



Herbivores and molecular clocks as tools in plant biogeography

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Historical biogeography plays an important role in understanding evolutionary processes and the history of life, with fossil data, plate tectonics, and palaeoclimatology offering major data bases for biogeographic analyses. Here we suggest that specialized interspecific interactions, in combination with molecular data, can play an important role in such analyses. We use the interaction between *Bowlesia incana* (Apiaceae) and the host-specific herbivore *Greya powelli* (Lepidoptera: Prodoxidae) in California to demonstrate the utility. Distributed in disjunct temperate parts of North and South America, *B. incana* has been proposed to have been introduced in historical time (<250 yrs BP) into North America. Three lines of evidence together suggest that the plant is of a far older age in North America. First, *G. powelli* is not known from the South American range and the genus is very unlikely to exist there, making introduction with the plant in North America unlikely. Second, divergence of mtDNA among members of the genus *Greya* suggests that the lineage leading to *G. powelli* originated 2.3–3.8 Mya, thus predating a proposed introduction by several orders of magnitude. Third, host shifts are consistently linked with species divergence within the genus *Greya*, suggesting that the *G. powelli* lineage has utilized *Bowlesia* since a time near its origin. We conclude that *B. incana* has been present in western North America for a long period of time, and that it did not arrive by human transport. The use of specialized herbivores and molecular data adds a powerful tool to historical plant biogeography.

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CONTENTS

Introduction	368
The organisms	369

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The plant	369
The herbivore	370
Rationale and results	370
Evidence against <i>Greya powelli</i> being present in South America	370
Evidence for old age of the <i>G. powelli</i> lineage	371
Evidence for colonization of <i>B. incana</i> near the origin of the <i>G. powelli</i> lineage	374
Discussion	376
Acknowledgments	376
References	376

INTRODUCTION

Biogeography has played an important part in analysing the historical record of life and mechanisms of evolution since the days of Darwin, Hooker, and Wallace (Darwin, 1859; Wallace, 1876; Turrill, 1953; Brooks & McLennan, 1991; Avise, 1994; Thompson, 1994). Records of historical ranges, dispersal paths, and timelines of change provide a template for interpreting the effects of abiotic change and species interactions on such fundamental processes as mechanisms and modes of speciation and principles of community composition. In this context, the fossil record, palaeoclimatological data, and plate tectonics have provided both a historical record of past organismal distributions and the changing continental stage on which life has evolved and spread (Wallace, 1876; Avise, 1994; Raven & Axelrod, 1978). But the incompleteness of the fossil record, with its taxonomic and temporal taphonomic biases, provides a sketchy record at best, and additional lines of evidence should be of great value.

Here we suggest that specialized interspecific interactions can provide such evidence, and in particular that historical plant biogeography can benefit from simultaneous analysis of plants and their associated specialized herbivores. We illustrate the approach using *Bowlesia incana* Ruiz & Pavon, an umbellifer suggested to have been introduced in North America in historical time (Raven & Axelrod, 1978; Mathias & Constance, 1965). We use a specialized herbivore and molecular data in conjunction to show that this association provides evidence for a far older age of presence in the North American flora.

Bowlesia incana is one of a large number of plants in the Americas that show amphitropical distribution, i.e. they have a disjunct distribution in the two hemispheres and are separated by tropical regions (Constance, 1963; Raven, 1963). Such distributions can be ascribed to past contiguous distribution, shared origins from a tropical ancestor, or long-distance dispersal events. The first explanation is inconsistent with the palaeoclimatological record, and the second is only rarely supported by phylogenetic affinities or the fossil record. Instead, animal-mediated long-distance dispersal has been suggested to explain the majority of these disjunct distributions (Raven, 1963; Lowry & Jones, 1984). But the situation is complicated by human interference in historical time, with inadvertent introduction of species into new areas. This is the case with many species now occurring in temperate South America and the North American southwest, where many species are known to have been carried from one region to the other by humans in the last 250 years, but there is also a large category of plants for which the native range remains unsettled.



Figure 1. Distribution of *Bowlesia incana* (positive slope) and *Greya powelli* (negative slope) in the Americas. Isolated *Bowlesia* collections have also been made in Florida and in French Guiana.

THE ORGANISMS

The plant

The genus *Bowlesia* consists of 14 species of slender, prostrate herbs with dichotomously branched trailing stems that rarely reach 30 cm above the ground (Mathias & Constance, 1965). Umbels arise from axillary pedicels, and are usually reduced to a single inconspicuous green flower. Species differ in regard to longevity and compatibility, with *B. incana* being a self-compatible annual.

All species occur in temperate portions of western South America, ranging from Patagonia to Ecuador, with one species reaching into central Mexico. *Bowlesia incana*, in addition to its southern South American range, also occurs in southwestern North America (Fig. 1). In California, the species is common in southern oak woodlands and coastal sage scrub, and in foothill woodlands of the southern Sierra Nevada. Because it has been found as a ruderal in New Zealand, Pakistan, French Guiana, Florida, and several sites in Europe (Mathias & Constance, 1965) and because many

other plants were introduced to California from this particular South American region (Raven, 1963), previous workers have suggested that it is an introduced weed in North America, with arrival through European settlers a few hundred years ago (Raven & Axelrod, 1978; Mathias & Constance, 1965).

The herbivore

Greya powelli Davis & Pellmyr is the smallest member of the genus *Greya* in the yucca moth family (Lepidoptera, Prodoxidae). This moth occurs in the coastal ranges from central California to Los Angeles, and in the south-central Sierra Nevada. Available material from the Sierra Nevada has a distinct wing pattern (Davis, Pellmyr & Thompson, 1992). New molecular data presented below suggests that these entities may represent distinct phylogenetic species, but whether they are or not is immaterial to the present argument.

Greya powelli belongs to a group of species that feed exclusively on umbellifer seeds (Davis *et al.*, 1992; Thompson, 1987), and it oviposits only into seeds of *B. incana*. Larvae feed on one or both of the developing seeds in a *Bowlesia* fruit during the first instars; subsequent biology is unknown. Males are readily seen flying just above grassy vegetation where *Bowlesia* is a component, whereas females mostly run along the stems of their hosts, searching for fruits in a suitable stage for oviposition. Although females are fully winged (wingspan *c.* 7 mm) and can fly, they usually walk on the ground between host plants, and have never been seen to fly more than a few centimeters (Davis *et al.*, 1992).

RATIONALE AND RESULTS

The obligate dependence of *G. powelli* on *B. incana* can potentially provide evidence for long-term existence of the plant in California. Three criteria must be met:

- (1) Evidence must show that *G. powelli* does not exist in the South American portion of the host range, and hence could not have moved with it. If the association predated a purported recent introduction in North America, the association in California would not be helpful to resolve its origins.
- (2) Evidence must show that substantial time has passed since the divergence of *G. powelli* from its sister group. If the lineage leading to *G. powelli* arose in recent time, it could be consistent with the recent-introduction hypothesis for *B. incana*.
- (3) Evidence must show that colonization of *B. incana* occurred near the point of divergence from the sister group of *G. powelli*. Even if the lineage leading to *G. powelli* is old, a recent switch to *Bowlesia* would be possible.

Evidence against Greya powelli being present in South America

None of the 18 identified *Greya* species is known to occur in the Southern hemisphere (Davis *et al.*, 1992; Kozlov, 1996), and there are several reasons to infer that this is not a sampling artifact. First, the distribution of *Greya* in the northern hemisphere is well known from extensive studies during the past decade; no species

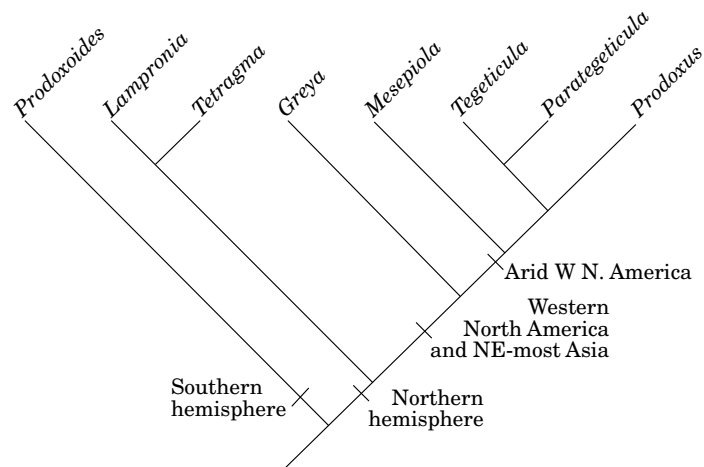


Figure 2. Proposed phylogeny of genera within the Prodoxidae, based on morphological and molecular data (Nielsen & Davis, 1985; Wagner & Powell, 1988; Davis *et al.*, 1992; Brown *et al.*, 1994b). Distribution of the different genera are indicated on internodes.

is known to extend south of the U.S.-Mexican border (Davis *et al.*, 1992; Kozlov, 1996). Likely candidate areas in the South American Andes, where *Bowlesia* is abundant in grassy woodlands at intermediate elevations, have been studied extensively for Prodoxidae and other Microlepidoptera (Nielsen, 1985). Although the search yielded the first, and so far only, known prodoxid from the southern hemisphere (Nielsen & Davis, 1985), no *Greya* species was ever found. A distinct biogeographic pattern within the family also argues against the presence of *Greya* in South America (Fig. 2). The South American *Prodoxoides* is probably basal within the family, whereas *Lampronia* and *Tetragma* are Holarctic in their distribution. Four or five basal *Greya* species show Transberingian distribution, whereas the more derived remainder of *Greya* and its sister group the yucca moths (*s.l.*) have diversified in the western North American semiarid and arid regions (Davis *et al.*, 1992; Kozlov, 1996; Nielsen, 1985). To make the presence of *G. powelli* in South America plausible within this biogeographic framework, it would be necessary to assume extensive extinction of more basal prodoxid taxa in the southern hemisphere, or a long-distance dispersal event without equal within the moth family. In conclusion, it is unlikely that *G. powelli* occurs on *Bowlesia* in South America and arrived recently in North America.

Evidence for old age of the G. powelli lineage

Molecular data originally gathered for phylogenetic reconstruction of the genus *Greya* in combination with new sequences can be used to establish a relative age of the lineage that led to *G. powelli*. A continuous 765-bp sequence of mitochondrial DNA data from the COI-COII region is available for this purpose. Technical details of data acquisition are provided elsewhere (Brown *et al.*, 1994a). Sample collection sites and GenBank numbers are provided in the Appendix. Two samples from the original *Greya* analysis were excluded because of uncertain host affinity and complete

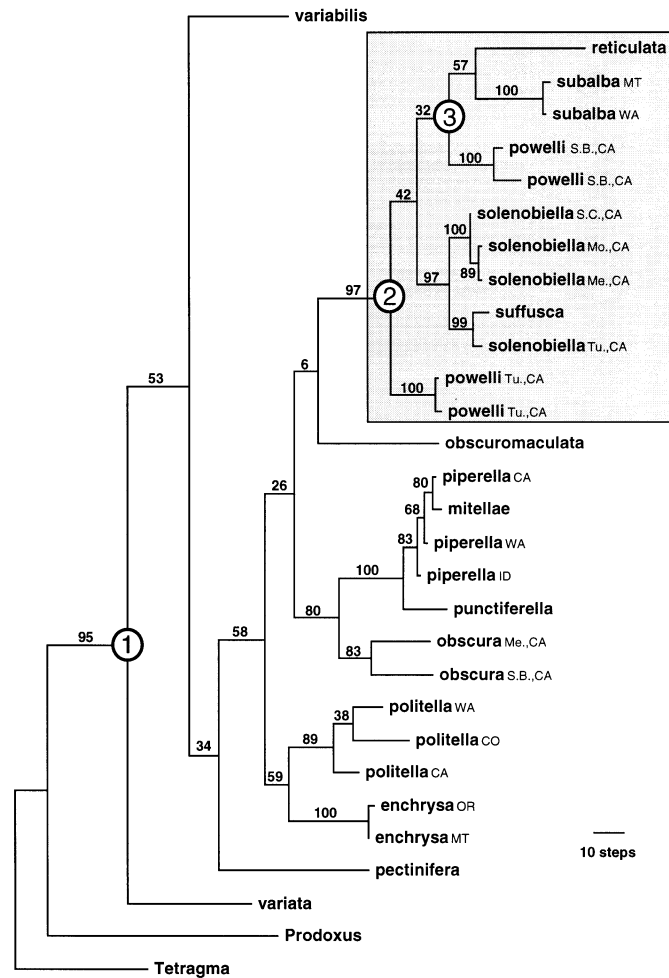


Figure 3. Phylogenetic hypothesis for all North American species of *Greya* based on mtDNA sequence; samples are largely from Brown *et al.* (1994a) with additions as noted in the text. *Tetragma* and *Prodoxus quinquepunctellus* were used as outgroups. This is a single most parsimonious tree. Taxon labels include state and county abbreviations when needed to distinguish among samples. Numbers on internodes are bootstrap values based on 100 iterations using maximum parsimony. Shaded area indicates the group of taxa that feed on umbellifers. Circled numbers indicate nodes used for calculation of relative ages of specific lineages (Table 1).

sequence identity with another sample, respectively. Two new *G. powelli*, two *G. solenobiella*, and one *G. politella* sequence were added from previously unrepresented parts of their ranges.

A single maximum-parsimony tree was obtained (Fig. 3). Comparison of likelihoods of a tree with *G. powelli* constrained to be monophyletic against the maximum-parsimony tree showed that monophyly could not be rejected ($P=0.095$; Kishino-Hasegawa test [Felsenstein, 1993]). Further data should be collected to resolve the issue of *G. powelli* monophyly.

Any estimation of relative age of a lineage assumes that the rate of molecular

TABLE 1. Mean node-to-tip distances and standard errors for three of the nodes in the maximum-parsimony tree shown in Figure 3. Distances were estimated using Kimura's 2-parameter correction. Relative age estimates are calculated as the ratio of each node-to-tip distance over the distance for the basal node within *Greya*. Significance level for rejecting the null hypothesis of equal rates between clades above the node is also shown

Node	Node-to-tip distance \pm SE, %	<i>P</i>	Relative age
1. <i>G. variata</i> <-> other <i>Greya</i>	6.25 \pm 0.65	0.52	1.0000
2. <i>G. powelli</i> <-> other umbellifer feeders	3.04 \pm 0.42	0.33	0.4864
3. <i>G. powelli</i> <-> <i>reticulata</i> + <i>subalba</i>	3.17 \pm 0.45	0.49	0.5072

evolution has been more or less stable for the group under study (Li & Graur, 1991). We tested the assumption of equal rates of sequence evolution in two ways. First, rate heterogeneity across all *Greya* species was tested by comparing estimated branch lengths calculated using a maximum likelihood model that imposes equal rates, with branch lengths estimated using a model that allows rates to vary (DNAML vs. DNAMLK [Felsenstein, 1993]). Because we were particularly interested in the relative rate of evolution on the *G. powelli* branches, we also tested for rate heterogeneity between *G. powelli* clades and their sister clades using the distance-based approach of Takezaki, Rzhetsky and Nei (1995). The topology used in both analyses was the maximum-parsimony tree (Fig. 3).

The null hypothesis that the sequenced mtDNA region is evolving at equal rates in all *Greya* species was rejected ($P < 0.05$; Kishino-Hasegawa test [Felsenstein, 1993]). The two-cluster relative rates test of Takezaki *et al.* (1995) was then performed on each node of the parsimony tree to identify sources of the rate heterogeneity. Distances along each branch were estimated using Kimura's 2-parameter estimation (Kimura, 1980). The equal rates hypothesis was rejected at two nodes: the branch leading to *G. punctiferella* was significantly longer than the average node-to-tip distance for the *piperella/mitellae* clade ($P < 0.013$), and the branch leading to *G. reticulata* is longer than the average node-to-tip distance for the *subalba* clade ($P < 0.05$; Fig. 3). The two-cluster test failed to reject the null hypothesis of equal rates between either of the distinct *G. powelli* clades and their sister clades (Table 1; labels 2 and 3 in Fig. 3), so average node-to-tip branch lengths reflect time since divergence between these clades. Similarly, the test failed to reject assumption of rate constancy at the node between the basal *Greya* and all other *Greya* species (Label 1 in Fig. 3). Thus the ratio of node-to-tip distance for the *G. powelli* clades over the node-to-tip distance for the basal node within *Greya* is an estimate of the origin of *G. powelli* relative to the age of the genus. Using this logic, the divergence of the *G. powelli* lineages from their sister clades occurred 48–50% of the time since the divergence time for the most basal node within the genus (*G. variata* + all other *Greya* species).

The absolute time of origin is difficult to ascertain, because the age of *Greya* is still unknown. One estimate can be obtained from published estimates of rates of mtDNA sequence evolution (Brower, 1994). Seven data sets from Diptera, Coleoptera, Homoptera, and Decapoda, where fossil or biogeographic data provided calibration, ranged in rates between 1.7 and 2.4% per million years. Using this range estimate, the observed distance between *G. powelli* and the other umbellifer feeders would infer an origin of the *G. powelli* lineages 2.3–3.8 Mya. There are reasons to regard this bracket with considerable caution; the published rate estimates

were based on different portions of the mtDNA genome, which may evolve at different rates (Moritz, Dowling & Brown, 1987; Li & Graur, 1991; Avise, 1994; Cummings, Otto & Wakeley, 1995), and the estimate also does not incorporate known sources of rate difference among lineages such as generation time (Gaut *et al.*, 1992; Hafner *et al.*, 1994). Nonetheless, this estimate suggests that the age of the *G. powelli* lineages exceeds the proposed age of *Bowlesia* introduction into California by several orders of magnitude.

Evidence for colonization of B. incana near the origin of the G. powelli lineage

Although the lineage leading to the extant *G. powelli* has existed for a very long time, recent introduction of *Bowlesia* into California could still be viable if the current association is the result of a recent host colonization and the moth ancestor fed on one or more different host species during its existence. Such ecological and evolutionary plasticity with regard to hosts is common among some groups of phytophagous insects (Powell, 1980; Carroll & Boyd, 1992; Thompson, 1994). Studies of host associations within *Euphydryas editha* (Boisduval) show that host utilization is highly plastic within the species, and that numerous populations in fact have switched to an introduced plant within recent decades (Thomas *et al.*, 1987; Radtkey & Singer, 1995). In contrast, host association is highly conservative in other groups (Ehrlich & Raven, 1964), with host shifts being directly associated with disrupted gene flow and sometimes speciation (Mitter, Farrell & Wiegmann, 1988; Thompson, 1994). Patterns of host utilization among *Greya* offer strong support for colonization of *Bowlesia* by *G. powelli* at a point in time close to the divergence point with its sister taxa.

A novel life history trait, such as a host shift in a herbivore, can be acquired at any time during the period that has passed since the divergence from a sister taxon. In the absence of historical information, which is usually the case, an approach can be taken to ask whether the trait consistently may have appeared at or near (and perhaps even played part in) the divergence of the lineages. If a consistent pattern of different hosts among sister species or larger clades is present within the group containing the organism of study, this could provide indirect evidence that host shifts are associated with the emergence of novel lineages within a group of herbivores. The underlying logic is as follows: if two sister taxa are specialized to feed on different hosts, they may have diverged in host use at any time since the divergence event that produced the lineages. If sampling of multiple populations throughout the ranges of these taxa fails to uncover any extant populations that use the host of the other species, then the shift of one of the taxa onto a novel host can be inferred to have arisen at or near the time of speciation. Alternatively, selective extinction of populations on a shared, ancestral host can explain the pattern. If at least one population uses a shared host species, then this may infer either more recent colonization of a unique host by the lineage or recolonization of an ancestral host. If either or both taxa use multiple hosts, and the intraspecific pattern of host colonization is not known, they should be treated conservatively as a polytomy, i.e. any one overlap in host use at the species level should be considered evidence against a host shift at or near the divergence point. That is, recolonization is only considered a possibility if intraspecific data is available to document such an origin.

The procedure of estimating the relative time of host shift on an internode is

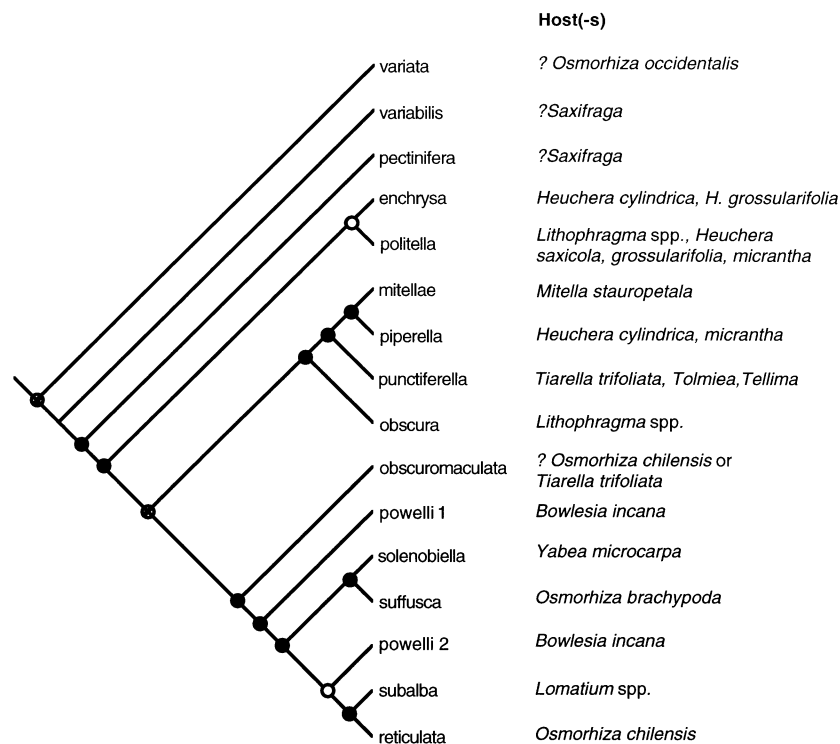


Figure 4. Parsimony mapping of host shifts for North American species of *Greya*, with known host information provided for all species. Host associations are based on checks of populations throughout the known geographic range of each moth, and in most instances represent all known populations (Davis *et al.*, 1992). Filled and crossed circles represent nodes where host differences can be confirmed by parsimonious host mapping; for the crossed circles, judgment is based on tentative host identification and absence of shared potential hosts in habitats. Open circles represent instances where a shared ancestral host cannot be excluded. Insufficient host information is available to assess host evolution for the node lacking a circle.

applied by determining for each pair of clades whether different or shared hosts are utilized. If most nodes show different hosts, this lowers the probability that selective extinction is an explanation and increases the probability that it reflects a pattern of host shift at or near the divergence point. Host information for *Greya* is sufficient to provide data for 14 of 15 nodes (Fig. 4). All but one species pair and all but one lower node differ in host usage, including ones that utilize more than one host. This nearly consistent pattern of host shifts associated with lineage divergences within *Greya* is a strong indication that host shifts occur near the basal node, and in fact may be a facilitating factor in causing divergence in the first place. It should be noted that two species, *G. mitellae* and *G. suffusca*, are of such recent origin as to have mitochondrial haplotypes nested within their sister taxa (Fig. 3), thus lending further support for rapid host shift at or near the point of divergence. The evidence suggests that the host shift by *G. powelli* onto *B. incana* occurred at or near the origin of the lineage leading to the extant species.

DISCUSSION

The data on *G. powelli* lend strong support to the suggestion that *B. incana* is an old member of the North American flora. Empirical and biogeographic data reject the notion that the association between *Bowlesia* and *G. powelli* was established in South America, the molecular data suggests that the origin of the *G. powelli* lineage diverged from its closest extant ancestors 2.3–3.8 Mya, and a strong argument can be made for a consistent pattern of host shifts associated with divergence within the entire genus *Greya*. The data cannot address the status of the disjunct ranges in Texas, Arizona, or adjacent Mexico (Fig. 1), because *Greya* is not known to exist in those areas.

Specialized herbivores appear never to have been used for the purpose of plant historical biogeography before, although Moran (1989) used the reverse argument of historical plant ranges to determine age of an insect-host association. Halbert and Voegtlin (1994) used a specialized herbivore to locate an introduced weed. These herbivores have the potential to be an important general indicator of native host plant ranges, as a large number of herbivorous insect groups meet the criterion of high specificity and conservatism in host utilization (Ehrlich & Raven, 1964; Thompson, 1994; Labandeira *et al.*, 1994; Becerra, 1997). Furthermore, the relative ease with which molecular phylogenetic hypotheses can be constructed and used for historical analysis has added a powerful quantitative tool for these purposes. While the present study used a case of recent, purported human transport, these tools can be useful also for older divergences; the utility depends on the availability of herbivore groups with high specificity, limited distribution, and limited means of dispersal.

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APPENDIX

Alphabetized list of specimens used for phylogenetic analyses, given with state and county (CA = California, CO = Colorado, ID = Idaho, MT = Montana, NY = New York, OR = Oregon, WA = Washington). All specimens are from the USA. GenBank acquisition number is provided in parentheses.

<i>Greya enchrysa</i>	MT: Glacier (L22221), OR: Umatilla (L22234)
<i>G. mitellae</i>	ID: Latah (L22220)
<i>G. obscura</i>	CA: Mendocino (L22223), Santa Barbara (L22222)
<i>G. obscuromaculata</i>	ID: Benewah (L22224)
<i>G. pectinifera</i>	WA: Clallam (L22225)
<i>G. piperella</i>	CA: Calaveras (L22237), ID: Clearwater (L22236), WA: Garfield (L22235)
<i>G. politella</i>	CA: Tulare (L22240), CO: San Juan (U49021), WA: Whitman (L22240)
<i>G. powelli</i>	CA: Santa Barbara (U91853, U91854), Tulare (L22239, U91852)
<i>G. punctiferella</i>	WA: Clallam (L22227)
<i>G. reticulata</i>	CA: Santa Clara (L22242)
<i>G. solenobiella</i>	CA: Santa Clara (L22230), Mendocino (U91856), Monterey (U91855), Tulare (L22229)
<i>G. subalba</i>	MT: Glacier (L22243), WA: Whitman (L22231)
<i>G. suffusca</i>	CA: Tulare (L22232)
<i>G. variabilis</i>	WA: Clallam (L22245)
<i>G. variata</i>	MT: Glacier (L22235)
<i>Prodoxus quinquepunctellus</i>	NY: Suffolk (L22241)
<i>Tétragma gei</i>	WA: Asotin (L22244)
