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ABSTRACT. Fruits of most fleshy-fruited yuccas host non-pollinating bogus yucca moths. A peculiar exception has been the widespread and abundant *Yucca schidigera* Roezl ex Ortgies (mojave yucca), where extensive search has failed to document a resident species. Here we report on the discovery of this predicted taxon, *Prodoxus praedictus* **n. sp.**, from a small geographic area in southern California, provide a formal description and results of a phylogenetic analysis, and information on species biology.

Additional key words: Prodoxidae, Agavaceae, mutualism

The pollinating yucca moths (*Tegeticula* Zeller and Parategeticula Davis; Prodoxidae) are perhaps the most widely recognized monotrysian moths, based on their obligate pollination mutualism with yuccas (Riley 1872, 1892, Powell & Mackie 1966, Davis 1967, Powell 1984, 1992, Pellmyr 2003). Containing at least 27 species (Davis 1967, Pellmyr et al. 2008), they constitute a mature system for ecological and evolutionary studies of diversification on several time scales. Meanwhile, the sister group of the pollinators, Prodoxus Riley, referred to as 'bogus yucca moths' (Riley 1880a, b) which coexist as non-pollinators with the pollinators on yuccas, have received less attention. They differ ecologically from the seed-feeding pollinators by feeding on plant parts not used by the pollinators, such as peduncles, non-seed parts of the fruit, and leaf tissue (Riley 1892, Powell and Mackie 1966, Davis 1967, Powell 1984, Wagner and Powell 1988). A recent revision recognized 22 species (Pellmyr et al. 2006). This diversity of life habits among the yucca moth community in its broadest sense will permit analyses of prodoxid community assembly; individual yucca species are known to host as many as six prodoxid species, thus offering sufficient diversity and near-complete information that is unique among recognized models of obligate mutualisms involving seed-parasitic pollinators (e.g., senita moths, gracillariids, fig wasps; Holland and Fleming 1999, 2002, Kato et al. 2003, Kawakita and Kato 2006, Machado et al. 2005).

Before a comprehensive diversification analysis can be done for the bogus yucca moths, it will be important

to identify all moth species. The number has accrued with several studies (e.g., Davis 1967, Powell 1984, Pellmyr et al. 2006), such that virtually all known feeding sites of prodoxids on all yucca species have been checked in the field. A puzzling observation has been the failure to find a fruit-feeding Prodoxus on Yucca schidigera, a common, wide-ranging fleshy-fruited yucca of the Mojave Desert and parts of adjacent deserts. Adult *Prodoxus* rest in the flowers during the day, and despite many lepidopterists checking yucca flowers over several decades, no one has reported a fruit-feeding species on the mojave yucca. Examination of prodoxid holdings in UCB revealed a series of six individuals of an undescribed species collected on Y. schidigera in the current Joshua Tree National Park in 1970 by J.A. Powell and R. Dietz. Subsequent fieldwork in 2006 and 2007 by the present authors recovered adult moths in the flowers and characteristic fruit fragments infested by Prodoxus larvae. Here we provide a description of the species. Descriptions of traits other than genitalia are based on three specimens per sex; for genitalia, one male and two females were used.

Prodoxus praedictus Pellmyr **new species** Fig. 1

Diagnosis. The species is superficially similar to the two *Prodoxus* species of *Yucca brevifolia* Engelmann, *P. sordidus* Riley and *P. weethumpi* Pellmyr (illustrated in Pellmyr *et al.*, 2006). It differs in habitus by having nearly white, more slender and more pointed forewings, and darker brown hindwings than the two *Y. brevifolia*

feeders. In the female, signum diameter is only 25–31% of that in *P. weethumpi*, and the apophyses posteriores are 47–57% as long as those of *P. sordidus*. Specimens of *P. coloradensis* Riley, a stalk-borer of *Y. schidigera* and other species, can occasionally be very pale in the Mojave Desert, but they invariably have at least a few dark brown scales scattered across the forewing.

Description. Wingspan: male 10.0-10.9 mm, female 11.4-12.8 mm; integument grayish brown. Head: with chalk white scales; antennae with basal half or more covered by pale tan scales, then bare. Thorax: with chalk white scales; legs very light tan. Wings: FW length in male 4.3-5.2 mm, female 5.3-5.9 mm; dorsal surface pale tan, with slightly darker tan toward apex in some individuals; underside solid tan; HW with light brownish (male) to darker brownish gray increasing distally (female); underside brownish grey, without pattern; fringes concolorous with adjacent wing regions. Abdomen: male with dorsal scaling brownish tan, mixed with white toward abdominal tip and gravish tan, ventrally white; abdominal brush of linear scales in male light tan with whiter scales mixed toward apex; in female solid brown with little or no brown scales. Male genitalia (Fig. 2): vinculumsaccus 0.68 mm in length; valvae with slightly tapering cucullus, with 5-7 stout spines scattered along outer ventral margin to a point near apex; phallus 0.30 mm long, 0.035 mm in diameter. Female genitalia (Fig. 3-5): apophyses posteriores 1.68-1.99 mm long; ovipositor 0.20 mm high, with a 0.16 mm long, 0.18-0.20 mm high serrated dorsal ridge with 23 asymmetric teeth starting immediately behind tip; ductus bursae with minutely rugose section of internal spinulae; corpus bursae 0.49-0.87 mm in length, 0.23-0.24 mm wide, with two 0.10 mm wide stellate signa with 8–12 spines each.

Type material. *Holotype*: male, UŜA: California. Riverside Co., Joshua Tree N.M. [currently National Park], 1 mi [1.6 km] W Cottonwood Spring, elev. 900 m, in *Yucca schidigera* flower. N 33.7363°, W 115.8266°, 31 Mar. 1970, leg. J. Powell. (UCB). *Paratypes*: 2 males, 3 females, same data, except 2 males leg. R.J. Dietz. (UCB).

Other specimens. Specimens for DNA study were gathered 15 Mar. 2006 (larva in old fruit fragment) in Joshua Tree National Park at Pinto Wye, N 34.0209°, W 116.0106°, and as 11 adults 25 Mar.–4 Apr. 2007 in *Y. schidigera* flowers, between Pinto Basin N 33.8185°, W 115.8106° and S of Cottonwood Spring, N 33.7335° W 115.48.639°. All



FIG. 1. Adult female *P. praedictus*, holotype. Forewing length 5.9 mm.

of these specimens are cryopreserved as whole specimens or DNA in the laboratory of the senior author. As a result of transport while frozen, the specimens were too fragmented to include in morphometric data collection.

Etymology. The host species alone among the fleshy-fruited yuccas of the section Sarcocarpa did not have a known fruit-feeding *Prodoxus* species, despite the yucca being widespread and subject to extensive observation because of its pollination association with yucca moths. The species epithet reflects that a fruit-feeding bogus yucca moth had been predicted, but never identified, to exist on *Y. schidigera* despite decades of attention by entomologists.

Known hosts, oviposition site, and immature biology. The larva feeds in a gallery inside the fruit wall of developing *Y. schidigera* fruits. Infested fruits often fall into the leaf rosette or onto the ground near the plant, where they can persist for several years. Dried fruits inhabited by diapausing larvae often display diagnostic bumps on the surface, as well as round emergence holes from eclosed individuals (Fig. 6).

Flight period. Late March–early April, coincident with flowering period of the only known host.

Distribution. The species is so far only known from the southernmost Mojave Desert and adjacent Colorado Desert, in the central portion of Joshua Tree National Park in Riverside Co, California. Elevational range, 900–1000 m. The restricted range is puzzling as the host species is a widespread and common component of the Mojave Desert and Colorado Desert, occurring from S Nevada, SW Utah, NE Arizona, in California north to near Los Angeles along the coast and to areas south of Death Valley in the eastern part of the state, as well as in the northern portion of Baja California of Mexico. In fact, the few known sites straddle the rather sharp Colorado-Mojave Desert transition within Joshua Tree National Park, suggesting that perhaps abiotic factors are unlikely to play a significant role in limiting the range. Flowers of Y. schidigera have been extensively examined for lepidopteran visitors across much of the host range by many investigators, yet the fruit-feeding Prodoxus has only been recovered in the area described in the present paper. Additional surveys will be required to determine its actual range, but it appears likely to be quite small.

Phylogenetic position. Phylogenetic relationships of 21 *Prodoxus* species were analyzed based on molecular data in a recent paper (Pellmyr *et al.*, 2006). Here we used the same data set—a 2105-bp region of the mitochondrial COI-COII regions—with addition of *P. praedictus* (GenBank accession numbers GQ981319 and GQ9881320). Bootstrap analyses with 100 replicates using maximum parsimony (MP) and maximum likelihood (ML) criteria, respectively, both

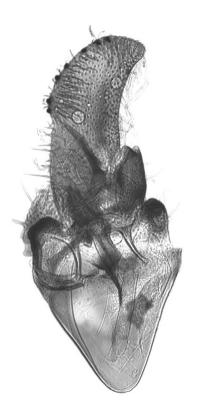


FIG. 2. Male genitalia. Vinculum-saccus, valva , and phallus. One valva removed, phallus not detached.

recovered *P. praedictus* as sister species of *P. y-inversus* Riley, a species with similar larval feeding biology on *Y. baccata* Torrey, a yucca with partly overlapping geographic range. Bootstrap values were 83% (MP) and 69% (ML), respectively, and in both analyses they were part of a clade with 100% support containing two other fruit feeders, *P. atascosanellus* Pellmyr and *P. carnerosanellus* Pellmyr.

DISCUSSION

With the discovery of *P. praedictus*, there is reason to believe that we have documented all extant yuccafeeding *Prodoxus* species in the northern part of its range. Surveys among the fleshy-fruited yuccas in the southern, mostly Mexican, part of the range have yielded both stem- and fruit-feeders in all taxa that have been reasonably well surveyed. They remain to be sought after in the epiphytic *Y. lacandonica* Pompa & Valdés, and in the recently discovered *Y. queretaroensis* Piña Lujan, neither of whose flowers have been available for examination. Meanwhile, the extent of *P. praedictus*' range remains exceptionally limited in the face of extended search by numerous investigators. Its



FIG. 3. Female genitalia, containing entire ovipositor and apophyses, and bursa with signa. For dimensions, see species description.

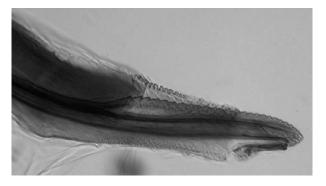


FIG. 4. Ovipositor tip, left lateral view. Dorsal serrated ridge of ovipositor protruding in part outside membranous portions of the abdomen.

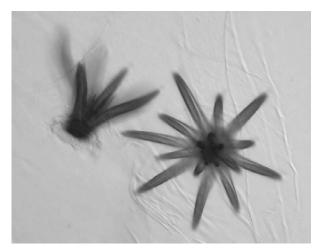


FIG. 5. Signa in lateral view and from below, respectively. Diameter 0.10 mm.

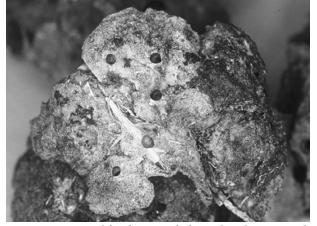


FIG. 6. Section of dried *Yucca schidigera* fruit fragment with several emergence holes created by individual *P. praedictus*. Exit hole diameter ~1 mm.

apparent absence in many areas begs an explanation.

In terms of life history diversification, the present analyses are consistent with previous analyses (Pellmyr *et al.* 2006), as it identifies stem feeding as the basal condition, with three separate origins of fruit feeding. The state of knowledge among the yucca moths in its broadest sense now is sufficiently complete as to permit analyses of diversification in this ecologically important group.

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