	189	34	<0.001

*Species forced into monophyly with the endemic Hawaiian species *T. perreirai*, *T. waikamoi*, *T. acuta*, and *T. stelarobusta*.

†Lengths of the shortest nonmonophyletic trees are 109 for the morphological data and 155 for the molecular data.

‡Only a subset of 10 of these species was used in the molecular analyses (see text).

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                                                                 50                                               100
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T.mandibulata   TAC*TTTTTTATAAATTTTATATACCTCCGTCC**AGAATAAATTTTTAATATTTTATTCAAAATAATATTATAATAATTTAGGTAAAGGTGTAGACTTT
T.acuta         C.......AAT..T............G.....T..T.....G..CA.A..*.....G..........A...C...A..................A...A.
D.raptor        ......GGA.T..T..........T......AT..C.....T..C.AA.T*..A.......C.............A......................AC
T.hawaiensis    C.......AATA.T............G....TT...........AAAA..*................AT..C..GA..................A...A.
T.nitens        C..........A...................AT........G....A..................................................A..
T.pallescens    C.......AAT..T............G.....T..T........CAAA..*................A...C...A..................A...A.
T.perreirai     C.......AAT..T............G.....T..T.....G....AA..*.............A..A...C...A..................A...A.
T.stelarobusta  C.......AAT..T............G.....T..T.....G..CA.A..*.....G..........A...C...A..................A...A.
T.versicolor    ......C.ACTA.T............G....TT...A.......A.AA..*........TTT..A..A...C...A..C...............A...A.
T.waikamoi      C.......ACT..T............G.....T..T.....G.CC.AA..*.............G..A...C...A..................A...A.
                                                               150                                               200
                         •         •         •         •         •         •         •         •         •         •
T.mandibulata   AAATTAG*TTTAAATGTGTTACATTAAAAATTATTTAAGAATTATTTTT*TATAACAATATATGAAAGAGGATTTATAAGCTACTTTTTAATTAAAATTTTAACTTG
T.acuta         CT.AA...A.G......A............AA.......G..C.AA..AAA...TA.T.T..A....A............*..T.A.............AA..T...
D.raptor        .TCCA.....A......A............CA.......GC...A.G.A...A.T.GCAT...A...AC...........*..TAA...TT......AAAA.GT...
T.hawaiensis    .T.AG...A.A......A............AA.......G....AAC.A.A.C.TAGT.T..A....A............*..TAA...T.........A...T...
T.nitens        ..T..........................TC..........A..A.A.....A..TG.*T..G.................*..T...................TA..
T.pallescens    TT.AA...A.A......A..........T.AA.......G....AA..A.A.A.TA.T.TC.C....A............*..T.A.........T...AA..T...
T.perreirai     TT.AA...ACA......A..........T.AA.......G..CGAG..A.A...TA.T.TC.A....A............*..T.A.........T...AA..T...
T.stelarobusta  CT.AA...A.G......A............AA.......G..C.AA..AAA...TA.T.C..A.................*..T.A......C......AA..T...
T.versicolor    GT.AA............TC.........T.AA.A..T.AGGAATAA.A..A.CT.T.TAT..A....AG...........*..T.A...T.....T...AA..T...
T.waikamoi      TT.AA...A.A......A..........T.AA.......G..CGGA..A.A...TA.T.TC.A....A............*..T.A.........T...AA..T...
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FIG. 2. mtDNA sequences of 10 tetragnathid spiders for 207 bp of the 12S ribosomal RNA gene (scale in units of 10). See ref. 26 for details.

Phylogenetic bootstrap values are much higher for the molecular data, which is commonly a consequence of the lower character/taxon ratios in the morphological as compared to the molecular data (40). Also, bootstrap values are highly conservative estimates of phylogenetic accuracy and, because biases differ from one study to the next, direct comparison among studies cannot be made (34). Because of these uncertainties about bootstrap values, we have provided several tests of artificial phylogenies that show that the data reject the hypothesis that the Hawaiian tetragnathids are monophyletic.

Biogeographic Implications. The phylogenetic analyses presented in the current study suggest that the Hawaiian tetragnathids are of multiple origin. Moreover, one or more founder events may have given rise to at least two independent species radiations, the spiny-leg clade (as represented by *T. waikamoi* and *T. perreirai*) (16) and the web-building species *T. stelarobusta* and *T. acuta* (both of which may represent species clades). In addition, it appears that two apparently "natural" colonizations may have resulted in the establishment of nonspeciose lineages, as represented by *T. hawaiensis* and *D. raptor*. Failure of secondary colonists to proliferate may arise from the effects of competition with congeners of an established species (41). Colonists might avoid the effects of competition through evolutionary innovations. Although the number of examples we have is small, we note that both instances of species proliferation are associated with evolutionary innovation, coupled with ecological and/or behavioral shifts. Continental *Tetragnatha* are characterized by their riparian habitat and sedentary, web-building foraging behavior (42). Among the Hawaiian endemics, the spiny-leg clade (including *T. waikamoi* and *T. perreirai*) comprises 12 species, all of which have abandoned the web-building behavior characteristic of the genus. In this clade, species appear to have proliferated as a result of repeated colonization and isolation on different islands along the Hawaiian chain (43). The diverse sister group of at least 50 web-building species (including *T. stelarobusta* and *T. acuta*) has exploited specialized forest microhabitats and may have speciated between favorable habitat patches within an island. An exception to the generalization that species formation is related to evolutionary innovation is the single species, *D. raptor*, which has abandoned web building and developed long claws at the ends of the tarsi of leg pairs I and II, which it uses to impale prey (20, 21). However, *D. raptor* has a relatively ancient phylogenetic position, is extraordinarily specialized in foraging behavior, and is confined to very small pockets of forest on the oldest of the main Hawaiian islands (Kauai). Thus, it may be a relic of a previously diverse radiation of *Tetragnatha* (44).

Table 2. Genetic distances among different species of Hawaiian tetragnathids

	Tpe	*Tw*	*Ta*	*Ts*	*Tp*	*Th*	*Tv*	*Tm*	*Tn*	*Dr*
T. perreirai	—	4	7	9	5	13	21	29	31	28
T. waikamoi	0	—	7	8	5	14	21	30	30	28
T. acuta	2	2	—	2	6	10	23	26	29	26
T. stelarobusta	2	3	0	—	7	12	25	26	30	28
T. pallescens	2	2	2	2	—	10	21	27	29	25
T. hawaiensis	6	6	4	4	6	—	22	35	27	25
T. versicolor	11	10	13	13	3	12	—	38	37	36
T. mandibulata	17	16	15	15	17	14	20	—	13	32
T. nitens	19	19	19	19	19	18	20	5	—	30
D. raptor	16	15	15	15	15	16	20	18	17	—

For each pairwise comparison, corrected percent differences appear in upper right of matrix, and percent transversions in lower left. At tops of columns, *Tpe* = *T. perreirai*, etc.

T. hawaiensis is the only endemic *Tetragnatha* species in the Hawaiian Islands that has not undergone radical shifts in its behavior or ecological affinities. Representatives of this small group (between one and four species) are widespread through the islands, associated with lowland riparian habitats. It may be the failure to develop any behavioral or ecological innovations that has prevented the radiation of this group. However, such an assertion begs the question why. The group may be a relatively recent arrival to the Hawaiian Islands and has had insufficient time to undergo ecological shifts and proliferation. Alternatively, gene flow between the islands may be acting to prevent differentiation (45).

T. mandibulata (and *T. macilenta* for the morphological analysis) are the only Hawaiian *Tetragnatha* we included that are found outside the Hawaiian Islands (Fig. 1). In the Hawaiian Islands, both species are confined to highly disturbed riparian and coastal habitats. Their widespread distribution and occupation of anthropogenically modified habitats support the contention that the species have gained access to the islands through recent human activity (46). Among the taxa we examined, the closest relatives to the endemic Hawaiian *Tetragnatha* are species from North

America (Fig. 1). However, the genus *Tetragnatha* is large and of worldwide distribution. Positive identification of the source(s) of the Hawaiian fauna will require a more comprehensive survey.

The biology of tetragnathid spiders is ideally suited for multiple colonizations. The genus *Tetragnatha* has been found on every habitable land mass examined to date. The ubiquity of the genus, as well as the absence of any known species radiation outside the Hawaiian Islands, may be a consequence of its dispersive capabilities. Aerial sampling has shown the genus *Tetragnatha* to comprise 96% of the aerial spider plankton collected offshore (400 km from land in the China Sea) (47). This extraordinarily high representation of *Tetragnatha* over the open sea suggests that the genus might be one of the most important for island colonization by spiders. Indeed, the genus was found to be among the first and most persistent colonists on mangrove islands in the Florida Bay (48). In addition, given the relative sizes and species numbers of continental versus Hawaiian source areas alone, multiple origins of the Hawaiian *Tetragnatha* would seem more likely than back colonization to the continental land mass (which is an alternative explanation for apparent polyphyly) (49).

In conclusion, the Hawaiian tetragnathid spider lineage appears to be derived from multiple origins. At least two groups (which may have arisen from one or more founders) are represented by many species inhabiting diverse habitats, while others may be monospecific. There is also some indication that species proliferation is connected to evolutionary innovation, coupled with ecological and/or behavioral shifts.

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