

Pollinator Divergence within an Obligate Mutualism: Two *Yucca* Moth Species (Lepidoptera; Prodoxidae: *Tegeticula*) on the Joshua Tree (*Yucca brevifolia*; Agavaceae)

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ABSTRACT *Yucca* moths are widely recognized for their role as highly specific pollinators and seed-eaters on yuccas, making them part of one of the major models of obligate mutualism. Here we describe *Tegeticula antiithetica* Pellmyr (Lepidoptera: Prodoxidae), a new pollinator species of *Yucca brevifolia* (Joshua tree). Biological information is provided. Molecular phylogenetic data show the two pollinators of *Y. brevifolia* to be sister taxa, and a molecular clock estimates their divergence to ≈ 10.7 million years ago. This is the first documented instance of pollinator moth divergence and speciation within a host plant. The known geographic ranges of the two species do not overlap. We discuss the historical biogeography of *Y. brevifolia* and its implications for moth diversification.

KEY WORDS *Tegeticula*, Prodoxidae, coevolution, phylogeography, Mojave desert

YUCCA MOTHS (*Tegeticula* and *Parategeticula*) are widely recognized in studies of coevolution because of their role as exclusive pollinators of yuccas (Riley 1892, Davis 1967, Powell 1992, Pellmyr 2003). At this time, 19 species are recognized, including 2 species that have lost the pollinator habit (Pellmyr 1999, Pellmyr and Balcázar-Lara 2000, Pellmyr and Leebens-Mack 2000). Like other seed-parasitic insects involved in obligate mutualism with their hosts (Fleming and Holland 1998, Weiblen 2002, Kato et al. 2003), these species are generally highly host-specific. More than two-thirds of the described pollinating yucca moths are monophagous (Pellmyr 2003), and the species with the broadest diet has been recorded from seven yuccas (Pellmyr 2003).

This kind of obligate mutualism is widely believed to increase the probability of parallel diversification between the interacting organisms, in part because of high specificity and the risks of extinction that derive from defection in obligate mutualism. In figs and fig wasps, reciprocal diversification has been detected at several taxonomic levels (Weiblen 2002), and unilateral diversification in the pollinators has recently been reported in pollinating wasps (Molbo et al. 2003). In yucca moths and yuccas, the lack of a well-resolved species-level phylogeny for yuccas has hampered analyses of reciprocal diversification. Here we report that one of the most phylogenetically isolated yuccas, *Yucca brevifolia* (Joshua tree), has two distinct pollinator species in different parts of its range. We describe the new pollinator species, provide phylogenetic data, and provide evidence for an old divergence

between the two pollinators of this prominent yucca. This is the first documented instance of pollinator speciation within a yucca species.

Materials and Methods

Specimens were collected as adults while resting inside flowers during the day or as larvae inside host fruit. Moths were either prepared for morphological study or placed in a -80°C freezer for subsequent molecular phylogenetic studies. Gross morphological measurements and genitalic dissections were performed as described in Pellmyr (1999), except that no staining was necessary for analysis. All specimens examined were used for gross morphology, and three sets of male and female genitalia were used for the two species under study. Whole-moth and slide-mounted genitalia illustrations were prepared by digital capture using a Nikon Coolpix 4500 camera (Nikon, Toyko, Japan) mounted on an Olympus SZX-9 microscope (Olympus Optical, Tokyo, Japan). Images were processed in Adobe Photoshop 7.0 (Adobe Systems, San Jose, CA). Collection abbreviations are as follows: LACM, Los Angeles Natural History Museum; UCB, University of California Berkeley; USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC; OP, Olle Pellmyr, to be transferred to USNM.

The phylogenetic position of the new species was estimated in a phylogenetic analysis based on mitochondrial DNA sequence data. Sequence data for a 1998-bp segment of the cytochrome oxidase I and II region of mtDNA were available for all described *Tegeticula* species and for the sister genus *Para-*

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Table 1. Samples used in phylogenetic analysis

Species	Locality	Genbank no.
<i>P. tzoyatllella</i> Pellmyr and Balcázar-Lara	Mexico: eastern Coahuila	AF150924
<i>T. m. maculata</i> (Riley)	USA: Tulare Co., CA	U49024
<i>T. m. extranea</i> (Edwards)	USA: Riverside Co., CA	U49023
<i>T. antithetica</i> Pellmyr	USA: Kern Co., NV	U49025
<i>T. synthetica</i> (Riley)	USA: Los Angeles Co., CA	AY327144
<i>T. treculeanella</i> Pellmyr	USA: Brewster Co., TX	U49041
<i>T. rostratella</i> Pellmyr	USA: Brewster Co., TX	AY004295
<i>T. yuccasella</i> (Riley)	USA: Wilson Co., TN	U49032

tegeticula (Pellmyr and Leebens-Mack 2000). The sequence, which was originally named *T. synthetica* in GenBank (U49025) and was from southern Nevada, was found to be the new species on re-examination. For this reason, a new sequence of *T. synthetica* was determined from a larva collected near Palmdale, CA, ≈ 50 km south of the type locality in Mojave, Kern Co. DNA extraction and sequencing protocol followed those described in Pellmyr and Leebens-Mack (2000). In addition to *T. antithetica* and *T. synthetica*, the analyses included three divergent species within the *T. yuccasella* complex and the two subspecies of the basal *T. maculata* (Table 1). *Parategeticula tzoyatllella* of the *Tegeticula* sister group was used as an outgroup based on the analysis by Pellmyr and Leebens-Mack (1999). Sample data and GenBank numbers are given in Table 1.

We used both maximum likelihood and Bayesian approaches (Huelsenbeck et al. 2001, Felsenstein 2003) to infer the phylogenetic relationships of the moths. The maximum likelihood analysis was implemented in PAUP* 4.0b10 (Swofford 2002). The model of evolution was selected using hierarchical likelihood-ratio tests involving an initial neighbor-joining search with LogDet distances to identify a tree. This model of evolution was used in a subsequent tree search under maximum likelihood to find the best tree. One hundred bootstrap replicates were generated to estimate support for the resulting tree topology. The Bayesian analysis was performed using MrBAYES 3.0* (Huelsenbeck and Ronquist 2001), and the same model of evolution was used from the maximum likelihood analysis. Starting trees were random and four Markov chains were run for 2,000,000 generations (three heated and one cold). Trees were sampled every 100 generations, producing an initial sample of 20,001 trees. The likelihood values stabilized after 40–50 trees; therefore, the first 100 trees were discarded. Posterior probabilities were thus determined from a sample of 19,901 trees. The Bayesian analysis was performed three times to ensure that the trees converged on similar results.

Results

Description of *Tegeticula antithetica* Pellmyr, new species (*Tegeticula synthetica* auct)

Wingspan in male, 13.5–15 mm; female, 13–16 mm (Fig. 1, A and C). Integument dark brown, contrib-

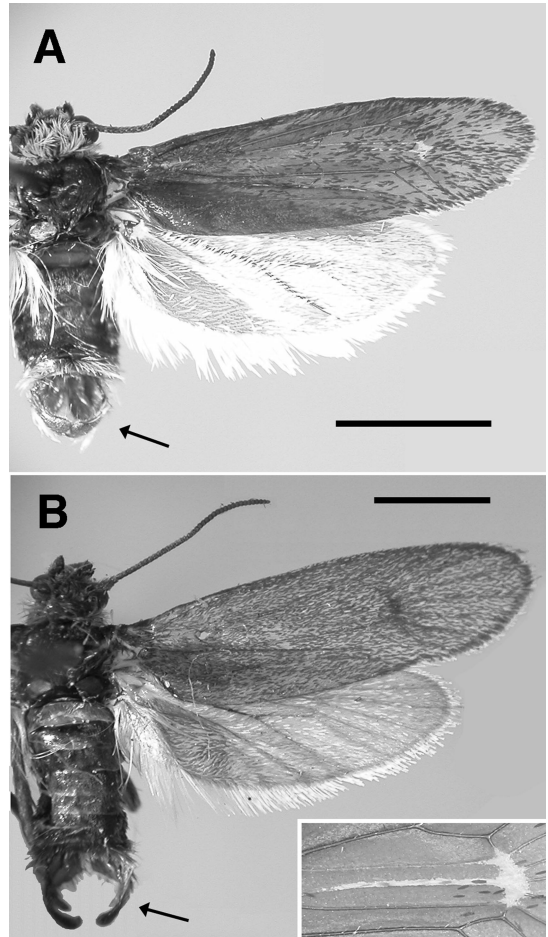


Fig. 1. Males of (A) *T. antithetica* and (B) *T. synthetica*. (C) Enlarged arrow-shaped mark in discal cell of *T. antithetica*. Scale bars in A and B are 2.5 mm. Note the different appearances of valvae (arrows) in A and B. Light hind wing in A results from reflecting glare; it is actually as dark overall as in the anal field.

uting strongly to perceived color because of limited vestiture. **Head.** With linear tan scales. Dark brown five-segmented maxillary palp with fully developed brown tentacle apically on first segment in female; at most a prominence in male. Labial palp three-segmented, with brown linear scales ventrally on second segment, narrow tan scales from distal second to terminal segments; female with 20–25 sensory setae ventrally on second segment; none in males. Proboscis amber, lighter than maxillary palp. Antenna ≈ 0.35 – $0.40\times$ length of forewing, with 33–34 segments; tan linear scales scattered dorsally on basal half, remainder dark brown. **Thorax.** Dark brown integument, very lightly covered with tan scales. Legs lighter distally, with dark brown femora and tibia, and brown tarsi. Epiphysis present. Forewing length in male 5.8–6.8 mm; female 5.6–7.0 mm; width in male 1.7–2.0 mm; female 1.8–1.9 mm; wing scaling quite sparse; integument dark gray except for a clear hemispheric or

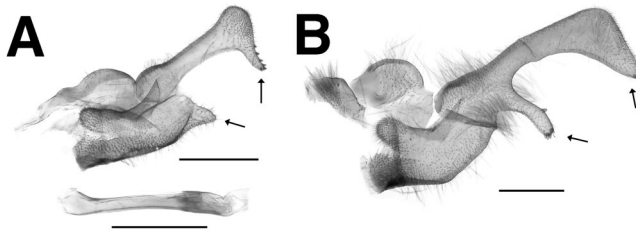


Fig. 2. Male genitalia of (A) *T. antithetica* and (B) *T. syntheticca*. Right valva (top) shown for both; aedeagus (below) only for *antithetica*. Note shape differences in ventral protrusions (arrows) of the valva and differences in spine number and distribution on those protrusions between the taxa. Scale bars = 0.5 mm.

blunt triangular patch distally in discal cell; in most specimens also a connected clear streak extending inward part of discal cell, creating the appearance of a blunt-tipped arrow. Cubital cell with narrow clear streak. Underside sparsely scaled in light tan. Fringe white. Hindwing with integument dark gray, with light tan scales above and below; fringe near white, with outer third near apex gray. *Abdomen*. With brownish black scaling. Seventh tergite in female broadly triangular, with dorsoventral regions lighter. In male, edge of last segment and valva with linear amber scales. In female, ovipositor angled downward 60–90° from abdominal axis. *Male genitalia* (Fig. 2, A and B). Apex of tegumen with two rounded setigerous lobes; valva length 0.98–1.0 mm; cucullus with two ventral protrusions, the inner narrowly triangular and tapering toward apex, without apical spines, the outer digitate, nearly pointed with 4–6 apical spines and a rounded dorsal bulb. Aedeagus 0.92–1.04 mm long, 0.055–0.065 mm in diameter at narrowest point. *Female genitalia* (Fig. 3, A–D). Posterior apophyses 2.20–2.25 mm long, anterior apophyses 1.52–1.69 mm long; ovipositor curved to 60–90° angle downward from body axis, 0.045–0.055 mm high near tip, with very low, finely serrated 0.15 mm long dorsal ridge starting 0.6 mm from tip; tip 0.06 mm in length, rounded, serrulate as in *T. syntheticca*; corpus bursae 1–75–1.95 mm long, 0.7–0.8 mm long when flattened, with two 0.28–0.37 mm signa; signum attachment to corpus wall a conspicuous circle, 0.05–0.08 mm in diameter.

GenBank accession number: U49025.

Etymology. The species epithet refers to the geographic distribution of the species, at the opposite margin of the Mojave desert from its sister species, *T. syntheticca*.

Material Examined. Pinned material: 23 males, 23 females.

Type Material. HOLOTYPE, male. USA: Utah, Washington Co. W Beaver Dam mountains. 1 km SW Castle Cliff, 1,075 m. In flower of *Y. brevifolia*. 21-III-2000. N 37°03.214' W 113°53.683'. O. Pellmyr and E. J. Augenstein, USNM. PARATYPES, 19 males and 14 females, same data as holotype.

Other Specimens. USA: Arizona. Mohave Co. Yucca. 14-III-32. one male, three females, McKelvey, USNM, 22-III-2000. two males, Pellmyr and Augenstein, OP; California. San Bernardino Co. 16 km NW Cima. 14-IV-67. two females, Davis, USNM; San Ber-

nardino Co. Cima Road. 18-IV-93. one female, Pellmyr and Augenstein, OP; San Bernardino Co. Clark Mountain 1.6 km NW Mountain Pass. 20–21-IV-80. one male, three females, Powell, UCB (Powell). For distribution records, numerous adults stored in freezer for DNA analysis in Pellmyr laboratory were included: Arizona. Yavapai Co. N Wickenburg. 22-III-2000, Pellmyr and Augenstein. Nevada. Clark Co. Kyle Canyon and Lee Canyon. 4-V-95, Pellmyr and Leebens-Mack.

Distribution and Biology. Eastern and northeastern portions of the Mojave desert (Wells 1979) in areas with *Y. brevifolia* variety *jaegeriana*. Altitudinal range 900–1,700 m. Flight period mid-March to mid-May (Fig. 4).

Diagnosis. The species is most similar to *T. syntheticca* (Fig. 1B), and specimens were included under that name in a prior revision (Davis 1967). A set of diagnostic traits are provided in Table 2 to distinguish between the two taxa. The new species is distinctly smaller and has a light gray arrow-shaped marking in the discal cell (Fig. 1C). In the male, valval protrusions are strikingly evident without dissection, and aedeagus length is also diagnostic (Figs. 1 and 2). In the female, both sets of apophyses are distinctly shorter and signa smaller, whereas general shape is similar. The only other *Tegeticula* species that slightly resembles *T. antithetica* is *T. maculata extranea*, but the latter has glossy and sooty black forewings, different ventral shape of the clasping valva in male genitalia, and a triangular as opposed to square apex of the ovipositor in lateral view (depicted in Powell and Mackie 1966, Davis 1967). No immatures of *T. antithetica* were available for comparative analysis, but larval morphology is generally highly conserved in *Tegeticula* (Fracck 1982).

Phylogenetic Position and Time of Divergence. The phylogenetic results provided a strongly supported tree where *T. antithetica* was the sister taxon of *T. syntheticca* (Fig. 5). The GTR + I (general time reversible model with estimated proportion of invariable sites) was the best model fitting the data (-lnL 4488.42), and the likelihood and Bayesian analyses produced the same tree topology. An earlier estimation of the timeline for diversification of yucca moths, based on clocklike sequence evolution and biogeographically based benchmark dates (Pellmyr and Leebens-Mack 1999), provided an opportunity to estimate time of divergence between the two Joshua tree pollinator species. We excluded third codon po-

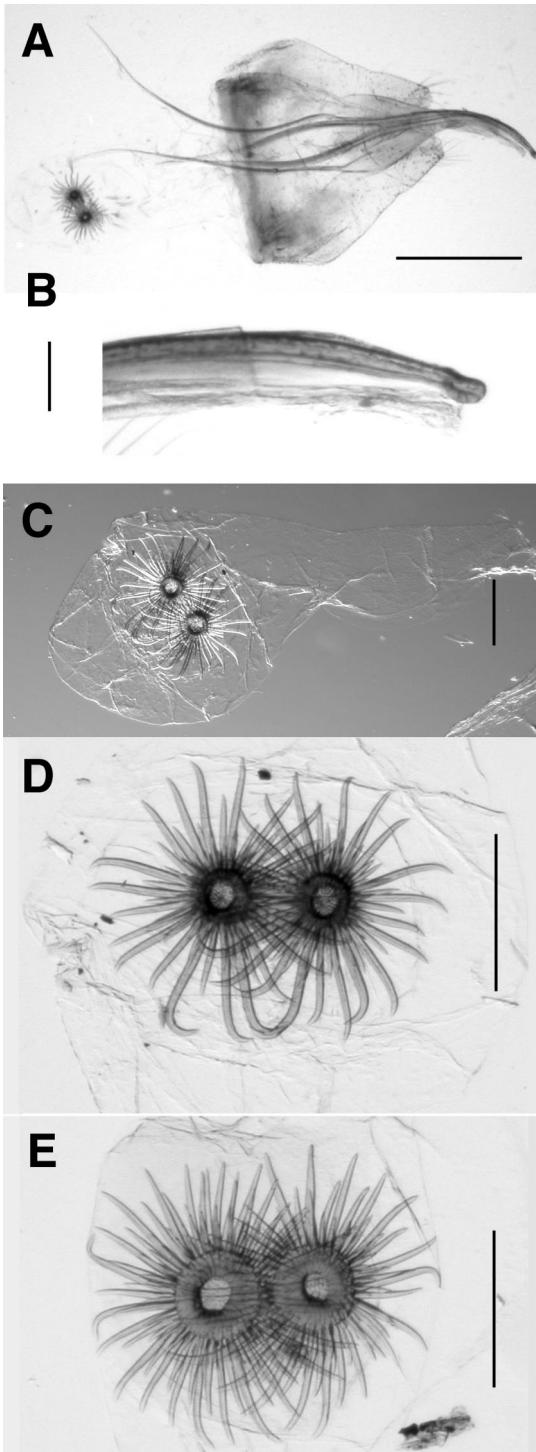


Fig. 3. Female genitalia of *T. antithetica* (A–D) and *T. syntheticca* (E). (A) Complete genitalia with last abdominal segment. (B) Ovipositor tip. (C) Bursa with signa. Enlarged signa of (D) *antithetica* and (E) *syntheticca*. Scale bars: A, 1 mm; B, 0.05 mm; C–E = 0.25 mm.

sitions to avoid the possibility of saturation and estimated the tree, assuming a molecular clock. This analysis failed to reject the clock model (likelihood-ratio test: $\chi^2 = 8.16$, $df = 6$, $P > 0.05$). Divergence times between *T. antithetica* and *T. syntheticca* were estimated using the node to tip heights provided in PAUP*. The relative age was determined by dividing the height of the node between *T. antithetica* and *T. syntheticca* by the height of the split between the *T. syntheticca* lineage and other *Tegeticula*. This relative age was multiplied by 21.9 million years (My; SE = ± 6.8 My), the approximate age of the root (Pellmyr and Leebens-Mack 1999). Thus, the split between *T. antithetica* and *T. syntheticca* was estimated to have occurred ≈ 10.7 My ago (range, 7.4–14.0 My).

Discussion

The discovery that two distinct *Y. brevifolia* pollinator species are concealed under one name is somewhat surprising, because *T. syntheticca* has been considered morphologically uniform (Davis 1967) and very distinct from all other pollinator species of other yuccas. In contrast, variation within the pollinator moth *T. yuccasella* was long recognized and eventually led to the identification of a large species complex (Pellmyr 1999), and discontinuous morphological variation within *T. maculata* has received taxonomic recognition at specific and subspecific levels (Busck 1947, Powell and Mackie 1966, Davis 1967, Segraives and Pellmyr 2001). Considering the symbolic status of the Joshua tree for the Mojave desert (Frémont 1845, Webber 1953, Bono et al. 1987), one might perhaps expect that ample pollinator material would be available; in reality, fewer than 150 specimens labeled as *T. syntheticca* exist in major public institutions. The oversight of the second species likely resulted because very few of those specimens had been collected in the northern portion of the host range. In USNM, holdings consist of four specimens in rather poor condition collected by yucca monographer Susan McKelvey and two other pinned but not spread specimens. One series of four specimens exists in UCB, whereas LACM holds many *T. syntheticca* from the southwestern portion of the host range but no specimens from the north. The two species are nonetheless distinguishable by general habitus in most instances, and differences in the clasping valvae of male genitalia are unusually apparent to the naked eye (Fig. 1, A and B).

In obligate mutualisms such as the one between yucca moths and yuccas, parallel diversification may be more likely than in other, less specific associations (Thompson 1994, Herre 1999, Weiblen 2002). There are no data supporting any instances of yucca-yucca moth cospeciation (Pellmyr and Leebens-Mack 2000). It deserves mention that phylogeny is still being established within two species-rich *Yucca* sections, so future analyses could reveal instances of reciprocal or unilateral speciation within them. Perhaps the strongest candidate at this time is *T. maculata*, the pollinator of *Hesperoyucca whipplei*. Morphological variation in *T. maculata* is spatially structured and may parallel

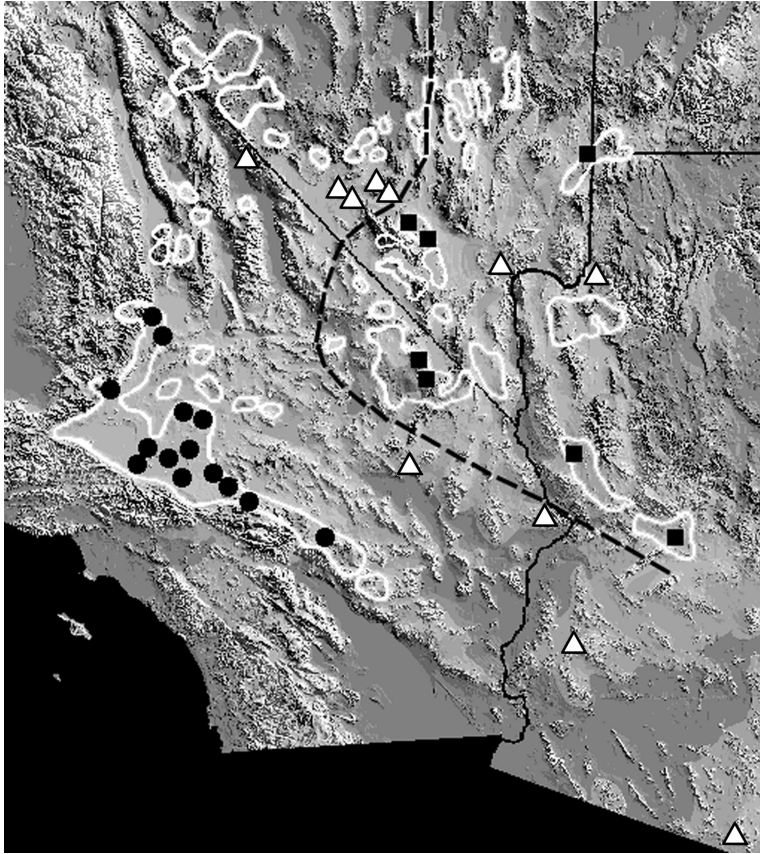


Fig. 4. Geographic distribution of *Y. brevifolia* and its two pollinators. Map area includes southern California, southern Nevada, southwestern Utah, and western Arizona. Extant *Y. brevifolia* distribution is outlined in white, with dashed line indicating split between the western variety *brevifolia* and the eastern variety *vespertina*; both varieties coexist in the areas split by the line at top. White triangles indicate subfossil records of *Y. brevifolia*; variety cannot be determined as fossils are minor leaf fragments in packrat middens, whereas the varieties are defined on growth form of the plant. Black circles, *T. synthetica*; black squares, *T. antithetica*. Plant distribution follows Rowlands (1978) and Spaulding (1990); moth distribution as compiled in current study.

variation in host reproductive habit (Davis 1967). As many as five varieties of *H. whipplei* have been described, primarily based on whether they are semelparous or iteroparous and their patterns of vegetative growth (Haines 1941), but whether this variation is discrete is a matter of debate among plant biologists (DeMason 1984, Keeley et al. 1986). Existing data are

insufficient to determine whether moths and plants have diversified in parallel, let alone whether they have coevolved. In *Y. brevifolia*, which is so distinct as to be placed in a separate series from all other *Yucca* species, the available records of the two pollinator species fall within the ranges of two *Y. brevifolia* varieties, variety *brevifolia* and variety *vespertina*, which

Table 2. Comparison of select morphological traits to distinguish between *T. antithetica* and *T. synthetica*

Trait	Antithetica	Synthetica
Forewing length, male/female (mm)	5.8–6.8/5.6–7.0	7.8–9.0/8.5–10.0
Valva length (mm)	0.98–1.00	2.11–2.13
Inner ventral point on cucullus	Narrow triangular point, without spines	Digitate with apical spines
Outer ventral protrusion on cucullus	Bulbous dorsally, tapering digitate ventrally	Blunt triangular
Spines on proximal/distal valva	0/4–6	3–5/2–3
Aedeagus length (mm)	0.92–1.04	1.18–1.20
Posterior apophyses length (mm)	2.20–2.25	3.55–3.77
Anterior apophyses length (mm)	1.52–1.69	2.96–3.15
Signum diameter (mm)	0.28–0.37	0.37–0.52
Round signum attachment diameter (mm)	0.046–0.083	0.093–0.130

All values are based on three specimens per sex, except the forewing, where all examined specimens were used.

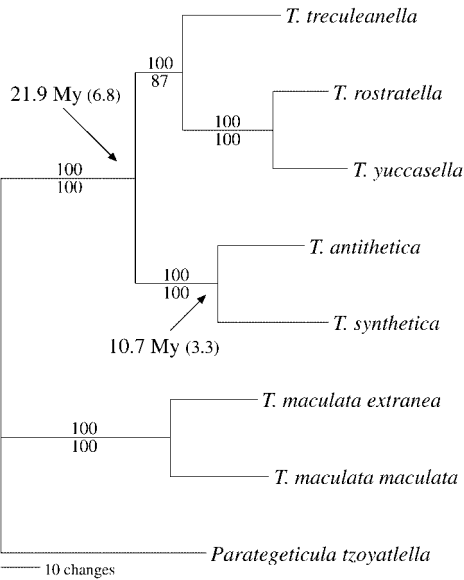


Fig. 5. Strict consensus phylogeny for a subset of *Tegeticula* species and one *Parategeticula* species used as outgroup. Parameters used were actual nucleotide frequencies (A, 0.331; C, 0.130; G, 0.128; T, 0.411), transition and transversion frequencies (AC, 1.123; AG, 5.217; AT, 5.288; CG, 0.990; CT, 20.900; GT, 1.000), and proportion of invariable sites (0.716). Posterior probabilities are above the branches, and likelihood bootstrap values are below the branches. Sample information is provided in Table 1. Estimated time of divergence of the *synthetica-antithetica* lineage from the *yuccasella* complex (upper arrow) taken from Pellmyr and Leebens-Mack (1999), time for *antithetica-synthetica* split (lower arrow) as computed here. Main figure is estimated age; number in parentheses is SEM. My, million years.

differ in growth form (Rowlands 1978). Further sampling is needed to determine whether moth specificity on the two varieties is maintained, particularly in a narrow region in Nevada where both varieties coexist. Growth form may be unlikely to affect moth specificity, and floral traits intuitively should be more likely candidates. *Yucca brevifolia* shows variation in flower size, petal length, and floral aperture size (Webber 1953), but there are no studies of how this variation is structured relative to the plant varieties and moth distribution.

Based on the available data, *T. antithetica* and *T. synthetica* represent the first unequivocal instance of unilateral speciation within a yucca host. This could have occurred through coevolution with the host, with or without a component of spatial isolation. At the present time, documented moth ranges are obviously disjunct, but divergence between the two lineages is estimated to have occurred in an unknown ecological context ≈ 10 My ago, in the late Miocene. This was a highly dynamic period in the evolution of western North American dry regions (Riddle 1995), with the gradual rise of the North American cordillera and the Colorado Plateau (Sahagian et al. 2002). In the Mojave region, woodland savanna gradually transformed into

xeric woodland and semideserts during the late Miocene. There is evidence that yucca-like plants were established in the area 14 My ago, in the form of a trunk fragment fossil from central Nevada, most closely resembling (but different from) extant *Y. brevifolia* (Tidwell and Parker 1990). Determination of whether *Y. brevifolia* distribution may have been fragmented in the window of time where pollinator divergence took place cannot be answered by available paleodata. A more recent marine incursion, referred to as the Bouse embayment, opened no later than 5.5 My ago and created a potential barrier from the Sea of Cortéz to southern Nevada (Lucchitta 1972). There is evidence that numerous less-vagile desert organisms diverged in disjunction during this incursion (Orange et al. 1999). Meanwhile, subfossil yucca fragments in packrat middens dating from the time period since the latest glacial maximum (18,000 years ago) to near-present (4,000 years ago) document range expansion and contraction of *Y. brevifolia* on a relatively short timescale, with the gap between northeastern and southwestern populations at the southern edge of the species range being smaller than present, and the plant being a component of xeric woodlands that extended into lower elevations between ranges during cooler pluvials (Spaulding 1990). Systematic sampling and phylogeographic analysis of moths and their hosts across isolated plant populations with different abiotic conditions (Rowlands et al. 1982) will be necessary to reconstruct the history of diversification of the pollinators of Joshua tree.

Acknowledgments

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