YUCCAS, YUCCA MOTHS, AND COEVOLUTION: A REVIEW[1]

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ABSTRACT

The obligate pollination mutualism between yuccas (Agavaceae) and yucca moths (Lepidoptera, Prodoxidae), in which the adult moth pollinates yucca flowers and her progeny feed on developing seeds, is one of the classically cited examples of coevolution. While known since 1872, our understanding of the ecology and evolution of this association has increased dramatically in the past decade. Here I review current information on organismal diversity and phylogenetic relationships, ecological relationships, origin and reversal of the mutualism, and the potential for analyzing patterns of co-speciation and the historical role of coevolution on specific traits in driving diversification in the interaction. Major novel developments in recent years include the recognition of a large species complex of pollinators, previously thought to be one polyphagous species; a majority of all moth species are monophagous. Considerable life history diversity has been unveiled, and mechanisms that maintain a mutualistic equilibrium by preventing overexploitation documented. Phylogenetic and ecological information, including data from other, newly discovered facultative pollinators in the Prodoxidae, have been used to erect a hypothesis for the evolution of obligate mutualism. Application of a molecular clock to phylogenetic data suggests that the plant-moth association arose at least 40 Mya, and that the obligate mutualism evolved very quickly after this event. Two separate events of reversal of mutualism have been identified, involving derived "cheater" moth species that oviposit into fruits resulting from pollination by other pollinator species. This appears to have happened not through selection for cheating, but rather as a byproduct of a phenological shift to an unexploited seed resource, in which case pollination behavior became redundant. Analyses of parallel diversification and character coevolution are hampered by incomplete phylogenetic information at the species level, especially for the plants, but also for the pollinators. Available data indicate considerable deviation from strict co-speciation, and no evident examples of this process. Analyses of the role of coevolutionary processes in driving the diversification of yuccas and yucca moths will be possible once fully resolved phylogenies become available.

Key words: coevolution, *Hesperoyucca*, mutualism, *Parategeticula*, Prodoxidae, *Tegeticula*, *Yucca*, yucca moth.

Coevolution, in the sense of reciprocally induced evolution, is one of the major processes driving diversification and speciation (Farrell & Mitter, 1993; Thompson, 1994, 1999a, b). Since first applied in plant-animal interactions as a hypothesis to explain diversification among butterflies and flowering plants (Ehrlich & Raven, 1964), it has been applied successfully in comparative analyses to test rates of diversification in ecologically defined groups, such as plant-feeding insects and parasitoids (Mitter et al., 1988; Wiegmann et al., 1993; Becerra, 1997; Farrell, 1998; Becerra & Venable, 1999). Several such studies show that plants and plant-feeding insects often have increased rates of diversification compared to sister groups with different life habits; thus one or more life history aspects of these groups appear to be important in driving diversification and speciation. This might involve, for example, chemical, physiological, and morphological arms races between the interacting organisms.

Our understanding of coevolutionary processes at populational and species levels is still in its infancy because identification of proximal factors of diversification relies on strong phylogenetic hypotheses for the interacting organisms (Barraclough et al.,

1998; Pagel, 1998, 1999a, b), extensive life history data, and ultimately experimental testing of emerging candidate traits (Armbruster et al., 1997). Often the phylogenetic frameworks are missing, and there are very few instances where all these criteria are met. A recent exception is the study of Becerra (1997), who used data for members of the plant genus *Bursera* (Burseraceae) and a group of specialist herbivorous beetles (*Blepharida*; Chrysomelidae) to suggest that chemical defenses and detoxification traits have been a major evolutionary factor in their diversification.

One of the most often cited cases of coevolution is the obligate mutualism between yuccas (*Yucca* and *Hesperoyucca,* Agavaceae) and yucca moths (*Tegeticula* and *Parategeticula,* Prodoxidae, Lepidoptera). In this association, the plants rely on adult moths for their pollination, while the moth larvae require developing seeds to complete their development. This association was first recognized over a century ago (Anonymous, 1872; Riley, 1872), and then served not only as an example of remarkable pollination mutualism, but also as one of the first and strongest examples of evolution by means of natural selection. Together with a few other models of obligate mutualism that involve seed-eating pollinators, the yuccas and yucca moths form a class of associations that are excellent systems for studies of coevolution, as well as of evolutionary and ecological dynamics of mutualism and its dissolution. This stems in part from the relative simplicity of measuring fitness costs and benefits in these interactions; in most instances both plant cost and benefit can be measured in seeds. Second, in contrast to most other plant-pollinator associations, these are relatively exclusive associations, often with a single pollinator species per plant species, making it easier to measure reciprocal effects than when webs of many, simultaneously interacting taxa have to be analyzed.

Considerable progress has been made in understanding this unusual type of obligate pollination mutualisms in the past 15 years. This is certainly true of the long-recognized yucca-yucca moth and fig-fig wasp associations (Riley, 1872; Weiblen, 2002). The two other documented examples of such obligate associations (*Trollius europaeus* L. [Ranunculaceae] and *Chiastocheta* flies [Diptera: Anthomyidae], and *Lophocereus schottii* (Engelm.) Britton & Rose [Cactaceae] and the moth *Upiga virescens* (Hulst) [Lepidoptera: Pyralidae]) were actually first documented during this period (Pellmyr, 1989, 1992; Fleming & Holland, 1998; Després & Jaeger, 1999; Jaeger et al., 2001). Here I will review our current understanding of the association between

Figure 1. *Tegeticula yuccasella* female collected by G. Engelmann on the first night that he observed moths on *Y. filamentosa* flowers. Label likely written by C. V. Riley, who received the moth. From the collections of USNM.

yucca moths and yuccas, and discuss its utility in exploring more general questions of coevolution. Since the latest reviews of this interaction, by Baker (1986) and Powell (1992), information on systematics, phylogenetic relationships, and life history has increased dramatically, especially in the moths, and the complexity of the association at different hierarchical levels is now quite different.

EARLY HISTORY OF STUDY OF THE PLANT-MOTH INTERACTION

The first observation of the yucca moths was made by George Engelmann in St. Louis in 1872 (Engelmann, 1872). Engelmann asked Charles Riley, then state entomologist of Missouri, to explore the relationship between the moths and the plants. Baker (1986) provided a passage from Engelmann's notes written on 13 June 1872 about the initial observations the previous night, and one of the moths observed from that initial set of observations appears to have survived. Riley donated his very large insect collection to the United States National Museum of Natural History (Smithsonian Institution), where it became the nucleus for the creation of the Department of Entomology. Among his yucca moth specimens is one female *Tegeticula yuccasella* (Riley) specimen labeled "found in Yucca flower—Engelm. June 12/72" (Fig. 1). This date coincides with that of Engelmann's original observations at the Missouri Botanical Garden, and is obviously a moth given to Riley by Engelmann. Although this would have been an obvious candidate for holotype, it is not. Riley, a driven and opinionated worker, never bothered to designate or label type material for any of the many species that he described, but instead would mention in his descriptions the number of specimens used for the description (Davis, 1967). A lectotype having already been designated for *T. yuccasella,* the surviving moth from Engelmann's

original observations has now been labeled to indicate its historical significance.

Charles Riley was to dominate the field of yucca moth studies up until his sudden death in 1895, despite this being a sideline in his job as the first federal entomologist (Sorensen, 1995). One of his most important contributions was his involvement in the salvation of the French wine industry (Smith, 1992). I mention it here because it indicates Riley's general understanding of the process of plant-insect coevolution. By the early 1870s, North American grape phylloxera aphids (*Daktulosphaira vitifoliae* (Fitch)) accidentally introduced in central Europe caused massive mortality of European grape cultivars by attacking their roots. Riley (1871) reasoned that American *Vitis* species had coevolved with phylloxera, and thus might tolerate them better. A grafting program with European cultivars and American roots proved highly successful in reducing phylloxera impact, and carried the industry to financial survival; Charles Valentine Riley may be the only individual to have received the French Legion of Honor for contributions to coevolution.

An extraordinary observer and able thinker, Riley unfolded the basic natural history of the plant-moth mutualism and documented the life histories of the pollinator *Tegeticula yuccasella* and the bogus yucca moth *Prodoxus decipiens* Riley within a decade of the initial discovery (Riley, 1880, 1881). In contrast to the records of most of his contemporaries, there are very few inaccuracies in his accounts, simply because of his reliance on empirical observation. In this, he arguably belonged in the exclusive group of exceptional naturalists with whom he regularly corresponded, such as Charles Darwin, Alfred Russell Wallace, Henry Walter Bates, Thomas Belt, Fritz and Hermann Müller, and Asa Gray. As one of the early protagonists of evolution by natural selection in the United States, Riley went beyond natural history to use the relationship between the yuccas and the moths in discussing more general issues such as mimicry and animal pollination (Riley, 1871, 1892).

The relationship between yuccas and yucca moths, characterized in an 1877 letter from Charles Darwin as "the most remarkable example of fertilisation ever published" (Burkhardt & Smith, 1994), drew the attention of many other naturalists in the first 15 years after the discovery. Riley was challenged on numerous occasions regarding the accuracy of his observations. This included the argument from P. C. Zeller, a German entomological authority whose experience with yucca moths was limited to three pinned specimens given to him, that it was simply too improbable to be true (Zeller,

1875: 340–342). Others charged not only that Riley was incorrect but that the very phenomenon of insect pollination was a dubious notion in the first place (Boll, 1876; Meehan, 1876); Boll went on to state that active pollination "belongs in the land of fables." Yet other critics challenged that his arguments about exclusivity of moths in pollinating yuccas were overstated (e.g., Hulst, 1886). Riley responded to his critics with experimental results, not always published in full, often with a singularly sharp pen (Davis, 1967). A prolific writer, with some 2400 entries in his bibliography (Ho & Yuille, 1990), Riley used the empirical data as he knew them to rebut and often scold his critics (e.g., Riley, 1877, 1881, 1887), and occasionally even stooped to ridicule.[3]

Following Riley's death, a hiatus arose in the empirical study of the association. Trelease worked with Riley on behavioral and botanical aspects, performing extensive fieldwork, and published detailed observations on pollinator behavior as well as plant morphology and systematics in his works (Trelease, 1893, 1902). Considerable collections of both moths and plants were made by Susan McKelvey for her monographs on southwestern *Yucca* (McKelvey, 1938, 1947). Busck (1947) attempted a reassessment of moth-plant associations based on McKelvey's insect material; his conclusions when correct generally followed those of Riley, but Busck misinterpreted morphological variation that he was the first to document among pollinator yucca moths, cheater yucca moths, and bogus yucca moths.

Since the 1960s, information about the association has accrued at an accelerating pace from several lines of investigation. This includes systematic and phylogenetic studies of the organisms, as well as the ecological and evolutionary studies of the interactions between the moths and the plants.

NATURAL HISTORY

ORGANISMAL DIVERSITY

The yuccas. The yuccas are part of the North and Central American family Agavaceae (Fig. 2). Recent data suggest that the sister group of Agavaceae may be the small family Camassiaceae, confined primarily to mesic habitats of western North America with the exception being one species in eastern North America (Pfosser & Speta, 1999).

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[3] V. T. Chambers, an amateur lepidopterist, mistakenly used the first non-pollinating bogus yucca moth to challenge Riley's description of pollinator yucca moths (Chambers, 1877). In a rebuttal, Riley (1880) untangled the confusion and used Chambers's moth to erect the new genus *Prodoxus* (Gr., "judging of a thing prior to experience").
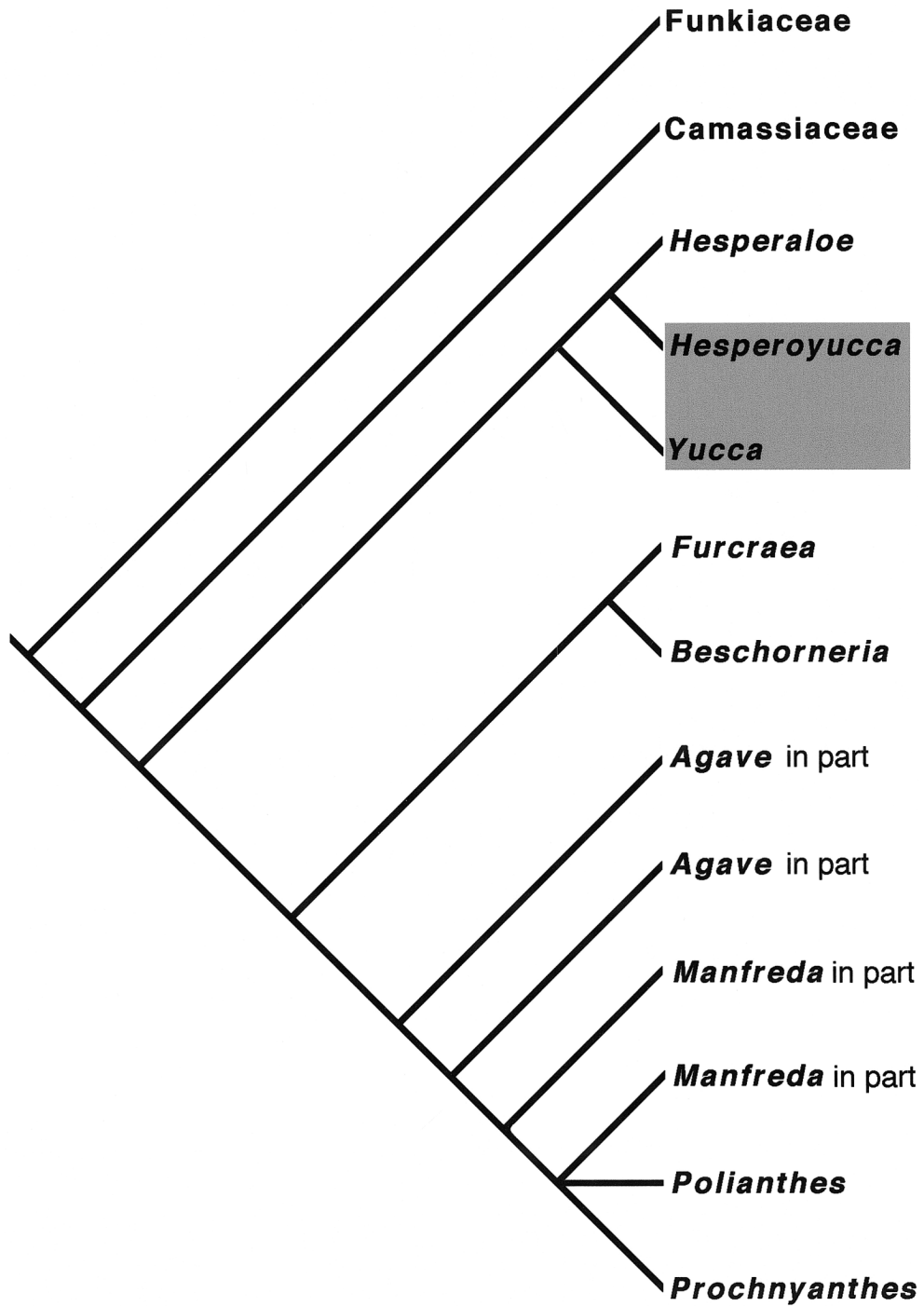
Figure 2. Tentative genus-level consensus phylogeny for Agavaceae and its sister families, adapted from Pfosser and Speta (1999), Bogler and Simpson (1996), and Eguiarte et al. (2000). The only two genera pollinated by prodoxid moths are indicated by gray box.

Generic-level relationships are partly unresolved within the family, but are robust among the taxa involved in the obligate mutualism with yucca moths (Bogler & Simpson, 1996; Clary, 1997). The monobasic *Hesperoyucca,* originally described as a distinct subgenus based on such features as a capitate stigma (Engelmann, 1871), was long considered a section within *Yucca* (Baker, 1986). Recent analyses show *Hesperoyucca* to be the sister group of *Hesperaloe,* a small genus of the Sonoran and Chihuahuan deserts (Bogler & Simpson, 1996). Importantly, *Hesperaloe* taxa are not associated with the yucca moths, and instead rely on hummingbirds (Pellmyr & Augenstein, 1997) and probably bats (Engard, 1980) for their pollination. Jointly, *Hesperoyucca* and *Hesperaloe* constitute the sister group of all remaining yuccas (Bogler & Simpson, 1996).

Yucca is divided into three sections: spongy-fruited section *Clistocarpa,* the fleshy-fruited section *Sarcocarpa,* and the capsular-fruited section *Chaenocarpa.* Section *Clistocarpa* consists solely of *Yucca brevifolia* Engelm., whereas the two other sections consist of no more than 20 to 25 species each (Clary, 1997). Section *Clistocarpa* is characterized by the single autapomorphy of a thickened exocarp, as observed by Trelease (1893). Its position relative to the other yuccas is uncertain but possibly tied to the series *Rupicolae* of capsular-fruited species (Clary, 1997). The longstanding interest in yuccas and their importance in many biological communities notwithstanding, *Yucca* taxonomy and systematics remain in a state of flux, with much need for a modern revision. Revisionary work is complicated by the relative scarcity of herbarium material, caused in part by the logistic problems of preparing specimens from these large, succulent plants. Horticultural interests in the group also have contributed to a plethora of names, with many taxa narrowly delineated using in effect a typological species concept (sensu Mayr, 1963). Observed variation frequently has been attributed to assumed hybridization and introgression (e.g., McKelvey, 1938, 1947; Webber, 1953), but this should be considered speculation as there is only one example where genetic evidence for introgression between two yucca species is provided (Hanson, 1992). Phylogenetic analyses are limited thus far, but appear not to violate assumptions of monophyly of both section *Sarcocarpa* and section *Chaenocarpa* (Clary, 1997). The use of horticultural material or yucca cultivars of unknown origin in some studies may contribute to historical confusion about relationships.

The *Hesperoyucca–Hesperaloe–Yucca* clade is native to North America (Fig. 3), and its contiguous range has been extended into Central America and northern South America through the cultivation of *Y. elephantipes* Regel for their edible flowers (Trelease, 1902; Matuda & Piña Lujan, 1980). Several species have been in cultivation on other continents, including in Europe since the late 1500s (Gerarde, 1633), but yucca moths have never been found either south of Mexico or on other continents. Riley (1881) attempted to establish them by sending batches of pollinator larvae in their cocoons to Darwin and Stainton in England, Planchon in France, H. Müller in Germany, and Asa Gray in Massachusetts, for establishment on cultivated yuccas. Müller (1874) reported that moths hatched, but no local ornamental plants were in flower. Darwin had no yuccas in cultivation, and forwarded his cocoons to Joseph Hooker at Kew, where their subsequent fate is unknown.

The two larger *Yucca* sections, section *Sarcocarpa* and section *Chaenocarpa,* have wide ranges that overlap in areas north and south of the border of Mexico and the United States (Fig. 3). The fleshy-fruited section *Sarcocarpa* is primarily southern, ranging throughout the Megamexico-1 biogeographic region of Rzedowski (1993), and extending in one species northward to southern Colorado. The aberrant *Y. aloifolia* L. occurs in the northern Caribbean and along the U.S. Mexican Gulf and southern Atlantic coasts; it reproduces vegetatively but is not known to have a native pollinator. Its origin is unclear, and I will return to it later. The capsular-fruited yuccas are more northern in distribution, ranging from the northern edge of the Great Plains in southern Canada southward to the Mexican High Plains.

Whereas yuccas generally are associated with shrub desert, chaparral, or grasslands, many Mexican species often grow in pine-oak woodland (Matuda & Piña Lujan, 1980; Gentry, 1982). Packrat midden data from the Wisconsin glacial show that species such as *Y. rostrata* Engelm. ex Trel. that currently inhabit shrub desert grew in pine-oak woodlands in areas such as the Big Bend region of Texas during wetter periods (Van Devender, 1990). The most unusual habitats are those of the southernmost yuccas, *Y. elephantipes* and *Y. lacandonica* G. Pompa & Valdés. Both occur in rainforest, with the former having a terrestrial habit whereas the latter is epiphytic or epilithic (Matuda & Piña Lujan, 1980; C. Beutelspacher, pers. comm.).

The yucca moths. The yucca moths belong to the Prodoxidae, a basal family within Lepidoptera of 78 described species (Davis, 1998; Pellmyr, 2002) and at least 15 additional undescribed spe-
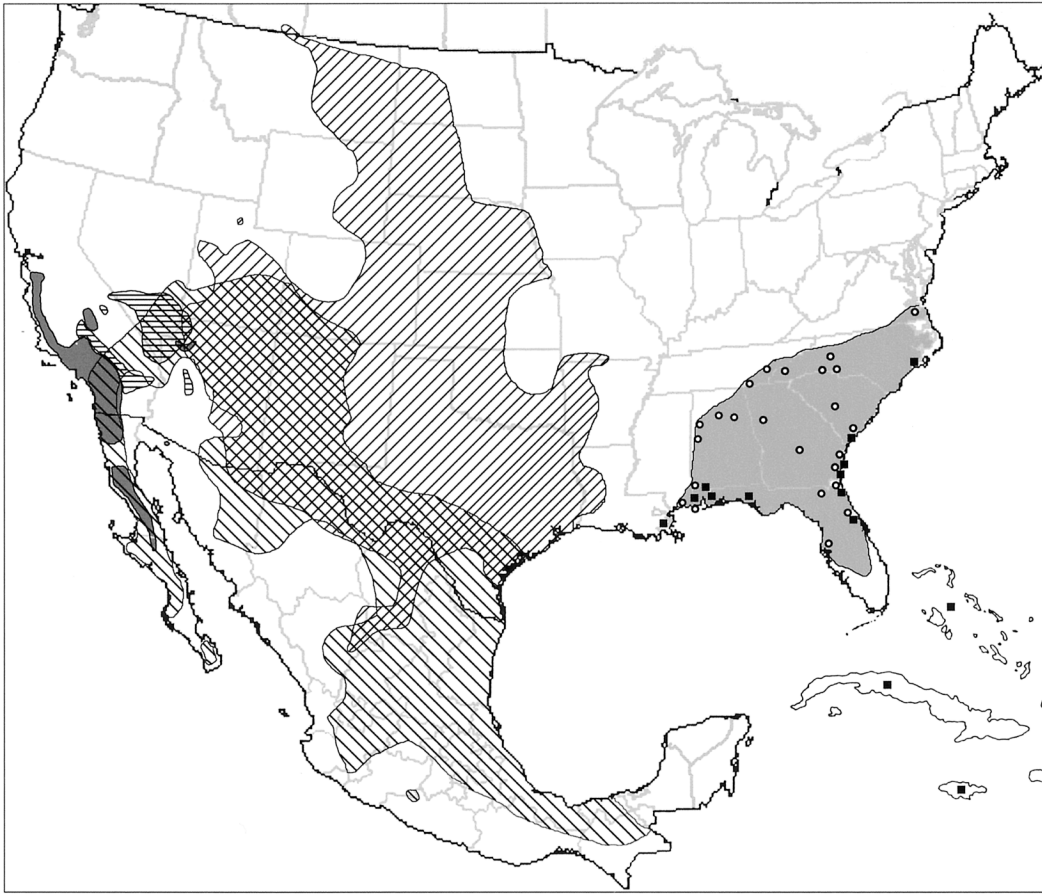
Figure 3.   Approximate limits of natural distributions of *Hesperoyucca* and the sections of *Yucca*. *Hesperoyucca*, dark gray (California, Baja California, Arizona); *Yucca* sect. *Clistocarpa*, horizontal lines; section *Chaenocarpa*, diagonal positive-slope lines and medium gray; and section *Sarcocarpa*, diagonal negative-slope lines and black squares (latter along southeast U.S. coast). Only published collection records from the wild, herbarium records from UNAM and MO, and a few records from J. A. Powell and my own fieldwork were included to avoid complications of extensive cultivation and escape. Published sources used were Engelmann (1873), McVaugh (1983), Mohr (1901), McKelvey (1938, 1947), Moss (1959), Steyermark (1963), Powell and Mackie (1966), Great Plains Flora Association (1977), Rowlands (1978), Matuda and Piña Lujan (1980), Turner et al. (1995), and García-Mendoza (1998). Special procedures were made for *Y. filamentosa* and *Y. aloifolia*. *Yucca filamentosa* (s.l.) has been naturalized by European settlers across the eastern U.S. and into adjacent parts of Canada, so I only used records from the oldest comprehensive published sources (Engelmann, 1873; Mohr, 1901; Trelease, 1902) to establish a conservative range (medium gray in southeastern U.S.; open circles give actual sites). For *Y. aloifolia* (black squares), the same sources plus Britton and Millspaugh (1962) were used; for records from the Antilles (Trelease, 1902), specific locations and circumstances of each collection are unknown. Land areas south of Mexico have been excluded.

cies (Frack, 1982; Nielsen, 1982; Pellmyr & Balcázar-Lara, in prep.). The sister family Cecidosidae consists of gall-makers feeding mostly on Anacardiaceae (Nielsen, 1985), and it shows a typical Gondwanan distribution. The presence of sister genera in Africa and South America of these moths, which are highly sedentary, strongly indicates an origin of this family, and by inference the Prodoxidae, before the South Atlantic breakup 95–100 million years ago (Pellmyr & Leebens-Mack, 1999).

Morphological (Nielsen & Davis, 1985) and mo-

lecular data (Brown et al., 1994; Pellmyr & Leebens-Mack, 1999) together suggest that the monobasic *Prodoxoides,* the only southern hemisphere prodoxid moth, is the basal genus in the family (Fig. 4). *Greya* is a diverse genus of boreal and temperate humid to semiarid areas of western North America (Davis et al., 1992), with the exception of a few basal members recently documented from easternmost Asia (Kozlov, 1996). *Tetragma* is confined to North America, whereas the large genus *Lampronia* is holarctic in distribution. These gen-

	Host families	Extant distribution
Cecidosidae	Anacardiaceae	S. America S. Africa New Zealand
Prodoxides (1)	Myrtaceae	S. America
Greya (18)	Saxifragaceae Apiaceae	W N. America E Asia
Tetragma (1)	Rosaceae	W N. America
Lampronia (27)	Rosaceae Grossulariaceae Saxifragaceae Betulaceae	Holarctic
Mesepiola (1)	Nolinaceae	W N. America
Prodoxus (11)	Agavaceae	N. America
Parategeticula (4)	Agavaceae	S N. America
Tegeticula (13)	Agavaceae	N. America

Cecidosidae-Prodoxidae split 95 Mya

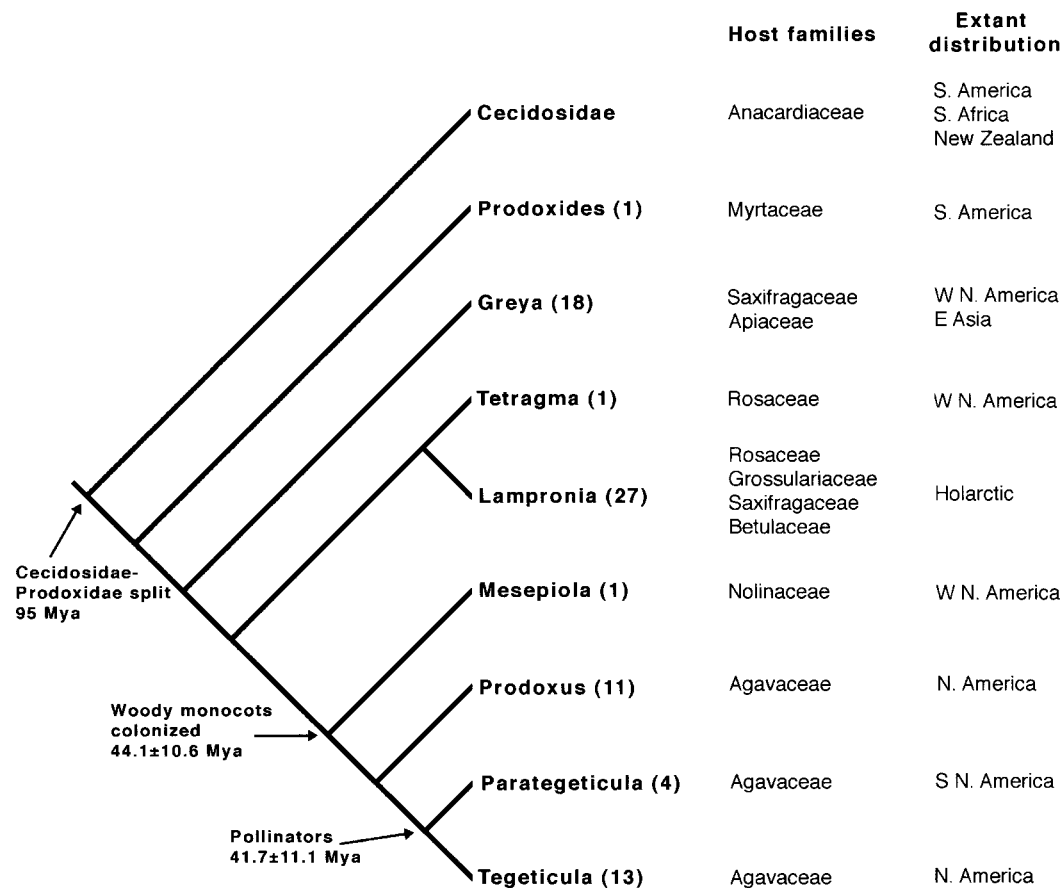Woody monocots colonized 44.1±10.6 Mya

Pollinators 41.7±11.1 Mya

Figure 4. Genus-level phylogeny for Prodoxidae, based on mtDNA and morphological data, with information on plant host families and extant distribution. Estimated minimum dates for seminal events and trait origins are based on a molecular clock, calibrated based on biogeographic data from the sister family Cecidosidae. Tree information and dates from Pellmyr and Leebens-Mack (1999). Numbers in parentheses are numbers of described species.

era use a remarkable variety of host plants, including species of the Myrtaceae, Apiaceae, Rosaceae, Grossulariaceae, and Saxifragaceae, i.e., representatives from four plant orders (APG, 1998). In cases where immature stages are known, the larva feeds inside plant tissue during early instars, and then from the outside while concealed inside folded leaves or cases during the final instars of development (Davis, 1987; Davis et al., 1992).

Colonization of woody monocots, first observed in *Mesepiola,* coincides with colonization of arid habitats and a concurrent change in life habit to having larvae that feed inside host tissue until feeding is complete (Davis, 1967; Frack, 1982). *Mesepiola* feed on members of Nolinaceae, whereas the three yucca moth genera *Prodoxus, Parategeticula,* and *Tegeticula* feed on members of Agavaceae. *Prodoxus* (the "bogus yucca moths" of Riley (1880)) coexist with the two other genera, but feed on tis-

sues other than the seeds. They are not involved in pollination. Virtually all yuccas host *Prodoxus* species that feed inside the inflorescence scape, and most fleshy-fruited and spongy-fruited yuccas also host species that feed inside hardening galls in the exo- or mesocarp portion of the fruit. The recently described *Prodoxus phylloryctus* Wagner & Powell is so far unique within the genus in feeding as a communal gall-maker in fleshy yucca leaves (Wagner & Powell, 1988). In addition, the peduncles of at least six *Agave* species are used (Frack, 1982) by some *Prodoxus* species. I will not deal with them further here, as they are not directly involved in the pollination mutualism.

The pollinating yucca moths belong in the genera *Parategeticula* and *Tegeticula. Parategeticula,* with four described species (Pellmyr & Balcázar-Lara, 2000), is unique in having lost the linear cutting ovipositor of prodoxid moths used for inserting eggs

into plant tissue, and instead their thick blunt ovipositor is used in creating a groove on the surface where eggs are laid (Davis, 1967; Powell, 1984). In species with known biology, they also differ in that the larva bores into the young fruit, where it causes the formation of a gall-like structure ("cyst" of Powell, 1984) formed from modified placental tissue and a few immature seeds that in effect fuse and are consumed from within. *Tegeticula* was until recently held to consist of three species (*T. maculata* (Riley), *T. synthetica* (Riley), and *T. yuccasella*) with broadly similar life histories (Baker, 1986). Morphological variation had long been reported within *T. yuccasella* but considered as intraspecific variation (Busck, 1947; Davis, 1967); Davis (1967: 53) stated that more than one "biological entity" may exist, but refrained from delimitation on the grounds of insufficient information. Miles (1983) used morphometric data to demonstrate the presence of at least three unnamed host-specific entities. Further studies using morphological and molecular tools have so far led to the description of 13 species (Pellmyr, 1999), and several additional taxa remain to be described (Pellmyr & Balcázar-Lara, in prep.). *Tegeticula maculata* is morphologically and molecularly highly divergent and may well consist of several biological species (Powell & Mackie, 1966; Segraves & Pellmyr, 2001), and *T. synthetica* as currently circumscribed contains two species (Pellmyr, in prep.). All species consume seeds as larvae, but there is variation in oviposition timing and location. Pollinators oviposit at the time of flowering, but *Tegeticula* species, sometimes referred to as "cheater yucca moths," delay oviposition to the fruit stage and have independently lost the behavioral and morphological traits of active pollination (Pellmyr et al., 1996a; Pellmyr & Krenn, 2002). Intrageneric phylogenetic information for *Parategeticula* and *Tegeticula* is relatively well established (Pellmyr & Leebens-Mack, 2000), with the major remaining uncertainties revolving around a rapid burst of radiation creating most lineages within the *T. yuccasella* complex and the inclusion of remaining undescribed species primarily from the southern portion of the range. A note of caution about older publications involving the moths of the *T. yuccasella* complex is indicated: because of the historical lumping, many studies must be interpreted very cautiously and are sometimes of little value, as studied species are not identifiable and because as many as three coexisting species may have been treated as one.

Basic ecology of the plant-pollinator interactions. There is considerable variation in the eco-

logical aspects of interactions among both yuccas and the moths, and here I only outline major shared elements. The female yucca moth of both pollinator genera is equipped with unique tentacular mouthparts that she uses for pollen handling (Riley, 1892; Davis, 1967; Fig. 5A). She collects pollen from yucca flowers by dragging her tentacles across the anthers. The pollen is embedded in copious pollen kitt, almost to the point of floating in a semiliquid matrix in *Hesperoyucca,* and often comes off as a unit from the anther. The moth compacts the pollen using the tentacles, and then stores it as a batch underneath her head (Fig. 5A, B). The pollen is kept in place by adhesion alone, and the tentacles play no part in holding it in place. This load can be substantial, reaching nearly 10,000 grains in *Tegeticula yuccasella* females, and constituting nearly 10 percent of the moth's body weight (Pellmyr, 1997). Pollen collection can recur on an occasional basis during the active life of the female, so her pollen load may consist of multiple pollen genotypes. Following pollen collection, the female seeks out flowers of her host species for the purpose of finding suitable oviposition sites. Under most circumstances, only first-night flowers tend to be accepted but under some circumstances older flowers may also be subject to oviposition (Riley, 1889). In *Tegeticula,* the female first walks around the ovary, and her decision whether to oviposit is influenced not only by the flower itself but at least in some species also by its visitation history (Addicott & Tyre, 1995; Huth & Pellmyr, 1999). In *T. yuccasella,* females deposit a host-marking pheromone during oviposition, and subsequent visitors perform a crude estimation of pheromone quantity (Huth & Pellmyr, 1999). Visitors become increasingly unlikely to accept a flower with increasing number of prior visits. In one case of two coexisting pollinators, one species responded to visitation history whereas the other made oviposition choices independent of number of prior visits (Addicott & Tyre, 1995). If the female decides to oviposit, she positions herself in a species-specific location on the ovary and cuts into it (Fig. 5C). Most species penetrate the ovary wall and lay eggs inside the locule, but a few species oviposit very superficially under the epidermis. The female then uses the tips of her tentacles to scrape off a small amount of pollen from her batch, walks up to the stigma, and places the pollen on the papillose internal surfaces of the perforate style using a series of 10–20 bobbing movements (Fig. 5C, E). The only exception in this regard is *T. maculata,* which pollinates the capitate stigma of *Hesperoyucca whipplei* Torr. using the same scraping behavior as is used for pollen col-
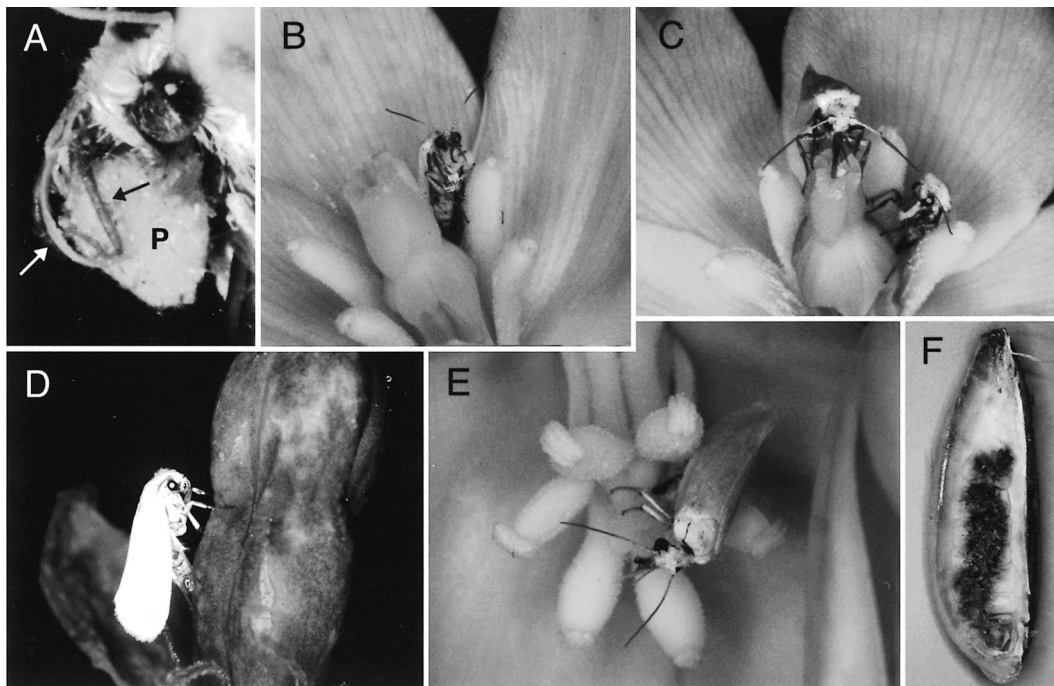
Figure 5. —A. Head of *Tegeticula carnerosanella* female. Large pollen load (P) held below the head, with left tentacle and proboscis indicated by black and white arrows. Cross section of tentacle 1.0 mm. —B. Female *T. yuccasella* compacting pollen just collected from a *Y. filamentosa* stamen. —C. Females of *T. yuccasella* pollinating (top) and ovipositing into (right) a *Y. filamentosa* ovary. —D. Female *T. intermedia* ovipositing into a ca. 8-day-old *Y. filamentosa* fruit; note constriction caused by *T. yuccasella* ovipositions. —E. *T. treculeanella* female pollinating *Y. treculeana* Carrière flower. Moth wing length in panels B–E 10–11 mm. —F. Longitudinal section through locule of mature *Y. carnerosana* (Trel.) McKelv. fruit, showing feeding path of *T. carnerosanella* larva that has destroyed seven seeds; fruit length 73 mm. For a set of color pictures of *T. yuccasella* behavior on *Y. filamentosa*, see Murawski (1997).

lection. A female may repeat oviposition and pollination many times on a flower, especially if she started on a virgin flower. In *T. yuccasella,* pollination almost invariably happens following the first oviposition on a flower, but females then become increasingly likely to skip pollination during subsequent oviposition bouts, and they also deposit less pollen per pollination event (Huth & Pellmyr, 1999). Females of the species that encounter a flower visited by one other female first typically perform about half as many ovipositions and pollinations as the first female (Huth & Pellmyr, 1999), and a smaller yet significant reduction was observed in *T. altiplanella* Pellmyr (Addicott & Tyre, 1995, referred to as "deeps"). Once a female moves on, she usually walks to adjacent flowers and inspects them for suitability, then visits other side branches, and eventually she flies off to other inflorescences. Consequently, females perform both geitonogamous and xenogamous pollinations (Riley, 1892; Fuller, 1990; Dodd & Linhart, 1994; Pellmyr et al., 1997; Marr et al., 2000); there is no experimental evidence of plant self-incompatibility and

fruit set readily occurs following both types of pollination, but selfed fruits are highly susceptible to abscission when they develop in competition with outcrossed fruits (Pellmyr et al., 1997; Richter & Weis, 1998; Huth & Pellmyr, 2000).

Eggs of *Tegeticula* hatch within a few days, and larvae of species that lay eggs inside the locule start feeding on seeds immediately. In species that oviposit superficially, the larva first burrows in the ovary wall before entering the locule to feed on seeds (Wilson & Addicott, 1998; Pellmyr & Leebens-Mack, 2000). Larvae consume a variable number of seeds (Fig. 5F), depending on the species and factors such as the presence of abortive seeds that can reduce per capita consumption (Powell, 1984; Ziv & Bronstein, 1996; Bronstein & Ziv, 1997). Upon completion of feeding, the larva creates an exit path. It preferentially exits during rain, either night or day (Whitten, 1894), but perhaps more commonly at night (Groman & Pellmyr, unpublished data), and can spend extended time waiting inside the fruit for optimal conditions (Powell & Mackie, 1966). The larva burrows into the

ground, where it creates a silk-lined cocoon covered with soil or sand particles. The exact location in the ground has never been reported, but from lab trials Riley (1873) reported depths of 7.5–10 cm and Rau (1945) 2.5–7.5 cm for *T. yuccasella* and perhaps also *T. intermedia* Pellmyr. Powell (1984) reported depths of 1–3 cm in shallow containers for *T. maderae* Pellmyr. The larvae of five *Tegeticula* species (*T. yuccasella, T. intermedia, T. cassandra* Pellmyr, *T. treculeanella* Pellmyr, *T. carnerosanella* Pellmyr) reared in my lab commonly created their cocoons at a depth of 20 cm where they reached the impenetrable bottom of the rearing canisters. The variation in reported depths among *Tegeticula* species may at least in part reflect depth of rearing canisters.

The larva enters diapause inside the cocoon and pupates a few weeks before emergence. This may happen after a one-year diapause, but the larvae can remain in diapause in lab conditions for at least four years (Riley, 1892). Very high fruit set during mass flowering episodes in yucca populations that then effectively cease flowering almost completely for several years (Pellmyr, unpublished data) suggests that the moth larvae are capable of diapausing for several years in the field as well, and that there are unidentified cues that trigger completion of development and adult moth emergence. This is not to suggest that moth emergence is perfectly synchronized with host flowering—we know it is not (Frack, 1982)—but rather that a sufficient number has remained in diapause to emerge at the time of mass flowering to cause high levels of pollination.

The life history of *Parategeticula* is known in less detail than that of *Tegeticula,* but oviposition and larval biology of one species, *P. pollenifera* Davis, has been described in detail by Davis (1967) and especially Powell (1984). The most obvious difference is that *Parategeticula* females oviposit on pedicels and in petals, rather than into the ovary. In this case, the larva chews its way into the ovary, and then proceeds to feed on partly modified seeds as described above. Larvae of *P. pollenifera* pupated at 1–3 cm in shallow containers (Powell, 1984), and *P. elephantipella* Pellmyr & Balcázar-Lara formed their cocoons at 2–4 cm depth in 15 cm of loose soil (Pellmyr & Balcázar-Lara, 2000). *Parategeticula pollenifera* from southern Arizona invariably required two years to complete development (Powell, 1984), whereas the tropical *P. elephantipella* emerged in the lab without a diapause (Pellmyr & Balcázar-Lara, 2000).

Patterns of host specificity. In the traditional recognition of four species of pollinating yucca moths, three species were monophagous and the fourth species (*T. yuccasella* s.l.) was held to pollinate all other yuccas. This appeared somewhat paradoxical, as most phytophagous insects show relatively high levels of host specificity (Ehrlich & Raven, 1964; Price, 1980; Farrell & Mitter, 1993; Thompson, 1994), especially when the phenological window for the insect to successfully oviposit is very narrow. Yucca moths, which only live for a few days (Kingsolver, 1984; Powell, 1984), must access the plant during the short flowering period, so moth populations would have to be locally adapted for the flowering periods of different hosts. For example, in areas such as the Big Bend region of the Chihuahuan desert, four yucca species coexist and have largely non-overlapping flowering periods spread out from February to early June. If a single pollinator species were to utilize all four species, this would require intraspecific polymorphism in emergence phenology with four distinct peaks in the moths. Busck (1947) and Davis (1967) speculated that *T. yuccasella* may be a complex, but suffered from a dearth of material available for study. The first solid data supporting the hypothesized complex were provided by Miles (1983), who showed that the pollinators of three sympatric yuccas in southern New Mexico differed greatly in morphology. She described the entities but did not formally name them. Addicott (1996) likewise provided morphometric data suggesting the existence of several more host-specific species, and Pellmyr et al. (1996a) provided molecular phylogenetic data indicating the presence of a large complex. Thirteen species, including eleven pollinator species, have since been described (Pellmyr, 1999).

Given the revised moth species delineation, diet breadth among the pollinators is now more uniform (Fig. 6). Using the yucca species delineations used in Pellmyr (1999), members of the *T. yuccasella* complex have been recorded from 17 host species. Seven of the eleven pollinator species within the complex are monophagous, one has two hosts, two have three hosts, and one has six recorded hosts. Thus more than 70% of all pollinator taxa are monophagous, and the most oligophagous species uses six host species. The reason for this level of specificity remains to be explored, but certainly involves phenological specialization on hosts and probably also selection for specialization on plants with critical differences in ovary morphology. Interestingly, the two derived non-pollinating yucca moth species are known to use four and six hosts, respectively, giving them a significantly broader host range than the pollinators with which they coexist (Kruskal-Wallis test, $\chi^2 = 5.68$, p = 0.017). Proximal rea-
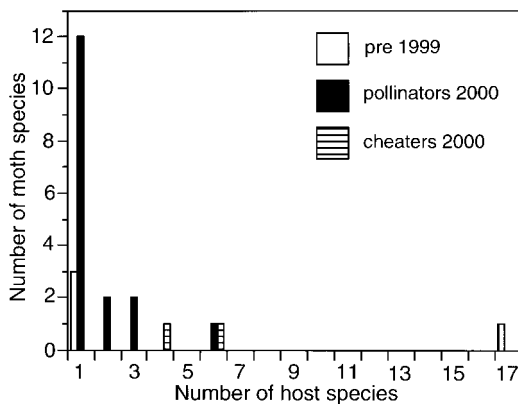
Figure 6. Number of recorded hosts of described *Tegeticula* and *Parategeticula* species. The two open bars give data for the four species recognized before 1999. Black bars give number of hosts for described pollinator species and striped bars derived non-pollinator species as of 2000. Cheater species have significantly more hosts per species than pollinator species (Kruskal-Wallis test, $\chi^2 = 5.68$, p = 0.017).

sons for the wider diet of non-pollinators remain to be explored. Because the non-pollinator larvae feed on seeds side by side with pollinators, diet is an unlikely explanation, but plausible hypotheses to test include a broader phenological window for species that oviposit into fruits, oviposition modes that are less likely to select for specialization, or higher potential for establishment on novel hosts through colonization because of limited resource competition with resident pollinators (Pellmyr & Leebens-Mack, 2000; Marr et al., 2001). Alternatively, it may reflect species age; because the non-pollinators are among the younger species in the complex, they have simply had less time available for potential diversification through host specialization.

The role of copollinators of yuccas. Suggestions of pollinators other than yucca moths appeared shortly after the original description of the plant-moth interaction, and this argument has resurfaced in the last decade, leading one monographer to the unfounded conclusion that "when moth populations are low, the fly *Pseudocalliope* may be an important alternate pollinator [of yuccas]" (Verhoek, 1998). For this reason, it is worth revisiting the support for this untested hypothesis.

I will discuss first all species other than *Yucca aloifolia,* which is a special case in this regard. The earliest claim of copollinators was made by Meehan (1879), who presented fruits resulting from geitonogamous hand-pollination on a cultivated *Y. glauca* Nutt. as evidence that other animals could serve as pollinators. In the absence of hand-pollination,

however, no fruit set occurred. Hulst (1886) was the first to use the fallacious argument of abundance of a particular visitor as evidence of pollinator function when stating that honey bees (*Apis mellifera* L.) can be copollinators. Frustrated with such untested hypotheses presumed to be true, Riley used a range of experimental and observational approaches to gather data to test them. Whereas he presented his conclusions in print (Riley, 1887, 1889, 1892), the original data were never published. Tabulated result sheets found in the archives of the Missouri Botanical Garden showed that inclusion experiments using two of the most common flower visitors, *A. mellifera* (25 bees, 72 hr.) and the soldier beetle *Chauliognathus pensylvanicus* de Geer (Cantharidae) (36 beetles, 24 hr.), in separate gauze bags containing single *Yucca filamentosa* L. inflorescences failed to result in any fruit development, whereas control inclusion experiments with yucca moths caused fruit production. Riley (1889, 1892) and Trelease (1893) further argued against copollinators on the basis of extensive visitor behavior observations. For example, honey bees were found to mostly lap the floral exterior for water and honeydew exudates, and when inside the flower probed the ovary base far away from the stigma. Similarly, other visitors also rarely moved close to the stigma. Riley (1881, 1892) also emphasized that plants in areas without moths, for example where plants recently had been put into cultivation, never had been found to set fruit, even though a wide array of other insects were found on the flowers. He also noted that in areas where an introduced yucca species coexisted with a native, moth-inhabited species with different flowering phenology, fruit set was never observed, whereas rare flowering coincidence of individual plants with a native yucca had been known to result in fruit set.

Speculation about copollinators was raised anew by Dodd and Linhart (1994). A lauxaniid fly (*Pseudocalliope* sp.) found in abundance on *Yucca glauca* flowers, with some individuals found to carry modest quantities of pollen on their bodies, was suggested as a possible vector. No attempt was made to test experimentally whether the flies cause pollination. There is reason for skepticism, because, as Riley (1892) first pointed out, lack of fruit set is common in yucca populations for a variety of reasons, yet flower visitors other than moths are often common in those same populations. Further, even if occasional modest pollen transfer were to take place through visitors other than the moths, it would likely be of little or no ecological and evolutionary significance. This follows because flowers

that receive small pollen loads or self pollen are highly susceptible to selective abscission (Richter & Weis, 1998; Huth & Pellmyr, 2000); thus a poor vector is expected to contribute minimally to plant fitness. The century-old hypothesis about existence of copollinators could readily be settled by the proper experiments. A simple experimental approach could exploit the size differences between yucca moths and proposed copollinators by using selective screens that permit entry to smaller visitors (such as the lauxaniid fly) but exclude the larger *Tegeticula* moths; this approach worked well in determining contributions to pollination by flies and bumblebees selectively screened on *Trollius europaeus* (Pellmyr, 1989). Given very high levels of genetic diversity in yuccas (Feist, 1995; Massey & Hamrick, 1998), routine genetic analyses of any resulting seed progenies could also provide information about selfing and outcrossing rates.

Yucca aloifolia is the single exception to the lack of evidence for pollinators other than the moths. Introduced as a garden plant in Europe no later than 1596, in Australia by 1885, and in Melanesia by 1880, it has been reported on several occasions to set fruit in locations outside North America even though there never have been any coincident moth reports. For example, Engelmann (1873) saw fruiting plants in Italy, Layard (1880) in gardens of New Caledonia on what undoubtedly was *Y. aloifolia* (MacKee, 1994), Riley (1891) conveyed a report from Australia, and Galil (1969) reported fruit set in a cultivated plant in Israel. The plant historically was scattered along the southeastern North American Atlantic and Gulf coast, especially along sandy shores from central North Carolina to eastern Louisiana (Fig. 3). Occasionally plants set fruit in parts of that range, typically as a result of colonization by *Tegeticula yuccasella* and *T. cassandra* from coexisting and simultaneously flowering *Y. filamentosa* (Engelmann, 1873; Riley, 1873; Pellmyr, 1999), but fruiting plants without oviposition scars or larval damage have also been reported (Riley, 1892; Groman, 1999). Riley hypothesized from floral structure that it may have resulted from autogamy, but Trelease (1893) found that he could prevent fruit set by excluding all floral visitors with a gauze bag in a plant that previously had produced fruit. This is the only reported experiment for any yucca that provides even moderate support for other visitors as copollinators. It needs to be replicated with reasonable sample size, and with inclusion as well as exclusion treatments.

The situation is more complex as *Yucca aloifolia* can have fruiting and non-fruiting inflorescences within populations and even individual plants

(Pellmyr, unpublished obs.). In sites with moths on other yuccas, it is generally explained by moths visiting only *Y. aloifolia* inflorescences that coincide with those of the native host (Riley, 1892). Elsewhere this cannot be the case. Conceivable explanations include intrapopulational variation in visitor guilds, and possibility of autogamy or geitonogamy, but they are relatively unlikely explanations in the first place, and no observational or experimental data exist to explore these or any other hypotheses. It is also possible that *Y. aloifolia* is under limited selection for maintaining sexual reproduction, as it reproduces very vigorously by vegetative propagation. This happens both through rapid clonal extension and establishment by broken-off plant parts (Brown, 1959); in coastal North Carolina, local residents disseminate the plant by cutting stems in 10-cm pieces that are tossed on the ground in disturbed sandy sites (J. Groman, pers. comm.). This habit of elevated vegetative propagation, absence of an endemic pollinator, core loss in the fruit, and poorly synchronized flowering spread across many months suggest that *Y. aloifolia* may be an escaped cultivar. Described from European gardens, Trelease (1893) referred to it as a species without a known geographical origin, and this is still the case. It is most closely related to *Y. elephantipes* and *Y. lacandonica,* which are tropical forest dwellers along the Gulf side of Mexico from Veracruz to Yucatan and into northern Belize (Matuda & Piña Lujan, 1980; Davidse et al., 1994); within this range, they set fruit through the actions of a specific yucca moth (Pellmyr & Balcázar-Lara, 2000, unpublished data) whereas plants are sterile elsewhere. This is most evident in *Y. elephantipes,* which is widely cultivated throughout Mexico and southward at least to Panama for its comestible flowers. *Yucca aloifolia* has been reported from Mexico (Matuda & Piña Lujan, 1980), but examination of available herbarium collections at UNAM for their records indicates that these refer to cultivated specimens and to *Y. elephantipes* (Pellmyr & Balcázar-Lara, unpublished data). In addition to its distribution along the shoreline of southeastern North America, *Y. aloifolia* is reportedly also established on Cuba, Jamaica, the Bahamas and Bermuda (Trelease, 1902), where pre-Hispanic cultures are suggested to have used its roots for soap (Engelmann, 1873). This use, together with a disjunct geographic range from the remainder of the genus and traits characteristic of cultivated plants, makes plausible a hypothesis that *Y. aloifolia* originated from *Y. elephantipes* as a cultivar selected for its high vegetative propagation. If correct, phylogeographic studies are predicted to show a ge-

netically depauperate *Y. aloifolia* nested within *Y. elephantipes*. This would be an important analysis to perform from the perspective of the plant-pollinator association, as possible corroboration would imply that occasional fruit set in the absence of moths in *Y. aloifolia* is irrelevant to understanding diversification and coevolution of the plant-moth mutualism.

EVOLUTION OF THE MUTUALISM AND ITS ECOLOGICAL CONTEXT

The origin of the mutualism long remained unknown, and was subject to little speculation for more than a century after its initial discovery. Two limiting factors loom important in this context. First, life history differences and variation in outcomes of yucca-yucca moth interactions had yet to be discovered. The interactions between the four historically recognized yucca moth species (Davis, 1967; Powell, 1992) and yuccas were held to be obligate mutualisms, so there was no apparent transformation series to analyze. Second, and perhaps more important in retrospect, the phylogenetic framework of the yucca moths at the family and genus level was not determined until the 1980s (Frack, 1982; Nielsen & Davis, 1985). At that time, life history data also started to appear for the closely related genera of prodoxid moths (Frack, 1982; Davis et al., 1992).

A timeline for establishment of the yucca-yucca moth mutualism. The fossil record is quite poor for these plants and effectively absent for the moths, providing little assistance in dating the establishment and diversification of the plant-pollinator association. The only pre-Pleistocene yucca macrofossil is a 14-My old trunk segment described as *Protoyucca shadishii* Tidwell & Parker from Nevada, most resembling the extant *Yucca brevifolia* (Tidwell & Parker, 1990). Fossil pollen described as *Agave* has been described from the mid Miocene (Axelrod, 1979; Palacios & Rzedowski, 1993). Bremer (2000) used clocklike behavior in *rbc*L to estimate the minimum age of the Funkiaceae, which is the sister family of Agavaceae + Camassiaceae (Pfosser & Speta, 1999), at 21 My, whereas Eguiarte (1995) provided an independent *rbc*L-based estimate for the Agavaceae of 14 My. For the moths, a mitochondrial DNA sequence data set was used to estimate age of their diversification, using biogeographic events for calibration (Fig. 4; Pellmyr & Leebens-Mack, 1999). Colonization of yuccas as a host was estimated at having occurred about 41.7 Mya, with the diversification of the three genera that inhabit yuccas being so rapid that their dates

overlap. Importantly, this narrow time window includes the split between the two pollinator genera as well as the most basal split within *Tegeticula* (between *T. maculata* and all other species), showing that the pollination habit was established in a common ancestor very close in time to the colonization of the yuccas by prodoxid moths. Given this rapid diversification of the moth lineages, we can infer that a basal radiation of yuccas was in existence by this mid Eocene date, pre-dating current independent estimates for the plants. For comparison, there is strong molecular data from several fig wasp lineages suggesting that the obligate mutualism between figs and fig wasps had originated by the late Cretaceous, some 90 Mya (Machado et al., 2001).

PATTERNS OF TRAIT EVOLUTION IN PRODOXIDAE LEADING TO OBLIGATE MUTUALISM

The obligate mutualism between the moths and yuccas could have originated either through extensive trait-level evolution, or it could have been precipitated in interactions where only minor quantitative changes in preexisting traits would be required to switch the outcome from antagonism to mutualism. This would happen, for example, by variation in outcome based on ecological context. Studies of the biology of more basal prodoxid moths that do not feed on yuccas lend support for this model of pre-adaptations, and also reveal two separate origins of pollination mutualism between three members of the genus *Greya* and their saxifragaceous hosts (Pellmyr et al., 1996a).

The first studies were made of *Greya politella* (Walsingham), a specialist of several species of *Lithophragma* (Saxifragaceae) (Pellmyr & Thompson, 1992; Thompson & Pellmyr, 1992). The female moth oviposits into the ovary through the tubular hypanthium, and pollen often is transported on an elongated abdominal segment. Experiments showed that oviposition was a highly effective pollination behavior. At study sites in Washington, an extensive guild of copollinators of mostly bombyliid flies and solitary bees also provided cross-pollination. Although none of the copollinator species was as effective per visit as the ovipositing moths, their relative abundance and far higher rate of visitation made them important contributors to pollination in the study population. In two years of study, *G. politella* was estimated to have contributed 0.8–2% of all seed set in the study population. Their positive effect was effectively masked, as there was no significant effect of moth oviposition on net seed set. Their negative effect through larval seed consump-

tion was also masked by other sources of variation in seed production. The outcome of this moth-plant interaction is thus strongly dependent on copollinator contributions, as there will be no selection on moths for improved pollination efficiency unless it is tied to fitness differences. The same result was found for *Greya enchrysa* Davis & Pellmyr, a highly effective pollinator of its hosts in *Heuchera,* where abundant bumblebee visitors masked beneficial effects on seed set (Pellmyr et al., 1996b). In these interactions, variation in outcomes can be expected across the ranges of the species (Thompson & Pellmyr, 1992; Gomulkiewicz et al., 2000), potentially leading to sustained selection for a stronger mutualistic equilibrium between the moths and plants. The third case and second origin of pollination in *Greya* involves *G. mitellae* Davis & Pellmyr, a species whose larvae feed inside the flowering stalk and in leaf peduncles of *Mitella stauropetala* Piper. Moths pollinate while drinking nectar from the flowers. Whereas virtually all pollination was provided by the moths in study populations, no selection on increased pollination efficiency is expected in this interaction as larval fitness is unaffected by the incidental seed production during adult nectaring bouts. This case indicated that there must be a direct link between female pollination efficiency and progeny fitness to cause selection toward increased pollination efficiency and potentially obligate mutualism (Pellmyr et al., 1996a).

Mapping of several life history traits that were necessary prerequisites for the origin of the mutualistic behavior by yucca moths indicated that most traits were basal to prodoxid moths or at least had evolved before the lineage leading to the common ancestor of the pollinator genera. Hence this supported a scenario in which the life habits of prodoxid moths commonly have states that make pollinator function easy to acquire. At the same time, obligate mutualism that requires novel traits for highly effective pollination has only arisen once in the family, in the true yucca moths. Why did this happen in the yucca-yucca moth association, but not in the others? Pellmyr et al. (1996a) used ancestor reconstruction of the yuccas to erect a hypothesis in which highly effective pollination in the moths evolved first, followed by exclusion of ancestral copollinators through effective cessation of nectar production in the plants. A general feature of the Agavaceae is resource-limited fruit set (Sutherland, 1982), where only a minor fraction of all flowers give rise to mature fruit. As prodoxid moths colonized yucca ovaries, they thus encountered a major new mortality factor for their progeny, because all eggs inside pollinated flowers subsequent-

ly abscised will perish. Floral abscission is highly selective, with fertilized flowers resulting from small pollen loads or self pollen having a much elevated risk of abscission (Pellmyr et al., 1997; Richter & Weis, 1998; Huth & Pellmyr, 2000). For this reason, variation in pollination efficiency provided by female yucca moths can result in differential abscission of flowers containing moth eggs, as females providing large amounts of pollen decrease the risk of abortion. Importantly, this trait could evolve in the females against a background of relatively inefficient, nectar- and pollen-consuming floral visitors. In a second step, reciprocal specialization in the plants on the increasingly effective yucca moths is expected as the net fitness contributions attributable to the ancestral nectar-consuming visitors relative to energetic investments in the nectar reward became negative. Both selective abscission as a mortality factor and high cost of nectar production were novel traits to the yucca-yucca moth association in the sense that they are not present in the plant-moth interactions immediately basal to it, and they may point to factors that could facilitate similar transitions in other associations. Consistent with this prediction, much reduced nectar production and low fruit : flower ratio are characteristic of the recently described obligate mutualism in the Sonoran desert between the columnar cactus *Lophocereus schottii* and its pollinating moth, *Upiga virescens* (Holland & Fleming, 1999).

REVERSAL OF MUTUALISM

Mutualistic interactions contain an underlying evolutionary conflict in that the interacting partners are under selection for increased exploitation of each other (Trivers, 1971; Bull & Rice, 1991; Pellmyr & Huth, 1994). In a plant-pollinator relationship, this might manifest as selection for higher efficiency in reward extraction among pollinators, and smaller or more inaccessible rewards in the plants. In facultative relationships, such conflicts may result in arms races that shut out excessive exploiters. For example, a decreasingly rewarding plant species may be abandoned by flower visitors that have a choice, while plant traits that reduce losses to poor pollinators in theory can evolve to complete exclusion. In obligate mutualisms that involve a single pollinator and plant, this conflict has a potentially different dynamic. In such instances, the evolution of a cheating mutant with a fitness advantage over mutualist individuals is expected to lead to reciprocal extinction of the mutualists, at least at the population level and possibly on a spe-

cies scale, depending on patterns of gene flow. For this reason, obligate mutualisms such as those between yuccas and yucca moths were long considered evolutionary dead ends (Soberon Mainero & Martinez del Rio, 1985; Bull & Rice, 1991). This is clearly not the case under all circumstances, as two distinct species of non-pollinating cheater yucca moths derived from pollinating ancestors have been identified (Pellmyr et al., 1996a). The two described species, *Tegeticula intermedia* and *T. corruptrix* Pellmyr, oviposit directly into fruits at different stages of development, and the larvae consume seeds in coexistence with larvae of the pollinator species (Fig. 5D). Their presence can be very costly for host seed production; in one study of *Y. filamentosa,* seed destruction was tripled in populations where cheater moths coexisted with pollinator moths (Pellmyr et al., 1996a). Ecological data did not reveal any competition between coexisting larvae of the pollinator *T. yuccasella* and the cheater *T. intermedia* (Marr et al., 2001), so coexistence is evidently not a problem, but the separate issue of an evolutionarily stable origin of the cheater life habit remains to be explained.

Phylogenetic analyses based on mitochondrial DNA sequence data suggest that the two species originated separately around 1.26 ± 0.9 Mya; thus these are not ephemeral lineages (Pellmyr et al., 1996a; Pellmyr & Leebens-Mack, 1999). A simple solution to the problem of escaping the evolutionary dead end of obligate mutualism is coexistence of two or more mutualists on a shared partner. For example, if two yucca moths were to coexist on one yucca species, one moth species could evolve the cheater habit without causing failure of sexual reproduction in the yucca. In this situation, reciprocal extinction is only expected if both mutualists independently abandon the pollinator habit. With the recent recognition of a large number of pollinator species, it has become apparent that coexistence of pollinator moth species is not uncommon, with at least five documented instances of two pollinators sharing a host in all or part of its range (Davis, 1967; Powell, 1984; Tyre & Addicott, 1993; Pellmyr, 1999; Pellmyr & Balcázar-Lara, 2000; Pellmyr & Leebens-Mack, 2000). One of those sympatry zones is implicated in the origin of *T. intermedia.* This species is most closely related to the pollinator *T. cassandra,* and available data suggest that it may have evolved where *T. cassandra* came into coexistence with *T. yuccasella* in part of its range. The pollinating sister species of both *T. intermedia* and the other cheater species oviposit in a way that distinguishes them from all other pollinator species, and they have a characteristic ovi-

positor that allows them to oviposit into either a flower or a young fruit. Thus, these pollinators may be preadapted for a switch to oviposition into fruit once a sympatric pollinator species is available to perpetuate pollination. Because of a selective abscission mechanism in the yuccas that causes flowers with many moth eggs of most pollinator species to be abscised within a few days of pollination, a large proportion of the seeds are simply not accessible for larval consumption by these pollinator species. Hence, a pollinator species that can delay oviposition by a few days and oviposits directly into young fruits can bypass the plant's abscission period and exploit a rich seed resource. In this scenario, the phenological shift can be an adaptive step into a novel niche that precedes the loss of pollination habit, which becomes redundant once fruits become the target of oviposition. Available data thus suggest that the origin of cheater yucca moths from pollinators did not result from selection for cheating per se, but rather as a byproduct of selection for exploitation of a previously untapped seed source (Pellmyr & Leebens-Mack, 2000).

By analogy to evolution of non-cooperative pollinators, it is in theory possible that cheating plants could arise in an obligate mutualism. In the case of yucca plants, that would entail the evolution of mechanisms that maintain pollination but prevent seed destruction by pollinator larvae. This could happen through mechanisms such as prevention of successful oviposition, or killing of the eggs or larvae. If an alternative, cooperative host species exists in the area, such cheating by plants could be evolutionarily stable, whereas evolution of cheating plants in a single plant-single pollinator scenario is predicted to lead to extinction (Bull & Rice, 1991). The only proposed case thus far involves a population of *Yucca baccata* Torr., where Bao and Addicott (1998) reported that the fruits of a substantial proportion of all plants lacked evidence of larval damage, and speculated that this might be evidence of a cheating mechanism in these plants. They did not speculate regarding a mechanistic basis, but mentioned that fruits without larvae had a distinctive shape. Further studies will be needed to determine whether a cheating mechanism indeed is in place.

It should be emphasized that the strongest, most direct evidence for selection for cheating in a mutualism would be direct evidence of individual lifetime fitness gains. Such data are wanting for both yuccas and moths, and it is difficult to accrue such data. The major obstacle in measuring moth lifetime fitness has been difficulty to track them during extended flight; it is likely a matter of time before
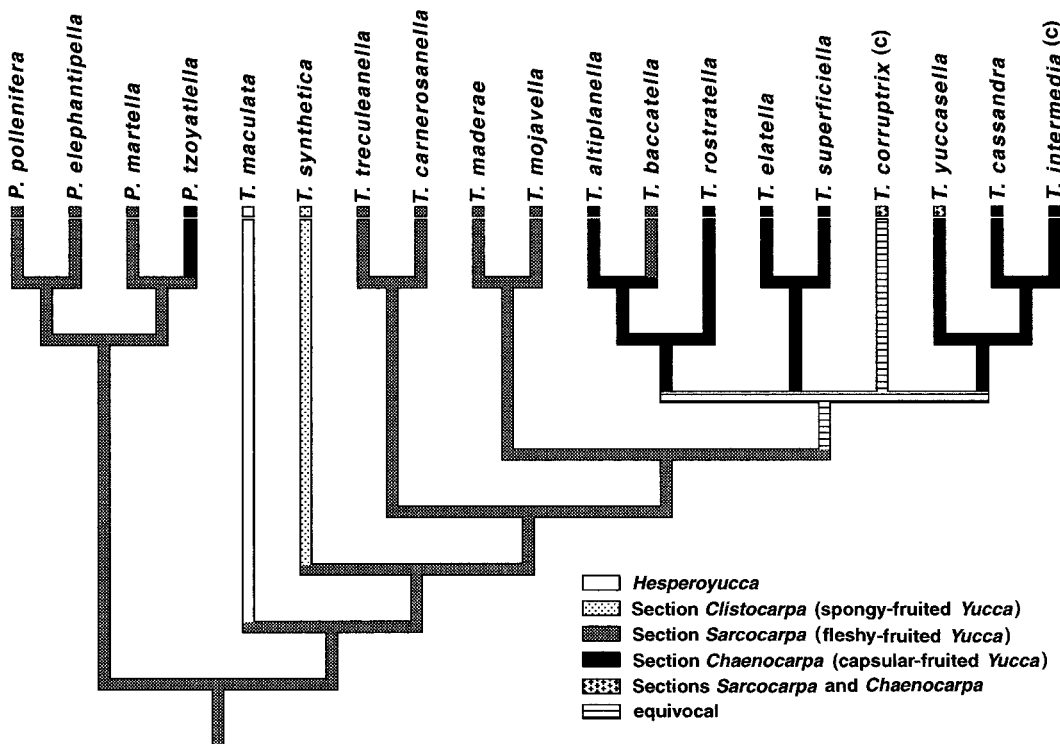
Figure 7. Phylogeny of *Parategeticula* and *Tegeticula*, tracking host use for each species. A "(c)" following the name indicates that it is a cheater species. Two, three, or four origins of *Yucca* sect. *Sarcocarpa* use are indicated and two or three origins of *Y.* sect. *Chaenocarpa* use. Phylogeny from Pellmyr and Leebens-Mack (2000), host records from Pellmyr (1999) and Pellmyr and Balcázar-Lara (2000).

suitable technological tools will be available to solve this problem. In the yuccas, longevity of decades or centuries (McKelvey, 1938; Webber, 1953; Matuda & Piña Lujan, 1980; Webb, 1996; Comanor & Clark, 2000), with iteroparity in all but one species, and also different magnitude and possible plasticity in vegetative propagation, makes it difficult ever to measure lifetime fitness. In consequence, surrogate measures, such as intact seed production in the plants, are the best available option.

PARALLEL SPECIATION AND THE ROLE OF COEVOLUTION IN PLANT-MOTH DIVERSIFICATION

When species are tightly associated, there is a probability that they may co-speciate (Eichler, 1948; Huelsenbeck et al., 2000). Such parallel diversification may result either from vicariance-based divergence or from coevolutionary processes between the species (Page, 1994). For this reason, obligate pollination mutualisms between seed-parasitic pollinators and their hosts should be good candidates for parallel diversification, as potential divergence may derive from linked host speciali-

zation in the pollinators and pollen-mediated gene flow in the plants (Bogler et al., 1995; Pellmyr et al., 1996a). The fig-fig wasp associations and yucca-yucca moth associations are sufficiently speciose that analysis of parallel diversification is possible. Analyses of the association between figs and fig wasps have indeed indicated a high level of parallel diversification at the level of fig genera and subgenera (Herre et al., 1996), while there is emerging evidence that this pattern breaks down to a fair degree at lower taxonomic levels (Lopez-Vaamonde et al., 2001; Machado et al., 2001). Analysis for the yuccas and yucca moths is still rudimentary as the yucca phylogeny is incompletely resolved, and the unresolved polytomy in the moth phylogeny also limits analysis (Fig. 7). Given the current unresolved plant relationships, there are no strong candidates for parallel diversification, although this may change with increasing phylogenetic information. Meanwhile, several lines of evidence indicate that there are numerous instances where colonization has occurred. The most obvious instance involves recent colonization by *Tegeticula yuccasella* of *Yucca aloifolia*. Similarly, *T. baccatella* Pellmyr,

which feeds on a fleshy-fruited host, is nested amid species that feed on capsular-fruited yuccas (Fig. 7), and thus supports a past shift assuming that monophyly of fleshy-fruited yuccas is upheld. The cheater *T. corruptrix,* also arising from an ancestor on a capsular-fruited yucca (Fig. 7), now utilizes both fleshy-fruited and capsular-fruited species. Second, the coexistence on a host of non-sister taxa of *Tegeticula* pollinators cannot be explained by parallel diversification; in principle, coexistence of a *Parategeticula* and a *Tegeticula* pollinator on a host could reflect two independent parallel diversifications with the hosts, but there is very little support from published host data for this explanation (Fig. 7). Third, instances where a pollinator species utilizes more than one host species (Fig. 6) cannot reflect parallel diversification, although they may possibly reflect an ancestral association with subsequent unilateral diversification in a monophyletic group of hosts.

Co-speciation does not require coevolutionary processes, and coevolution can act on organisms regardless of their history of association; thus the role of coevolution in driving diversification between the plants and the pollinators is an altogether separate matter. Selection on plant and moth traits that vary among species may arise either from the interacting partners or from factors extrinsic to the interaction. For example, traits likely to affect moth oviposition success, such as floral ovary morphology and moth ovipositor morphology, may be strong candidates for reciprocal selection as they directly affect plant and pollinator fitness. Meanwhile, traits such as petal shape and color may be more likely to be under selection based on a wide range of antagonistic interactions with other herbivores, as well as abiotic factors. To determine the historical role of coevolution in the diversification of an interaction, variation in divergent traits must be partitioned to remove extrinsic components, i.e., in essence to remove background evolution in the interacting groups attributable to other factors. This obviously requires groups of plants and pollinators that have coexisted during much or all of their diversification, as is the case for yuccas and yucca moths. It also requires well-resolved phylogenies, preferably with estimates of internal branch lengths. This criterion is not yet met for the yucca-yucca moth association, nor for any other similar plant-pollinator association. Such analyses will be highly useful in evaluating the historical role of coevolution in driving diversification and speciation in plants and pollinators.

CONCLUSION

It may seem a somewhat subdued note on which to end, that we cannot yet perform rigorous tests of the role of coevolution in the diversification of yuccas and yucca moths. But the reason is simply that a large amount of information about morphology, ecology, natural history, and phylogeny is required for any one association before analyses of the historical impact of coevolution can be explored. Most, but not all, of these requirements are now largely met. The last 15 years have seen a dramatic increase in our understanding of organismal diversity, especially among the insects, although much information from the Mexican range of the yucca-yucca moth associations remains to be published. Ecological and evolutionary dynamics have also become far better understood in the last decade, including the expansion into the realm of reversal of mutualism. Phylogenetic information is now arguably the primary limiting factor for analyses of coevolution and several other major questions, but there is reason to hope that robust information soon will be available for both groups. Ongoing parallel projects on subsets of fig-fig wasp associations (e.g., Lopez-Vaamonde et al., 2001; Machado et al., 2001; Weiblen & Bush, 2002) as well as other mutualisms involving seed-parasitic pollinators (Després et al., 2002) also offer possibilities for grander comparisons across mutualisms in the next few years. Whatever generalizations about factors mediating plant-pollinator mutualisms emerge from these highly specific associations can soon be used as a template in analyzing other, more complex plant-pollinator mutualisms.

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