Thorn-like prickles and heterophylly in *Cyanea*: Adaptations to extinct avian browsers on Hawaii?

(anti-herbivore defenses/geese/leaf form/moa-nalos/paedomorphosis)

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ABSTRACT   The evolution of thorn-like structures in plants on oceanic islands that lack mammalian and reptilian herbivores is puzzling, as is their tendency toward juvenile-adult leaf dimorphism. We propose that these traits arose in *Cyanea* (Campanulaceae) on Hawaii as mechanical and visual defenses against herbivory by flightless geese and goose-like ducks that were extirpated by Polynesians within the last 1600 years. A chloroplast DNA phylogeny indicates that thorn-like prickles evolved at least four times and leaf dimorphism at least three times during the last 3.7 million years. The incidence of both traits increases from Oahu eastward toward younger islands, paralleling the distribution of avian species apparently adapted for browsing. The effectiveness of visual defenses against avian browsers (once dominant on many oceanic islands, based on the vagility of their ancestors) may provide a general explanation for insular heterophylly: the other islands on which this previously unexplained phenomenon is marked (New Zealand, New Caledonia, Madagascar, Mascarene Islands) are exactly those on which one or more large flightless avian browsers evolved.

Cyanea (Campanulaceae: Lobelioideae), the largest genus of plants endemic to the Hawaiian archipelago, has undergone striking adaptive radiations in growth form, leaf size and shape, and floral morphology (1–5). Most of its 55 species are unbranched or sparsely branched trees and treelets of mesic and wet forests at roughly 1000- to 2000-m elevation; 89% occur on only one island each, and all appear to have coevolved with honeycreepers (Fringillidae: Drepanidini) and other endemic birds that served as pollinators and frugivores. Perhaps most remarkably, 18 species possess thorn-like prickles (conical outgrowths of underlying ground tissue up to 1 cm in length) on their leaves and/or stems, especially on juvenile shoots (Fig. 1). These prickles are especially dense on leaf veins and developing shoot apices (1). Many species also exhibit developmental heterophylly (i.e., heteroblasty), with juvenile leaves being more deeply lobed or divided than those of adults (6, 7). No compelling explanation has been advanced to account for the adaptive significance of the latter phenomenon—one instance of a general tendency toward heterophylly on oceanic islands (8)—and *Cyanea*'s prickles are an evolutionary enigma, given the absence of native mammalian or reptilian browsers in the archipelago (9). Carlquist (1–3) suggested that they may have evolved to deter herbivory by endemic land snails and specifically noted succinids. Yet succinid snails have never been observed to consume lobelioid leaves and, like achatinellid snails (the largest group of terrestrial mollusks native to Hawaii), usually graze on epiphyllic films of fungi and algae instead (refs. 10 and 11; M. G. Hadfield, personal communication).

FIG. 1. Juvenile shoots of *Cyanea solanacea* on Molokai (Kamakoa Reserve, The Nature Conservancy), showing dense aggregation of thorn-like prickles (≈1 cm long) and deeply lobed juvenile foliage. These shoots are sprouts from an adult axis (visible at the bottom of the photograph) that had been mechanically damaged by feral pigs, a recently introduced alien herbivore. Note the loss of prickles toward the tip of the juvenile shoots, signaling the beginning of the shift toward adult morphology.

As a basis for studying adaptive radiation in *Cyanea* in a noncircular fashion, we (12) developed a molecular phylogeny for this group and other fleshy-fruited lobelioid genera endemic to Hawaii, based on a cladistic analysis of restriction-site variation in chloroplast DNA. Our data indicate that *Cyanea* is composed of two clades, one characterized by orange fruits, and the other by purple fruits (Fig. 2). The endemic genus *Rollandia*, which differs from *Cyanea* in having the staminal tube adnate to the corolla, is wholly embedded within the orange-fruited clade and includes three additional species with prickles. Fully 52 of the 63 species in *Cyanea–Rollandia* bear orange fruits (4) and presumably belong to the orange-fruited clade. Most of the dispersal events inferred from our molecular phylogeny (Fig. 3) involve movements from one island to the next younger island to the southeast, paralleling the pattern seen in other Hawaiian groups, such as *Drosophila* (13) and the silversword alliance (14, 15). This trend is thought to reflect the greater chance of establishment and subsequent radiation by colonists on nearby, newly

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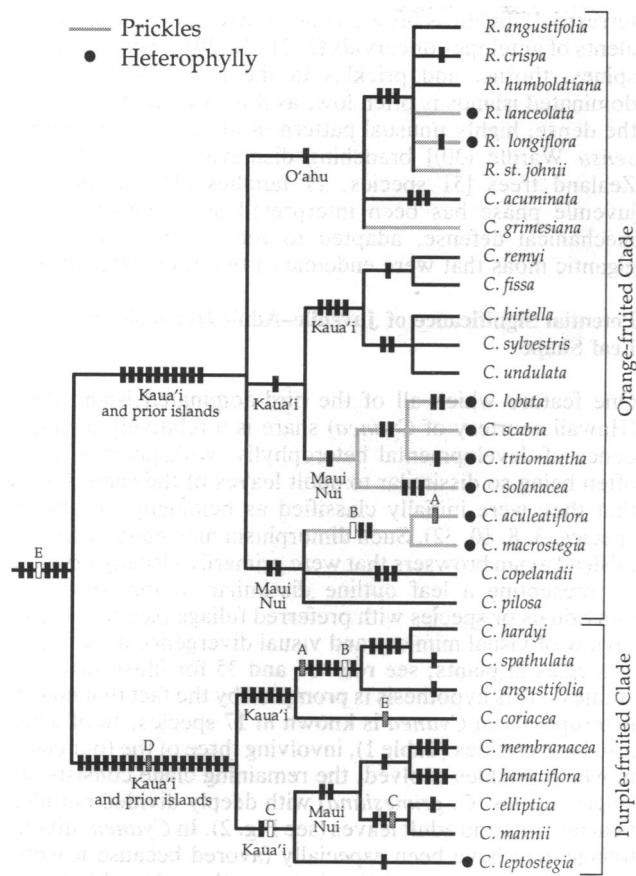‡Present address: Department of Botany, Smithsonian Institution, Washington, DC 20560.

FIG. 2. Possession of prickles (gray lines) and marked juvenile-adult heterophylly (●) superimposed on the phylogeny of *Cyanea–Rollandia* derived by Givnish *et al.* (12). Vertical bars indicate synapomorphies, reflecting shared derived chloroplast DNA restriction-site gains or losses. Hollow bars indicate convergent site losses; gray bars, convergent site gains; and solid bars, unreversed site gains or losses. Prickles arose at least four times independently (indicated in gray); heterophylly evolved in two of these lineages, and co-occurred with prickles in 13 of 14 instances (see text). Several prickle-bearing species are extinct or extremely rare and their chloroplast DNA has not been examined; most of these species seem morphologically related to the *C. solanacea* or *C. aculeatiflora* clades (7, 12). Including them in the analysis could only increase or leave unchanged the number of independent evolutionary origins of prickles.

formed, relatively unoccupied islands created as the oceanic crust moves past the Hawaiian "hot spot" at 8.6 cm/year (16). The repeated creation and destruction of habitat pockets and associated populations by lava flows may accelerate speciation and genetic evolution on the youngest islands (17).

Origin of Prickles and Their Potential Adaptive Significance

Prickles arose independently at least four times in *Cyanea–Rollandia*, all within the orange-fruited clade (Fig. 2), and are unique in the Lobelioideae (1). It is remarkable that the great majority of prickle-bearing species occur on relatively young islands and that the fraction of species with prickles increases toward younger islands: 0 of 16 species on Kauai bear prickles, 5 of 14 on Oahu, 11 of 26 on Maui Nui [including Maui, Molokai, and Lanai, all connected by exposed sea bottom during the Pleistocene (18)], and 6 of 12 on Hawaii (Fig. 4). One explanation for this pattern might be that a group of terrestrial herbivores appeared first on Oahu and then moved down the chain as younger islands appeared to the southeast, evolving into an increasingly potent set of herbivores as time proceeded. An alternative hypothesis—more complex, but we
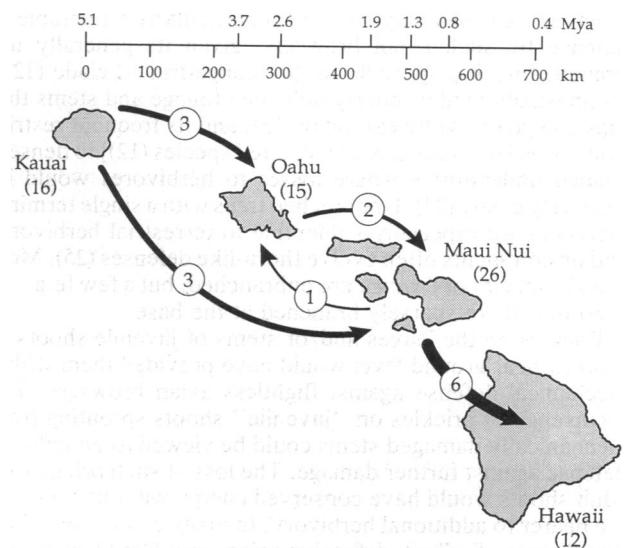

FIG. 3. Minimal number of interisland dispersal events for *Cyanea–Rollandia* inferred by Givnish *et al.* (12), illustrating tendency for dispersal from one island to the next younger island in the archipelago. Width of each arrow is proportional to the number of dispersal events between the corresponding pair of islands; the number of species found on each island or island group is indicated in parentheses. Mya, million years ago.

believe more compelling—would have the herbivores arrive on Oahu [above water for the last 3.7 million years (16)] and cause the origin of prickly lineages of *Cyanea*. Subsequently, the herbivores may have spread throughout the chain unopposed, but *Cyanea* dispersed mainly to newly formed islands to the southeast (12); presumably, members of prickly lineages would have been more likely to establish themselves, radiate, and then produce colonists that moved on to the next island, favoring an increase in the incidence of prickliness by species-level selection (19) as well as by traditional natural selection operating within populations. Both proposed mechanisms agree in having the herbivores arrive (or at least exert selection) first on Oahu.

But what were those herbivores? We propose that *Cyanea* prickles evolved as a mechanical defense against browsing by the extinct flightless geese and goose-like ducks ("moa-nalos") that were endemic to Hawaii and then exterminated during the last 1600 years by the arriving Polynesians (20). Eight species of these birds, as well as a series of volant relatives, have recently been described by Olson and James (21) from subfossil remains in lava tubes and calcified sand dunes; they were relatively massive birds, with a vertical reach of nearly 1 m. Goose herbivory can exert widespread damage and profound ecological effects in certain ecosys-
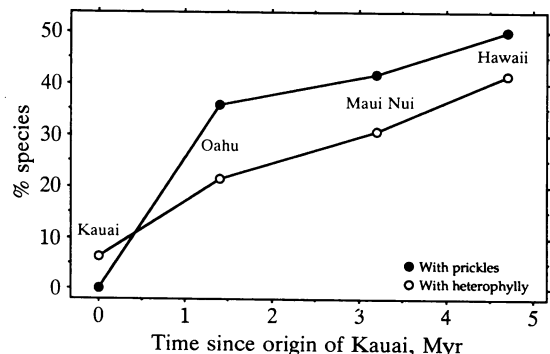

FIG. 4. Percentages of species of *Cyanea–Rollandia* with prickles (●) or with heterophylly (○), plotted as a function of the time of island origin, in millions of years since the origin of Kauai.

tems (22). *Cyanea* may have been particularly vulnerable to damage by such avian browsers, given its generally unbranched habit [especially in the orange-fruited clade (12)], its unusually tender, poorly defended foliage and stems that pigs and goats avidly eat today (23), and its frequent restriction [especially among orange-fruited species (12)] to densely shaded understories where losses to herbivores would be relatively costly (24). Unbranched trees with a single terminal meristem are especially vulnerable to terrestrial herbivores and on continents often evolve thorn-like defenses (25). Most prickly species of *Cyanea* are unbranched, but a few [e.g., *C. marksii* (1)] are sparsely branched at the base.

Prickles on the leaves and/or stems of juvenile shoots of *Cyanea* near ground level would have provided them with a mechanical defense against flightless avian browsers. The recurrence of prickles on "juvenile" shoots sprouting from mechanically damaged stems could be viewed as an induced defense against further damage. The loss of such prickles on adult shoots would have conserved energy without exposing the bearer to additional herbivory. In many continental plant genera (e.g., *Smilax*), defensive spines (modified leaves) are often borne only near ground level, where plants are vulnerable to terrestrial mammalian browsers. Several woody plants in Central America bear such spines and prickles up to 3 m or more above the ground, presumably defensive adaptations to a mammalian megafauna extirpated at the end of the Pleistocene (26). The retention of such defenses for 10,000 years after the Central American megafauna disappeared suggests that *Cyanea* might easily have retained its prickles for the much shorter period (<1600 years) following the extinction of flightless geese and moa-nalos.

Of the eight flightless avian browsers formerly found in the Hawaiian archipelago, only one (*Chelychelynechen quassus*) occurred on Kauai, as did a flying relative of the nene (*Branta sandvicensis*) (21). These Kauaian species may not, however, have exerted much pressure on *Cyanea–Rollandia*. The nene occurs primarily in rather open habitats today and feeds on grass, other herbage, and fruits. *Chelychelynechen* possessed a remarkable tortoise-like bill with a linear occlusion, unlike that of the other flightless geese and moa-nalos (21); we infer that it may have been more adapted to grazing than browsing. Other moa-nalos had mandibles and maxillae with tooth-like projections (which would help shear twigs) that were strongly decurved. Decurved mandibles and maxillae increase the range of cutting forces exerted along their length, resulting in a secateur-like action (see ref. 27), and may be better adapted than linear mandibles for handling the combination of soft leaves and hard twigs that browsers consume. Comparative morphology supports this view: the extinct moas of New Zealand, identified as browsers by fossilized coprolites, also possessed decurved mandibles (27, 28); decurvature was most strongly developed in the largest species, which presumably would have consumed the coarsest mix of twigs and leaves. In the Hawaiian archipelago, the seven flightless avian browsers [*Thambetochen, Ptaiochen, Geochen*, and unnamed taxa (browsing in the last has been inferred from body size)] other than *Chelychelynechen* are known only from the younger islands, with two species each on Oahu, Maui Nui, and Hawaii. These are just the islands to which prickly species are restricted. It is impossible to exclude the chance that further paleontological research may uncover an extinct avian browser on Kauai (where only one fossil site is now known); however, the current data indicate a parallel distribution of prickly *Cyanea* and flightless browsing birds, in accord with our hypothesis.

Several extinct groups of birds (i.e., moas on New Zealand; elephant birds on Madagascar; *Sylviornis* on New Caledonia; possibly rails, dodos, or solitaires on the Mascarene Islands) were able to disperse to oceanic islands inaccessible to nonflying mammals and then evolve into terrestrial, flightless browsers and grazers, the insular equivalents of antelopes or cervids (2, 21, 27–29). The incidence of spines, thorns, and prickles in the floras of these bird-dominated islands is often low, as it is in Hawaii. However, the dense, highly unusual pattern of divaricate [filiramulate *sensu* Wardle (30)] branching displayed by several New Zealand trees [51 species, 21 families (31)] during their juvenile phase has been interpreted as a similar kind of mechanical defense, adapted to reduce browsing by the gigantic moas that were endemic to that archipelago (28).

Potential Significance of Juvenile–Adult Dimorphism in Leaf Shape

One feature which all of the bird-dominated island floras (Hawaii courtesy of *Cyanea*) share is a relatively high incidence of developmental heterophylly, with juvenile leaves often being so dissimilar to adult leaves of the same species that they were initially classified as belonging to different species (3, 8, 10, 32). Such dimorphism may have evolved to mislead avian browsers that were primarily visually oriented, by presenting a leaf outline dissimilar to that of related individuals or species with preferred foliage (see ref. 33 for a review of visual mimicry and visual divergence as defensive strategies in plants; see refs. 34 and 35 for illustrative case studies). This hypothesis is prompted by the fact that marked heterophylly in *Cyanea* is known in 17 species, 16 of which also bear prickles (Table 1), involving three of the four clades in which prickles evolved; the remaining clade consists of a single species (*C. grimesiana*) with deeply divided but identical juvenile and adult leaves (see Fig. 2). In *Cyanea*, divided foliage may have been especially favored because it would result in a closer association between the vulnerable lamina and the defensive prickles on leaf veins and/or rachises.

This hypothesis would explain why juveniles, near ground level and within range of flightless avian browsers, bear "unusual" foliage dissimilar to that of adults (and juveniles

Table 1. Occurrence of prickles and marked juvenile–adult heterophylly in species of *Cyanea–Rollandia*, together with their geographic distribution

Prickles	Heterophylly	Geographic distribution*
C. aculeatiflora		M
C. asplenifolia	*C. asplenifolia*	M
C. grimesiana		O, Mo, L, H
C. horrida	*C. horrida*	M
	C. leptostegia	K
C. lobata	*C. lobata*	M, L
C. marksii	*C. marksii*	H
C. macrostegia†		M, L
C. mceldowneyi	*C. mceldowneyi*	M
C. pinnatifida	*C. pinnatifida*	O
C. platyphylla	*C. platyphylla*	H
C. quercifolia	*C. quercifolia*	H
C. scabra		M
C. shipmanii	*C. shipmanii*	H
C. solanacea	*C. solanacea*	Mo, M
C. solenocalyx	*C. solenocalyx*	Mo
C. stictophylla	*C. stictophylla*	H
C. tritomantha	*C. tirtomantha*	H
C. truncata		O
R. lanceolata		O
R. longiflora		O
R. st.-johnii		O

Data were compiled from refs. 4, 6, and 7.
*K, Kauai; O, Oahu; Mo, Molokai; L, Lanai; M, Maui; H, Hawaii; Maui Nui, Mo + L + M + Kahoolawe.
†Roughly hispid, but no thorn-like prickles present.

of other *Cyanea*) and why oceanic islands, colonized by birds that became the dominant terrestrial herbivores, have floras with a relatively high incidence of developmental heterophylly. Many of the divaricately branched juveniles of New Zealand woody plants, apparently adapted to reduce herbivory by the extinct moas, have leaves that are markedly divergent from adults of the same species and appear to visually mimic leafless branches and/or the foliage of other plant species (28). One of the three native species of Hawaiian plants outside *Cyanea–Rollandia* that bears thorn-like organs (*Solanum anomala*) also shows marked juvenile–adult leaf dimorphism (5).

Selection for visual divergence may have provided the engine needed to drive the neotenic evolution of leaf form seen in *C. solanacea* and its relatives (Fig. 5), brilliantly documented by Lammers (7). A series of five closely related species, endemic to increasingly younger areas ranging from Molokai to Hawaii, share a pattern in which (*i*) the juvenile foliage of each species is more divided than its adult foliage, (*ii*) the adult foliage of each species closely resembles the juvenile foliage of the preceding species in the series, and, hence, (*iii*) the juvenile foliage of each species in the series is progressively more divided. Continued selection for visually divergent leaf outlines could have helped to generate such a pattern, by favoring retention of visually divergent foliage in adults while promoting even greater visual divergence in juveniles of the same species. Such a process, involving an interplay between selective pressures and developmental constraints, might proceed with a few simple heterochronic shifts (36) in leaf (and prickle) development, entailing changes at only one or a few loci and resulting in increased expression of the juvenilized characters of leaf division and prickliness.

Alternative Hypotheses

Prickles. Plausible alternative hypotheses for the origin of prickles in *Cyanea* seem few, if any. The large size of prickles

C. profuga   C. solanacea   C. solanacea   C. asplenifolia   C. shipmanii
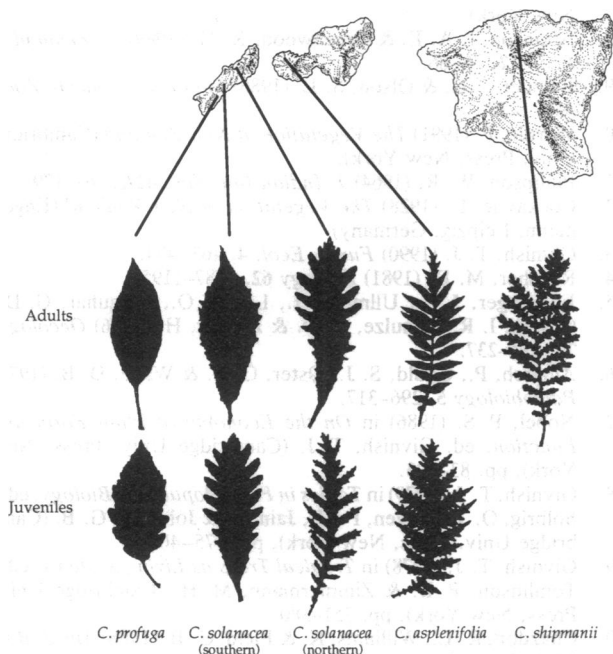   (southern)   (northern)

FIG. 5. Apparent paedomorphosis of leaf form in a suite of species occupying a sequence of progressively younger terrains from southeastern Molokai to Mauna Kea on Hawaii (redrawn from ref. 7). Note that the juvenile foliage of each species is more divided than the adult foliage of the same species and that the adult foliage of each species strongly resembles the juvenile foliage of the preceding species in the sequence.

(up to 1 cm in length) and their frequent restriction to juvenile shoots <1 m in height argue against their role as a defense against herbivory by tree snails, insects, or flying birds. It is suggestive that achatinellid snails occur on every tall island except Kauai (10, 11), but such snails have never been observed to consume foliage and are rarely even found on *Cyanea* (M. G. Hadfield, personal communication).

Browsing pressure by native terrestrial mammals or reptiles is excluded by the lack of extant or fossil species and by the recent evolution (on Oahu and Maui Nui; see Fig. 2) of prickles in *Cyanea–Rollandia* inferred from our molecular phylogeny. Browsing pressure by flightless birds other than geese and moa-nalos is excluded by a lack of appropriate extant or fossil species and by the recent origin of prickles. The inability of flightless birds to disperse between islands, combined with (*i*) the ephemeral life (≈5 million years) of tall Hawaiian islands, (*ii*) their small area, and (*iii*) the limited rate at which avian body size can increase through evolution, may help explain the absence of gigantic flightless birds on Hawaii, such as the moas and elephant birds of larger, geologically much older New Zealand and Madagascar. The only remaining argument for an adaptive value of prickles—namely, to reduce insolation and water loss in arid sites (37)—is excluded by the fact that *Cyanea–Rollandia* is almost entirely restricted to densely shaded, moist or wet montane rain forests.

Divided Leaves and Heterophylly. Carlquist (2, 3) proposed that leaf dissection in *Cyanea* is an adaptation to shady conditions, ensuring that the "leaf tissue is spread thin." Two interpretations can be placed on this statement, with leaf dissection resulting in either (*i*) a thinner leaf cross section or (*ii*) a broader space sampled for light. With regard to the first interpretation, there is no obvious reason why a dentate or lobed leaf margin is required to reduce leaf cross-sectional thickness, and many thin leaves have entire margins. Givnish (38) documented a tendency for nonentire leaf margins to be more common in thinner foliage but argued that the optimal area served by a midrib and its secondary veins should become dissected as a consequence of the mechanical properties of a thinner leaf cross section, not that leaf dissection is a means of reducing leaf thickness.

The validity of the second interpretation of Carlquist's argument hinges on a dissected leaf sampling a broader space than an undivided one of equal photosynthetic area, thereby hedging against its being shaded by a single leaf or branch of a taller individual; the advantage of such a strategy would be greatest in unbranched plants such as palms (39). For such a bet-hedging strategy to work, however, dissection must spread leaf tissue over an area that is large relative to the distances over which photon flux densities are highly autocorrelated. Such distances appear to be on the order of a few decimeters in tropical forest understories (40); thus, while a few *Cyanea* species with large, highly dissected leaves (e.g., *C. grimesiana* and *C. shipmanii*) may sample a large enough space to yield a bet-hedging advantage, it seems implausible that others (including all ancestral forms, Fig. 2) would gain any significant advantage by toothing or lobing their leaf margins on the scale of only a few millimeters or centimeters. Hence, neither interpretation of Carlquist's argument seems compelling. However, it is possible that leaf dissection arose in some *Cyanea* juveniles for *both* its biomechanical advantage (38) in thin, shade-adapted foliage *and* its beneficial effect in reducing herbivory via visual divergence.

It seems unlikely that heterophylly is a selectively neutral trait genetically or developmentally linked to prickle production, given its three or more origins in *Cyanea* and the lack of a general association between prickle- or thorn-like organs and heterophylly in angiosperms. Any adaptive argument for the evolution of heterophylly in *Cyanea* which is unrelated to herbivory must somehow explain (*i*) the almost complete

restriction of heterophylly to species bearing prickles; (*ii*) the general restriction of divided juvenile leaves to shoots ≤1 m in height, within reach of the putative avian browsers; and (*iii*) the global restriction of insular heterophylly to island groups on which flightless avian browsers evolved. No such explanation is today evident.

Conclusions

Prickles evolved at least four times and juvenile–adult leaf dimorphism at least three times during the last 3.7 million years in *Cyanea–Rollandia* in the Hawaiian Islands. These traits, expressed principally in juvenile shoots near ground level, appear to have been mechanical and visual defenses against browsing by flightless geese and moa-nalos extirpated during the last 1600 years. The proportion of species with prickles and developmental heterophylly increases from Oahu eastward toward younger islands, paralleling the distribution of extinct avian browsers. Continued selection for dissected, visually divergent foliage may have led to the paedomorphic evolution of increasingly divided leaves in a series of species occupying progressively younger terrains. Finally, the effectiveness of visual defenses against avian browsers may account for the previously unexplained phenomenon of insular heterophylly, in that the islands and archipelagos where this phenomenon is marked are just those where one or more large, flightless avian browsers evolved in the absence of herbivorous mammals and reptiles.

Cyanea provides superb material for additional studies of speciation, adaptive radiation, and related evolutionary phenomena (12). It is extraordinary that two classic patterns of insular evolution (flightlessness in birds and arborescence in plants), as well as three previously unexplained patterns (insular heterophylly, neotenic evolution of leaf form, and origin of prickles in the absence of native terrestrial mammals and reptiles), are brought together in *Cyanea* by an extinct group of avian herbivores that apparently played a pivotal role in shaping its evolution.

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