

Phylogeny and life history evolution of *Prodoxus yucca* moths (Lepidoptera: Prodoxidae)

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Abstract. *Yucca* moths (Lep., Prodoxidae) are well-known for their obligate pollination mutualism with yuccas. In addition to the pollinators, yuccas also host many non-pollinating yucca moths. Here the genus *Prodoxus*, the non-pollinating sister group of the pollinators, is revised using morphological and molecular data, their phylogenetic relationships are analysed, and the evolution of host tissue specialization explored. Twenty-two species are recognized, including nine new species: *Prodoxus gypsicolor* sp.n., *P. sonorensis* sp.n., *P. carnerosnellus* sp.n., *P. tamaulipellus* sp.n., *P. weethumpi* sp.n., *P. tehuacanensis* sp.n., *P. californicus* sp.n., *P. mapimiensis* sp.n. and *P. atascosanellus* sp.n. *Prodoxus y-inversus* Riley, *P. coloradensis* Riley and *P. sordidus* Riley are redescribed. The genus *Agavenema* is synonymized with *Prodoxus*. Phylogenetic analyses indicated that stalk-feeding is basal within the group, that there are three separate origins of fruit-feeding, and one origin of leaf-mining from a stalk-feeding ancestor. Although species with different feeding habits often coexist within hosts, the analyses suggest that ecological specialization and diversification within a host only may have occurred within one or possibly two hosts.

Introduction

Obligate interactions between seed-eating pollinators and their host plants have played a major role in the development of our understanding of mutualism (Bronstein, 1994; Herre, 1999; Pellmyr, 2003). There are now five phylogenetically independent models of such relationships, including yucca moths and yuccas (Pellmyr, 2003), agaonine fig wasps and figs (Weiblen, 2002), gracillariid *Epicephala* moths and euphorb shrubs (Kato *et al.*, 2003; Kawakita & Kato, 2004), anthomyiid *Chiastocheta* flies and *Trollius* (Pellmyr, 1992; Després & Jaeger, 1999; Després *et al.*, 2002), and the pyralid moth *Upiga virescens* and the cactus *Pachycereus* (*Lophocereus*) *schottii* (Holland & Fleming, 1999). The purpose of the present paper is to establish a systematic and phylogenetic basis for forthcoming analyses of life history evolution in yucca

moths and yuccas, a model system in which studies in the last decade have revealed considerable biological diversity in the moths (Pellmyr, 1999; Pellmyr & Balcázar-Lara, 2000). In this system, female yucca moths serve as the exclusive pollinators and, in turn, rely on the host for larval development. The female uses unique mouthparts to gather pollen actively from host flowers, oviposit into or adjacent to ovaries, and then actively pollinate the flower. Larvae feed on host seeds or tissue that replaces seeds; thus, pollination is critical for larval survival (Powell, 1992; Pellmyr, 2003).

This paper provides a modern synthesis of *Prodoxus* Riley, 1880, the non-pollinating sister group of the pollinating yucca moths (*Tegeticula* Zeller and *Parategeticula* Davis; Prodoxidae). This biologically diverse genus is roughly as rich in species as the pollinators. Although *Prodoxus* coexists with the pollinators they do not participate in the pollination mutualism and feed on plant parts other than seeds, which are the main fare of pollinators. Two or three different *Prodoxus* species often coexist on yuccas, being host-specific to either fruit, flowering stalk, or leaf tissue. For this reason, yucca moths provide an excellent contrast for comparative analyses of mutualists vs. non-mutualists that share specific host plants (Althoff *et al.*,

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2001). Here, we provide a systematic revision of the genus *Prodoxus*, including descriptions that nearly double the number of named species, and use phylogenetic analyses to test explicit hypotheses based on earlier work about the evolution of host shifts and plant part utilization. The data presented are used to test whether this diversity reflects within-host diversification or more conservative life history evolution. The results reported here also will be central to forthcoming comparative analyses with the pollinator sister group and their shared yucca hosts, to explore patterns of diversification and coevolution.

The genus *Prodoxus* has been revised previously by Davis (1967). Systematic considerations and mention of known unpublished taxa also have been provided, mostly in the context of biological studies, by Powell & Mackie (1966), Frack (1982), Powell (1984, 1992) and Wagner & Powell (1988). Previous reconstructions of species relationships and life history evolution have been proposed by Davis (1967) and Frack (1982).

Materials and methods

A total of 1065 specimens from the following collections were used in the study: Edward Knudson, Houston, Texas (EK); Los Angeles County Museum of Natural History (LACM); Olle Pellmyr (OP; will eventually be transferred to USNM); University of California, Berkeley (UCB); Universidad Nacional Autónoma de México, Mexico City, Mexico (UNAM); National Museum of Natural History (Smithsonian Institution), Washington, DC (USNM). As the primary purpose of the present study is to analyse life history evolution, collections were screened for new taxa or for samples providing important range extension. Much of the material has been used previously in earlier revisions and biological studies, and the amount of new material is limited. In this paper, only type material is reported, but data for all additional collections used are provided as an electronic supplement and included also in the distribution maps.

Morphology

Gross morphological data were collected from specimens representing the twelve species described or redescribed here, using an Olympus[®] SZX-9 dissection microscope when needed. From these specimens, genital dissections were made of three individuals of each sex. The entire abdomen was removed and boiled for 5 min in 10% aqueous potassium hydroxide. Female genitalia were stained for 3 min with Chlorazol black. After dissection, measurements were made using the Olympus microscope at 10–80× magnification fitted with a micrometer scale. Each specimen was subsequently mounted in polyvinyl lactophenol on a glass slide.

For figure preparation, wing images were captured using a Nikon[®] Coolpix[®] 4500 digital camera mounted on the Olympus microscope, and genitalic mounts were captured

using a Spot[®] 1.1.0 digital camera mounted on a Leica[®] DMR microscope.

DNA data acquisition

Prior to DNA extraction, the head, wings and genitalia was removed from adults and kept as vouchers. Total genomic DNA from the remaining thorax and abdomen was extracted using Isoquick DNA Isolation Kits (Orca Research Inc., Bothell, WA, U.S.A.). For larvae, the entire individual was used. We used PCR to amplify the 3' end of mtDNA cytochrome oxidase I, the intervening tRNA lysine, and the 5' end of cytochrome oxidase II, which yielded a 2105-bp region. This region was amplified with four pairs of PCR primers that produced overlapping regions of sequence. The primer pairs were 1461F-2302R, 2231F-3020R, 2638F-3306R and 3252F-3371R, in which the numbers refer to the nucleotide positions in the *Drosophila yakuba* mtDNA genome (Clary & Wolstenholme, 1985). Primer sequences are available upon request from the authors. PCR was conducted in 30 µL reaction volumes containing 50 mM KCl, 10 mM Tris (pH=9.0), 2.5 mM MgCl₂, 0.2 mM dNTPs, 0.25 mM of each primer, one unit of Promega B Taq polymerase, and 10 ng of genomic DNA. The thermal cycler profile was one cycle at 95 °C for 2 min, 35 cycles at 95 °C for 1 min, 52 °C for 1 min, 72 °C for 1 min 30 s, and a final extension at 72 °C for 10 min. PCR products were cleaned using the Qiagen PCR purification columns (Qiagen Inc., Valencia, CA, U.S.A.). Dye terminator reactions were carried out following the Dye terminator protocol (Applied Biosystems, Foster City, CA, U.S.A.) with the exception that $\frac{1}{4}$ reactions were conducted. The thermal cycler profile was one cycle at 96 °C for 2 min, 25 cycles at 96 °C for 30 s, 50 °C for 30 s and 60 °C for 4 min. Sequencing products were cleaned using Centri-sep Sephadex columns (Princeton Separations, Adelphia, NJ, U.S.A.), and both forward and reverse strands were sequenced on an ABI 377 automated DNA sequencer (Applied Biosystems). Forward and reverse sequences for each individual were combined into contigs using Sequencher 3.1 (Gene Codes Corporation, Ann Arbor, MI, U.S.A.). The consensus sequence for each individual was then aligned by eye in PAUP* version 4.0b10 (Swofford, 2000). There were no insertions or deletions.

Phylogenetic analysis and life history analysis

DNA-based phylogenetic reconstruction used individuals of twenty-one of the twenty-two described *Prodoxus* species, including those treated in this paper. No sample of *P. barberella* was available for analysis. Samples and sequence references are listed in the Appendix. For all phylogenetic analyses, *Mesepiola* was used as outgroup based on prior studies of prodoxid phylogeny that consistently showed it to be the sister group of the yucca moths (Frack, 1982; Wagner & Powell, 1988; Brown *et al.*, 1994; Pellmyr &

Leebens-Mack, 1999). The DNA sequence data were analysed using parsimony and maximum likelihood following the procedures and recommendations in Sullivan (in press). For the maximum likelihood analyses, the model of sequence evolution was determined using the DT-ModSel program (Minin *et al.*, 2003); the selected model, GTR + G + I, was used in a heuristic search with random addition of taxa, ten replicate searches, and TBR branch swapping in PAUP 4.0b10 (Swofford, 2002). The resulting tree and parameter estimates of the model were then used in Seq-Gen 1.2.7 (Rambaut & Grassly, 1997) to generate 100 replicate data sets. An absolute goodness of fit test was used to determine the suitability of model selection, conducted by performing 100 parametric bootstrap replicates on a Beowulf computer cluster at the University of Idaho. Once the model was confirmed to be appropriate for the sequence data, another heuristic search was run using maximum likelihood and the non-parametric bootstrap procedure (Felsenstein, 1985) to assess support for the nodes in the resulting topologies.

Within the *Yucca* feeding clade, we tested whether species with particular oviposition habits (fruit or stalk oviposition) could be considered monophyletic groups. Parametric bootstrapping was used to test two specific hypotheses. First, we tested whether the fruit-feeding species constitute a monophyletic group, which would suggest that fruit-feeding arose only once within this species complex. Second, we tested whether the two *Prodoxus* species that coexist on *Y. brevifolia* could be considered sister species. The results from these two tests could then be used to infer the number of origins of fruit feeding within *Prodoxus* as a whole, and to infer the ancestral condition. To test each hypothesis, the topology was constrained to be consistent with the hypothesis, and another heuristic search was run under maximum likelihood and the model parameters re-estimated. The resulting tree and model parameters then were used in Seq-Gen 1.2.7 (Rambaut & Grassly, 1997) to generate 100 replicate datasets. Each dataset then was subjected to an unconstrained heuristic search, and another search that was constrained to the tree consistent with the hypothesis. The differences in log likelihood scores between the unconstrained and constrained searches for each replicate were used to generate a null distribution. The difference in log likelihood scores between an unconstrained and constrained search using the original dataset then was compared to this distribution to determine if the hypothesis could be rejected.

Results and discussion

General life history of the moths

Life history has been described in great detail for some species (Powell & Mackie, 1966; Davis, 1967; Powell, 1984; Wagner & Powell, 1988), and what follows is a general account. Eggs of *Prodoxus* are laid individually inside host tissue, with the female using her serrated ovipositor to cut with a sawing motion into the tissue. Different species

oviposit into and feed as larvae in one of three plant parts. Most species use the inflorescence stalk, several feed inside the fleshy outer layer of the fruit, and a single species mines yucca leaves. The larva generally completes feeding within a few weeks, and then enters diapause. This diapause may last only one year, but is known to commonly last for 3–5 years in many species, and has been extended to 30 years in one species (Powell, 2001), in a life habit that presumably reflects the habit of sporadic flowering in most yuccas and of episodic droughts in the regions that many species inhabit. Once diapause is broken, some species complete a final path to the tissue surface where an operculum invariably is left for the pupa to breach. After a brief pupal period, lasting a few weeks at most, the pupa breaks the operculum and the adult emerges, generally during the early to peak period of local flowering phenology. Moth activity is crepuscular and nocturnal, with the exception of three diurnal species that inhabit *Hesperoyucca whipplei* (Torr.), and at least one other species that has been observed to oviposit during the day as well as night. Resting moths are found commonly inside flowers of the host, and mating occurs inside flowers if available. The short mouthparts are functional, with adults imbibing fluids mostly at the ovary base. Oviposition commonly takes from less than a minute up to several minutes, especially in the stalk-ovipositing species that pierce into hard, fibrous tissue.

Descriptions, redescrptions, and taxonomic changes

For the redescrbed species, now known to have consisted of more than one species as originally described, only a cursory redescription is provided to indicate changes needed from the previous description. The same applies for two species in which generic affinity has been restored and changed, respectively.

Davis (1967) erected *Agavenema* for two *Agave*-feeding species, including a new species and one previously described as a *Prodoxus*. They differ in having conserved male genital morphology similar to that in *Mesepiola* and some *Tegeticula*. Meanwhile, their larval morphology is synapomorphic with some *Prodoxus* species in sharing elongate body form and loss of seta L2 (Frack, 1982). For this reason, and because the molecular data (see below) nest the genus within *Prodoxus*, *Agavenema* is synonymized here. Paratypes to complement current holdings will be placed in LACM, UCB, UNAM, the American Museum of Natural History (AMNH), the Australian National Insect Collection (ANIC), and The Natural History Museum, London (BMNH).

Diagnostic key to all Prodoxus species

This diagnostic key is based solely on morphology, but for several taxa information on host and host part will greatly facilitate identification, as would analysis of even

a short segment of mtDNA (as below in phylogenetic analysis).

Males

1. Forewing solid tan 2
 - Forewing patterned or of other colour 3
2. Aedeagus 0.98–1.04 mm long *sordidus*
 - Aedeagus 0.78–0.84 mm long *weethumpi*
3. Cucullus with a ventral digitate lobe 4
 - Cucullus without such a lobe 6
4. FW ground colour chalk white, with very few dark markings *gypsicolor*
 - FW ground colour greyish tan, with sometimes extensive dark markings 5
5. Vinculum-saccus > 2.25 mm long *pallida*
 - Vinculum-saccus < 1.75 mm long *barberella*
6. FW all white or with scattered minute dark dots 7
 - FW not white or with extensive dark markings 8
7. FW completely white, signa 0.10–0.22 mm in diameter *decepiens*
 - FW with 0–18 dark spots, signa 0.27–0.42 mm in diameter *quinquepunctellus*
8. FW with inverse dark Y from costa to tornum 9
 - FW without inverse dark Y from costa to tornum .. 10
9. Aedeagus 0.82–0.84 mm long *y-inversus*
 - Aedeagus 0.96–1.02 mm long *sonorensis*
10. FW unicolorous brownish grey to dark grey 11
 - FW not unicolorous 12
11. Sacculus with prominent lobe, valva constricted near middle *aenescens*
 - Sacculus without prominent lobe, valva not constricted near middle *cinereus*
12. FW all white or with scattered minute dark dots... *marginatus*
 - FW dark or with extensive dark markings 13
13. FW white with dark brown band along outer margin and dark spot in discal region, sometimes fused near tornum *carnerosanellus*
 - FW with different pattern 14
14. FW mostly dark, with light areas yellow 15
 - FW with light areas white, without yellowish tinge. 16
15. Aedeagus length 1.1–1.25 mm *ochrocarus*
 - Aedeagus length 2.3–2.5 mm *intricatus*
16. Tegumen width = 0.05 mm; FW basally white, diffused dark brown distally *tamaulipellus*
 - Tegumen width = 0.08 mm 17
17. Aedeagus length ≤ 0.95 mm *californicus*
 - Aedeagus length ≥ 0.95 mm 18
18. Teeth on ventral margin of valva more or less evenly spaced; aedeagus 0.04–0.05 mm wide ... *atascosanellus*
 - Teeth on ventral margin of valva in part clustered near outer ventral corner 19
19. FW mostly light, with diffuse tan and light brown checkerspot pattern *tehuacanensis*
 - FW with distinct brown and white checkerspot pattern 20

20. FW narrow, with drawn-out apex, creating lanceolate wing shape *mapimiensis*
 - FW wider, with more vertical outer edge, creating stocky wing shape 21
21. Thorax dorsally without white scales; FW usually darker than in *coloradensis* *phylloryctus*
 - Thorax dorsally with few white scales; FW lighter or much lighter than in *phylloryctus* *coloradensis*

Females

1. FW solid tan 2
 - FW patterned or of other colour 3
2. Corpus bursae with 2-to-6-spined signa 0.08–0.14 mm in size *sordidus*
 - Corpus bursae with 12-to-19-spined signa 0.39–0.52 mm in size *weethumpi*
3. Corpus bursae without signa 4
 - Corpus bursae with signa 8
4. FW with checkerspot pattern *intricatus*
 - FW uniform grey or with scattered dark spots and streaks on light background 5
5. FW uniform light or medium grey, length < 5 mm ... *cinereus*
 - FW elongate, white or tan with dark spots and streaks, length > 6 mm 6
6. FW ground colour chalk white, with very few dark markings *gypsicolor*
 - FW ground colour greyish tan, with sometimes extensive dark markings 7
7. Apophyses posteriores > 6 mm long *pallida*
 - Apophyses posteriores < 4 mm long *barberella*
8. FW all white or with scattered minute dark dots 9
 - FW dark or with extensive dark markings 10
9. FW completely white, signa 0.10–0.22 mm in diameter *decepiens*
 - FW with 0–18 dark spots, signa 0.27–0.42 mm in diameter *quinquepunctellus*
10. FW solid medium to dark grey *aenescens*
 - FW with some pattern elements 11
11. FW with inverse dark Y from costa to tornum 12
 - FW without inverse dark Y from costa to tornum .. 13
12. Signa 0.12–0.16 mm in diameter *y-inversus*
 - Signa 0.36–0.42 mm in diameter *sonorensis*
13. FW white with dark brown band along outer margin and dark spot in discal region, sometimes fused near tornum *carnerosanellus*
 - FW with different pattern 14
14. FW white with more or less scattered fuscous scales; signum < 0.04 mm *marginatus*
 - FW usually with more dark regions; signum > 0.15 mm 15
15. FW mostly dark, with light areas yellow *ochrocarus*
 - FW with light areas white, without yellowish tinge 16
16. Ovipositor serrated ridge with 28–35 teeth *tamaulipellus*
 - Ovipositor serrated ridge with 15–22 teeth 17
17. Apophyses posteriores length > 2.25 mm .. *californicus*
 - Apophyses posteriores length < 2.20 mm 18

18. FW mostly dark brown, distinctly patterned and signum ≤ 10 spines *atascosanellus*
 – FW mostly light, or signum with 12–16 spines 19
19. FW light to medium brown, with diffuse checkerspot pattern; signum with 10–12 spines *tehuacanensis*
 – FW with distinct brown and white checkerspot pattern; signum with 12–16 spines 20
20. FW narrow, with drawn-out apex, creating lanceolate wing shape *mapimiensis*
 – FW wider, with more vertical outer edge, creating stocky wing shape 21
21. Thorax dorsally without white scales; FW usually darker than in *coloradensis* *phylloryctus*
 – Thorax dorsally with few white scales; FW lighter or much lighter than in *phylloryctus* *coloradensis*

Prodoxus (Riley, 1892)

Agavenema Davis, 1967:99, **syn. n.**

Prodoxus barberellus (Busck, 1915), **rev. comb.**

Agavenema barberella (Busck), Davis, 1967:101.

Prodoxus pallidus (Davis, 1967), **comb. n.**

Agavenema pallida, Davis, 1967:102

Prodoxus marginatus (Riley, 1892)

Prodoxus pulverulentus, Riley, 1892:150, **syn. n.**

***Prodoxus gypsicolor* Pellmyr, sp.n. (Fig. 1R)**

Wingspan. ♂ 11.2–16.2 mm, ♀ 12–19.1 mm. Integument dark brown.

Head. With linear, erect white scales, nearly bare medio-dorsally. Antenna sparsely scaled up to 70% of full length, with coverage densest at base.

Thorax. With chalk-white scales. Legs lighter than thorax, with brown pretarsi. FW length in male 5.3–7.7 mm, female 5.6–9.1 mm; width in male 1.6–2.2 mm, female 1.9–2.2 mm; dorsal surface solid calcareous white, with some individuals having a dark grey spot made up of 1–5 scales in the outer discal region. Underside lightly scaled with pale brown scales, lighter region below discal spot of upperside. HW brownish grey. Underside very sparsely scaled with narrow light brown scales. Fringes on both wings white.

Abdomen. With dorsal scaling tan to brown tan on upperside, underside white to light tan. In male, valva with white or light tan scales.

Male genitalia (Fig. 2A). Vinculum-saccus 1.32–1.34 mm in length. Valvae with sacculus produced into a rounded lobe; cucullus narrow and linear, with a ventral digitate lobe with an apical, slightly symmetrical pectinifer consisting of 14–17 spines. Aedeagus 1.36–1.44 mm long, 0.05–0.06 mm in diameter.

Female genitalia (Fig. 3G) Apophyses posteriores 3.2–3.7 mm long; ovipositor 0.05–0.06 mm in height, with 0.43–0.52 mm long, 0.02–0.03 mm high serrated dorsal ridge with 20–23 teeth starting by tip; corpus bursae 0.76–1.00 mm long, 0.25–0.38 mm wide, without signa.

Type material. *Holotype*, ♀, USA: California, San Bernardino Co., E side of Kingston Range, 1100 m.

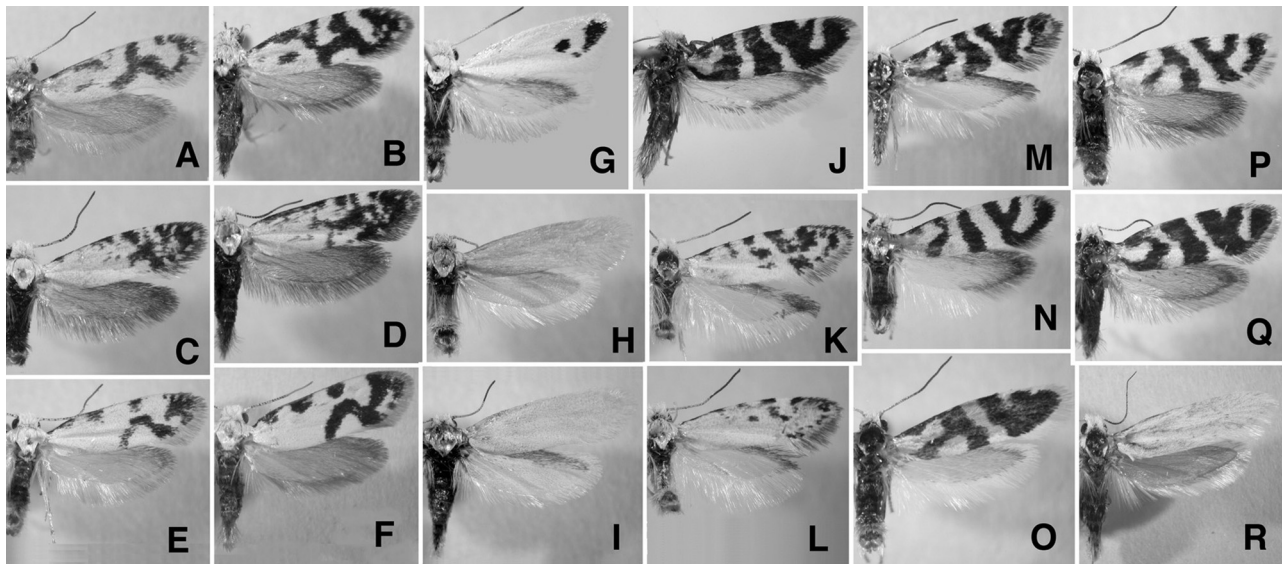


Fig. 1. Adults of described and redescribed *Prodoxus* species. A, B, *y-inversus* ♂, ♀; C, D, *tamaulipellus* ♂, ♀; E, F, *sonorensis* ♂, ♀; G, *carnerosanellus* ♂; H, *sordidus* ♂; I, *weethumpi* ♀; J, *californicus* ♀; K–M, *tehuacanensis*, 2♂, ♀; N, *coloradensis* ♂; O, P, *mapimiensis* ♂, ♀; Q, *atascosanellus* ♀; R, *gypsicolor* ♀.

N35°42'–W115°48', in old stalks of *Agave utahensis* harvested 28.iv.1994 by J. P. Donahue, em. 19–28.iv.1995 (*Pellmyr*) (USNM). *Paratypes*. 4 ♂ 5 ♀, same data.

Etymology. The species name refers to the chalk white colour of the FW.

Known hosts and oviposition site. In the inflorescence trunk of *Agave utahensis* Engelm.

Flight period. Emerged in captivity in mid-April, caught at high elevation near end of May; likely to be coincident with flowering period of host.

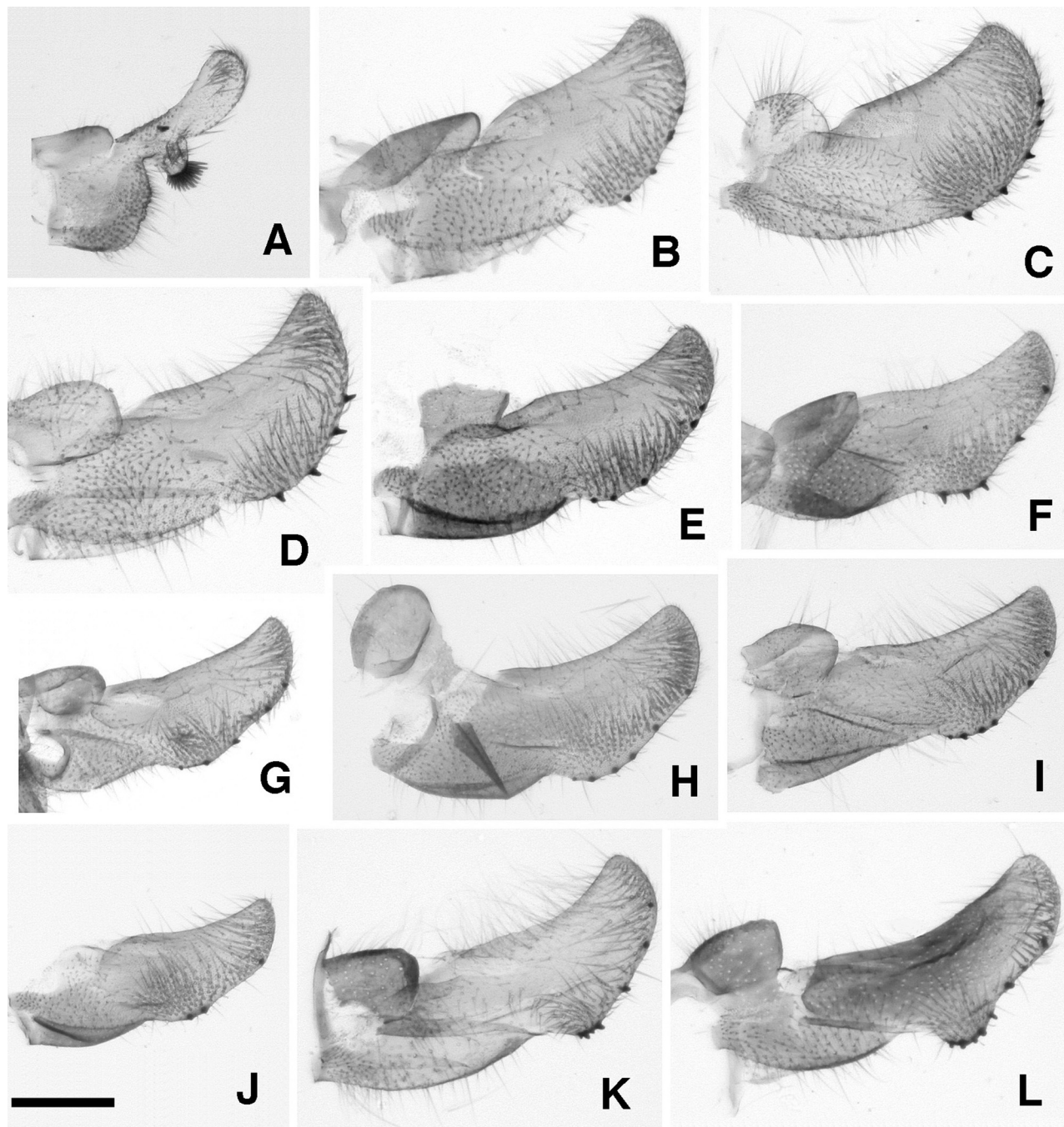


Fig. 2. Right valva of male genitalia of described and redescribed *Prodoxus* species. A, *gypsicolor*; B, *y-inversus*; C, *sonorensis*; D, *tamaulipellus*; E, *carnerosanellus*; F, *mapimiensis*; G, *atascosanellus*; H, *californicus*; I, *coloradensis*; J, *tehuacanensis*; K, *sordidus*; L, *weethumpi*. Scale bar = 0.25 mm.

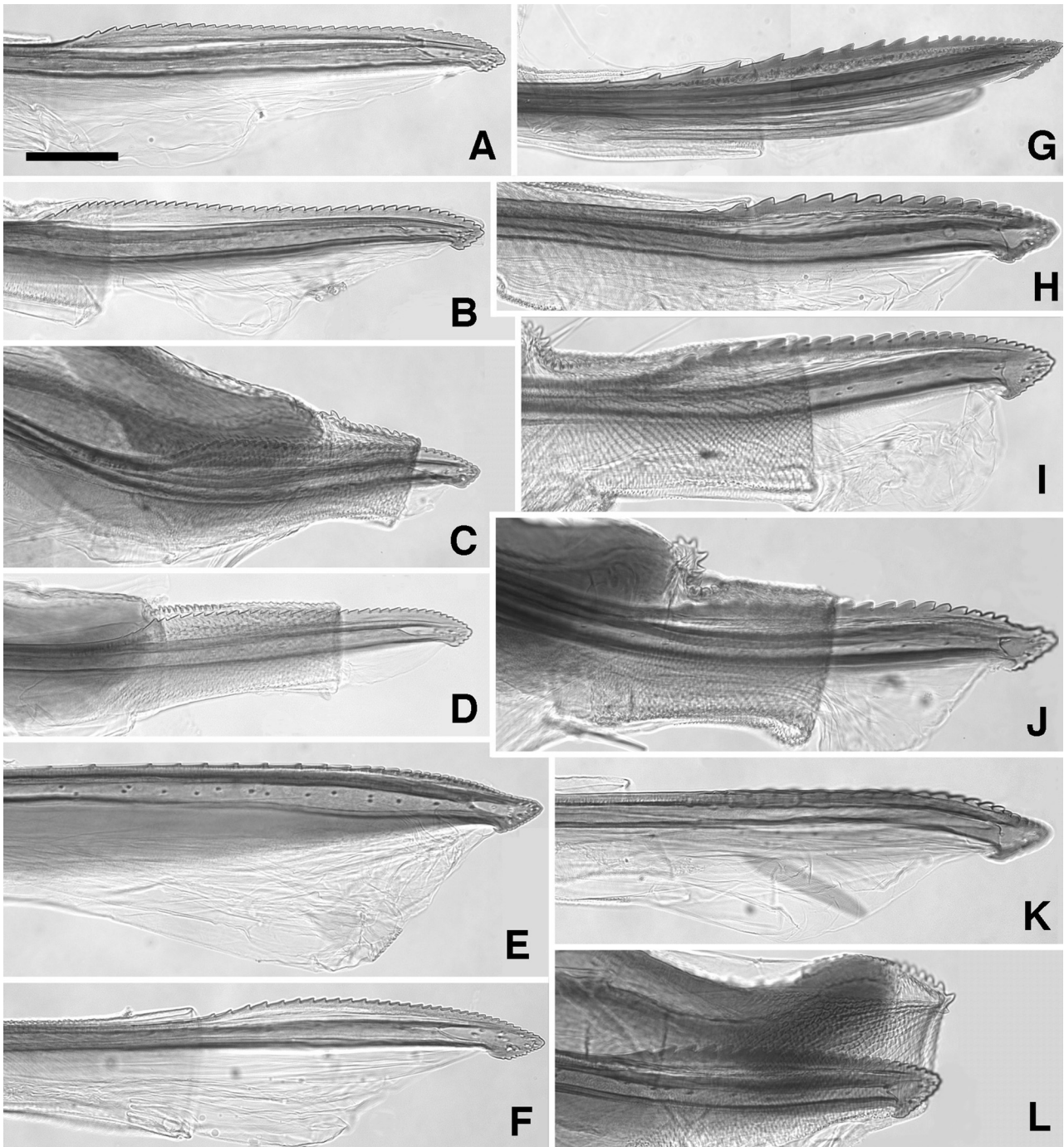


Fig. 3. Ovipositor tips of female genitalia of described and redescribed *Prodoxus* species; intersegmental membrane retracted to varying degrees, with part of the tip inside the membrane in most species. A, *y-inversus*; B, *sonorensis*; C, *carnerosanellus*; D, *tamaulipellus*; E, *sordidus*; F, *weethumpi*; G, *gypsicolor*; H, *mapimiensis*; I, *coloradensis*; J, *californicus*; K, *atascosanellus*; L, *tehuacanensis*. Scale bar in A = 0.05 mm for all panels except G, where = 0.10 mm.

Distribution (Fig 4) So far known only from the Kingston Range of NE Mojave Desert. Specimens reared by OP from *A. utahensis* at Tuweep, Grand Canyon National Park, in central northern Arizona may belong to this species. Elevational range 1100–1750 m.

Comments. The species is unique among the *Agave*-feeding species in having a nearly to completely white FW, and it differs also from *P. pallida* in the male by a shorter aedeagus and vinculum-saccus and from the female by shorter apophyses. Whereas the genitalia of this species virtually are identical to

those of *P. barberella*, wing coloration is very different. *Prodoxus barberella* has the most contrasting pattern of the three *Agave* feeders, with dark brown to black streaks and dots on a brownish grey background. As evidenced in many other *Prodoxus* species, there can be little variation in the genital traits even among distantly related species that are otherwise morphologically and biologically highly distinct.

Prodoxus y-inversus Riley (1892) (Figs 1A, B)

Wingspan. ♂ 10.2–12.5 mm, ♀ 11.3–15.0 mm. Integument brown to dark brown.

Head. With white scales. Antenna with basal half covered by scales, then bare; basally all scales white, distally increasingly often tan

Thorax. With white scales. Legs with some white scales, darker brown pretarsi than remainder. FW length in male 4.8–6.1 mm, female 5.2–6.7 mm; width in male 1.5–1.6 mm, female 1.5–1.8 mm; dorsal surface white, with dark brown pattern, more dominant in female; two basal costal spots usually fused, sometimes connected to left leg of more distal inverse Y that reaches from costa and has right lower branch at tornum. Outer edge solid brown. Underside light to medium brown mirroring upperside pattern. HW greyish brown on both upper and lower surface. Fringe of both wings greyish brown.

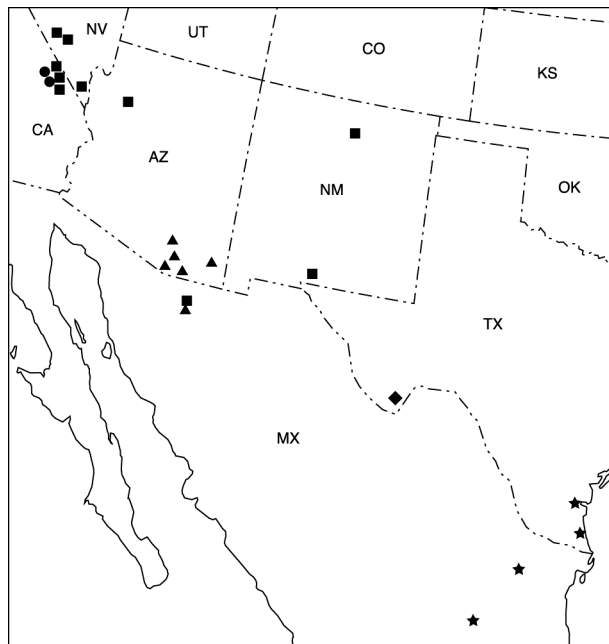


Fig. 4. Documented sites for five species of *Prodoxus*. Samples include all examined dried material in collections as well as frozen specimens used for DNA analyses in the Pellmyr lab. ●, *gypsicolor*; ■, *y-inversus*; ▲, *sonorensis*; ◆, *carnerosanellus*; ★, *tamaulipellus*. Abbreviations are: NV = Nevada, UT = Utah, CO = Colorado, KS = Kansas, CA = California, AZ = Arizona, NM = New Mexico, TX = Texas, OK = Oklahoma, MX = Mexico.

Abdomen. With dorsal scaling light to yellowish brown, ventrally near white. Abdominal brush of linear scales very light brown.

Male genitalia (Fig. 2B). Vinculum-saccus 0.64–0.68 mm in length. Valvae with equally broad cucullus and a broadly rounded outer edge, with 5–6 stout spines scattered along lower two-thirds of outer margin. Aedeagus 0.82–0.84 mm long, 0.05–0.06 mm in diameter.

Female genitalia (Figs 3A and 5B). Apophyses posteriores 1.88–2.06 mm long; ovipositor 0.015–0.020 mm high, with a 0.24–0.26 mm long, 0.009–0.012 mm high finely serrated dorsal ridge with 34–35 densely spaced teeth starting immediately behind tip; ductus bursae without rugose section of internal short points; corpus bursae 0.56–1.06 mm in length, 0.36–0.50 mm wide, with two 0.12–0.16 mm wide stellate signa with 8–9 spines each.

Type material. *Lectotype*, ♂, designated by Davis (1967), from an unspecified location in New Mexico, U.S.A.

Known hosts, oviposition site, and immature biology. The larva feeds in a gallery inside developing fruits of *Y. baccata* Torr. (Powell, 1984), including *Y. arizonica* McKelvey. Single fruits can host many larvae, with at least 235 larval galleries documented in a single fruit gathered at Cima, California, by DMA in 2003. Larval cohorts of the species emerge as adults over several years even when artificial winter and water is provided. Simulating native conditions of extended droughts, Powell (1986, 1989, 2001) could extend diapause to 30 years, at which point the material was exhausted. This arguably makes *P. y-inversus* one of the most long-lived known insects.

Flight period. April–May.

Distribution (Fig. 4). This species has thus far been documented from a modest number of sites, but they are distributed across a very substantial part of the range of the host species. Elevational range 800–1470 m.

Comments. The species is characterized by the inverse Y pattern on the FW, a trait shared only with *P. sonorensis*. The two species are readily separated by genital traits, including signum size in the female and aedeagus length in the male. On examining Riley's type material, and being unaware of the existence of a fruit feeder on *Y. baccata*, Davis (1967) assumed that Riley had obtained material collected on *Y. schottii* Engelm. in extreme SW New Mexico. The lectotype is a *P. y-inversus*, however, and the precise New Mexico location where it was collected is unknown.

Prodoxus sonorensis Pellmyr & Balcázar-Lara, sp.n. (Figs 1E, F)

Wingspan. ♂ 8.9–12.8 mm, ♀ 10.9–15.6 mm. Integument amber brown.

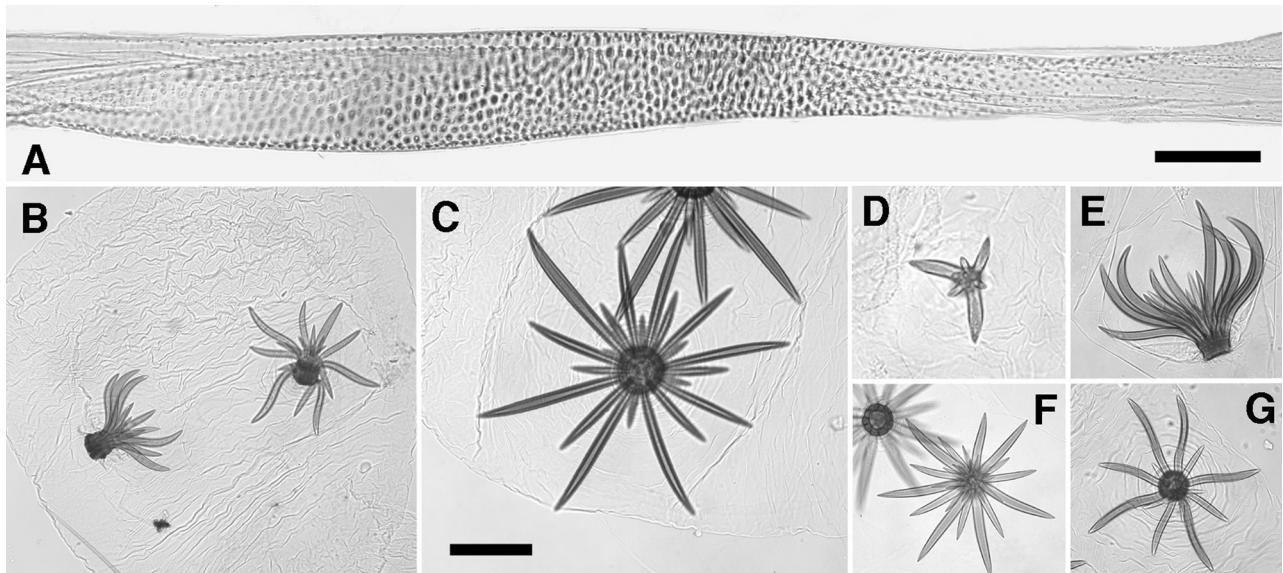


Fig. 5. Components of female genitalia. A, Ductus bursae of *P. weethumpi*, showing rugose section with internal points that characterizes this species and members of stalk-feeding checkerspot-patterned species; scale bar = 0.025 mm. B–G, Signa of different species, top view except where indicated. B, *γ-inversus*, side and top views; C, *weethumpi*; D, *sordidus*; E, *mapimiensis*, side view; F, *tamaulipellus*; G, *carnerosanellus*. Scale bar in C = 0.10 mm, applies to all signa.

Head. With white scales. Antenna with basal half covered by scales, then bare; basally all scales white, distally proportionately more brown ones.

Thorax. With white scales. Legs with yellowish white scales, some brown on tibiae and ventrally, darker brown pretarsi than remainder of integument. FW length in male 4.2–5.9 mm, female 5.3–7.2 mm; width in male 1.8–1.9 mm, female 1.8–1.9 mm; dorsal surface white, with dark brown pattern, more dominant in female; two basal costal spots usually separate, distal inverse Y beyond those spots that reaches from costa and has right lower branch at tornum sometimes broken above fork. Outer edge brown, mirroring upperside pattern. Underside tan to brown, mirroring upperside pattern. HW greyish brown on both upper and lower surface, darker toward edge. Fringe of both wings greyish brown.

Abdomen. With dorsal scaling greyish yellow brown, ventrally lighter. Abdominal brush of linear scales yellowish brown.

Male genitalia (Fig. 2C). Vinculum-saccus 0.76–0.82 mm in length. Valvae with a broad cucullus without an obvious ventroapical bend, with 5–6 stout spines scattered in outer half from base to near apex. Aedeagus 0.96–1.02 mm long, 0.06 mm in diameter.

Female genitalia (Fig. 3B). Apophyses posteriores 2.04–2.18 mm long; ovipositor 0.020–0.030 mm high, with a 0.24–0.27 mm long, 0.015–0.020 mm high serrated dorsal ridge with 23–47 densely spaced teeth starting immediately behind tip; ductus bursae without rugose section of internal

fine points; corpus bursae 0.80–1.06 mm in length, 0.50–0.60 mm wide, with two 0.36–0.42 mm wide stellate signa with 15–18 spines each.

Type material. Holotype, ♀, Arizona. Pima Co. Santa Catalina Mts. 6.9 rd-km above Molino Basin, 1700 m 26.vii.1991, in flower of *Y. schottii* (Pellmyr) (USNM). **Paratypes**, 4♂ 5♀, MEXICO: Sonora. Son Rte 89 km 182 La Churea to km 162 S Cerro Colorado Ranch, 1200–1300 m. From infested fruits collected 22.iv.1997, emerged 14.vii.1997, 30.iii–8.v.1998, 5♂ 4♀ (Pellmyr) (OP).

Etymology. The name refers to the Sonoran desert, where all known populations are found.

Known hosts, oviposition site, and immature biology. The larva feeds in a gallery in the wall of the developing fruit of *Y. schottii*, and the life history has been described and depicted in part by Davis (1967) and in superb detail by Powell (1984). Larval cohorts of the species emerge as adults over at least 6 years even when artificial winter and water is provided. Additional comments on the immature stages have been provided by Bronstein & Ziv (1997), who proposed that its presence might reduce feeding damage on seeds inflicted by *Tegeticula* larvae.

Flight period. Late June–mid-August.

Distribution (Fig. 4). Confined to pine-oak woodlands with *Y. schottii* in the isolated ‘sky islands’ of south-eastern Arizona and southward into northernmost Sonora, Mexico. Elevational range 1200–2200 m.

Comments. The species is characterized by the inverse Y pattern on the FW, a trait shared only with *P. γ -inversus*. The two species are readily separated by genital traits, including signum size in the female and aedeagus length in the male; adults of this species also are somewhat bigger in size. A light spot in the outer dark field of the FW also distinguishes *sonorensis* from *γ -inversus*. This is the species studied in the papers of Ziv & Bronstein (1996) and Bronstein & Ziv (1997).

***Prodoxus carnerosanellus* Pellmyr & Balcázar-Lara, sp. n. (Fig. 1G)**

Wingspan. ♂ 8.1–10.9 mm, ♀ 8.9–12.8 mm. Integument light amber.

Head. With white scales. Antenna with basal two thirds covered by white scales, then bare.

Thorax. With white scales. Legs pallid yellow, with darker brown pretarsi than remainder. FW length in male 3.6–5.2 mm, female 4.2–5.9 mm; width in male 1.4–1.6 mm, female 1.4–1.5 mm; dorsal surface white, with chocolate brown area from apex about two-thirds of distance to tornum; dark spot in discal region, occasionally fusing at lower edge with apical streak. Female generally with more dark pattern than male. Underside tan to dark grey, pattern mirroring upper side. HW with light grey shading near front edge, more so toward apex, remainder of wing white. Underside with grey shading along front, elsewhere white. Fringes of both wings white.

Abdomen. With dorsal scaling white and greyish tan, ventrally white. Abdominal brush of linear scales in male light tan.

Male genitalia (Fig. 2E). Vinculum-saccus 0.64–0.66 mm in length. Valvae with slightly tapering cucullus, with 4–5 stout spines scattered along outer ventral margin to a point near apex. Aedeagus 0.76–0.78 mm long, 0.04–0.05 mm in diameter.

Female genitalia (Figs 3C and 5G). Apophyses posteriores 1.70–1.74 mm long; ovipositor 0.020 mm high, with a 0.16–0.19 mm long, 0.018–0.020 mm high serrated dorsal ridge with 33–34 densely spaced fine teeth starting immediately behind tip; ductus bursae without rugose section of internal short points; corpus bursae 0.78–0.96 mm in length, 0.30–0.36 mm wide, with two 0.21–0.26 mm wide stellate signa with 11–18 spines each.

Type material. *Holotype*, ♂, USA: Texas. Brewster Co. Big Bend National Park. Dagger Flat Road, 10.4 km from Rte 385, elev. 800 m, emerged from dried *Y. carnerosana* fruit. N29°30.946'–W103°03.011', 1.i.1998, em. 10–22.ii.2001 (Pellmyr & Augenstein) (USNM). *Paratypes*, 4♂ 5♀, same data.

Etymology. The species name is derived from its only known host, *Y. carnerosana*.

Known hosts, oviposition site, and immature biology. The larva feeds in a hardening gallery inside the fruit wall of developing *Y. carnerosana* fruits. Infested fruits often fall into the leaf rosette or onto the ground, where they can persist for several years. Larval cohorts of the species emerge as adults over several years even when artificial winter and water is provided. In a large 1997 cohort, a single adult emerged by 2000, and then was followed by mass emergence of about 250 moths in 2001, thus roughly tracking the local flowering frequency of its host. Individuals from a 2001 cohort began emerging in 2003. The species can diapause for at least 7 years.

Flight period. April, coincident with flowering period of the only known host.

Distribution (Fig. 4). So far recorded only from the Big Bend region of west Texas. As the host ranges southward in the Chihuahuan desert to San Luis Potosi, the species may well extend a considerable distance into Mexico. Elevational range, 750–800 m.

***Prodoxus tamaulipellus* Pellmyr & Balcázar-Lara, sp. n. (Figs 1C, D)**

Wingspan. ♂ 8.4–11.1 mm, ♀ 9.4–12.5 mm. Integument brown to dark brown.

Head. With white scales. Antenna with basal 50–60% section covered by white scales, then scattered brownish scales before altogether bare.

Thorax. With white scales. Legs with darker brown pretarsi than remainder, white scales on all legs but darker toward apices. FW length in male 3.75–5.3 mm, female 4.2–5.9 mm; width in male 1.4–1.6 mm, female 1.4 mm; dorsal colour white, with speckles of brown along costa, and dark brown discal spot, sometimes fusing to form fragmentary inverse Y to tornum well above inner leg of fork. Coloration creates general appearance of speckled dark region outside a line at right angle to costa from tornum. Female generally darker than male. Underside tan to dark brown, mirroring upperside pattern. FW fringe concolorous with adjacent region. HW grey, darker along outer edge. Underside similar to upperside, but somewhat lighter. Fringes on both wings concolorous with adjacent regions.

Abdomen. With dorsal scaling flat brown, mixture of white and brown scales on back section; ventrally lighter coloration. Abdominal brush of linear scales dark brown at base, then yellowish brown.

Male genitalia (Fig. 2D). Vinculum-saccus 0.68–0.70 mm in length. Valvae with relative broad basal cucullus, then tapering to a blunt point, with 4–6 stout spines broadly spaced along outer third quartile of ventral margin. Aedeagus 0.76–0.82 mm long, 0.04–0.05 mm in diameter.

Female genitalia (Figs 3D and 5F). Apophyses posteriores 1.80–1.96 mm long; ovipositor 0.015–0.025 mm high, with a 0.20–0.22 mm long, 0.010–0.015 mm high serrated dorsal ridge with 28–35 densely spaced fine teeth starting immediately behind tip; ductus bursae without rugose section of internal short points; corpus bursae 0.88–1.30 mm in length, 0.36–0.64 mm wide, with two 0.17–0.18 mm wide stellate signa with 12–15 spines each.

Type material. Holotype, ♂, USA: Texas. Cameron Co. Laguna Atascosa National Wildlife Refuge, elev. 0–10 m. N26°15′–W97°21′. 8.iii.1995. (*Pellmyr*) (USNM). Paratypes, 4♂ 5♀, same data except emer. 12.iii.–2.iv.1995, 26.ii–5.iii.1996, 12–15.iii.1997.

Etymology. The species is named for the Tamaulipan biotic province, which contains the handful of known sites for the species thus far. Whereas *Y. treculeana* extends westward from the Tamaulipan province into the Chihuahuan desert, there is no evidence that *P. tamaulipellus* occurs in that area.

Known hosts, oviposition site, and immature biology. At the type locality, oviposition on *Y. treculeana* was observed to take place both during the day and night, in flowers as well as young fruits. The larva feeds in a gallery inside the fruit wall of developing fruits of *Y. treculeana* and *Y. filifera*. Larval cohorts of the species emerge as adults over at least 2 years even when artificial winter and water is provided.

Flight period. Late February–early March.

Distribution (Fig. 4). So far known only from host populations in thorn scrub interspersed with grasslands in the Tamaulipan biotic province. Elevational range 0–250 m.

***Prodoxus sordidus* Riley (1892) (Fig. 1H)**

Wingspan. ♂ 8.0–9.8 mm, ♀ 9.4–12.3 mm. Integument medium to dark brown.

Head. With light to medium tan scales. Antenna with basal 50–65% portion with tan scales matching FW colour, then bare.

Thorax. With light to medium tan scales. Legs with darker brown pretarsi than remainder. FW length in male 3.75–4.5 mm, female 4.5–5.9 mm; width in male 1.2–1.6 mm, female 1.2–1.5 mm; dorsal surface uniform light or occasionally medium tan, with concolorous fringe. Underside drab light brown, lighter toward apex where

concolorous with fringe. HW light grey along front edge, gradually fading to light greyish white on rest of wing; underside brownish grey.

Abdomen. With thin dorsal scaling greyish brown, ventrally off-white. Abdominal brush and valval scales very light tan.

Male genitalia (Fig. 2K). Vinculum-saccus 0.62–0.76 mm in length. Valvae with cucullus bending dorsad in outer section, creating ventroapical edge at about 45° angle to remainder; edge with 4–6 stout spines, some tightly clustered around ventroapical corner and then spaced along lower outer margin. Aedeagus 0.98–1.04 mm long, 0.04–0.05 mm in diameter.

Female genitalia (Figs 3E and 5D). Apophyses posteriores 3.52–3.60 mm long; ovipositor 0.06 mm high, with a 0.18–0.32 mm long, 0.003–0.005 mm high serrated dorsal ridge with 16–35 minute teeth starting immediately behind tip and becoming increasingly spaced apart forward; ductus bursae without rugose section of internal short points; corpus bursae 1.30–1.62 mm in length, 0.26–0.34 mm wide, with two 0.08–0.14 mm wide stellate signa with 2–6 spines each.

Type material. Lectotype, ♀, designated by Davis (1967).

Known hosts, oviposition site, and immature biology. In the flowering stalk of *Y. brevifolia* Engelm. Oviposition occurs during the flowering period. The larva feeds superficially inside the stalk, and can diapause for at least 6 years before pupation and emergence.

Flight period. March–mid-May.

Distribution (Fig. 6). Throughout the range of *Y. brevifolia*, including the south-western and north-eastern edges of the Mojave Desert in southern California and Nevada, north-western Arizona, and extreme south-western Utah. Two distinct pollinating prodoxids occupy different parts of the *Y. brevifolia* range (Pellmyr & Segraves, 2003), so comparative analyses of phylogeographical structure of this and the other *Prodoxus* inhabitant may prove of interest. Elevational range 800–1540 m.

Comments. Two externally similar species have been known for some time to be conflated under the name of *P. sordidus* (Frack, 1982; Powell, 1992). This is apparent also from Riley's (1892) reference to exitholes from emerging adults in stalks, whereas Davis reported larvae as feeding in the fruits. The two ovipositors depicted by Davis (1967) in fact belong to the two different species; Fig. 143 is *P. sordidus*. Examination of the lectotype designated by Davis (1967) revealed that the genitalia, which would provide certain identification, had been dissected, possibly by Riley. The resulting mount has not been recovered, and attempted recovery of DNA from the specimen would significantly damage the specimen and success would be highly

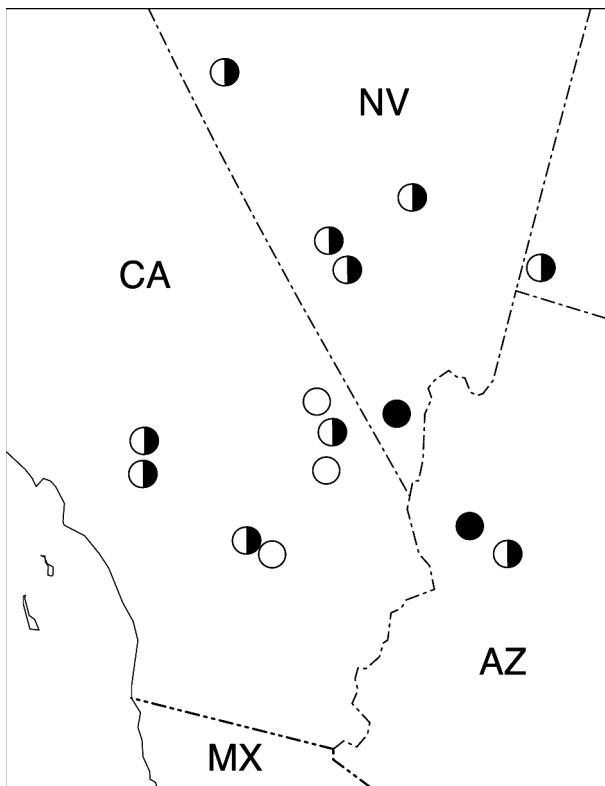


Fig. 6. Documented sites for the two *Prodoxus* species of *Y. brevifolia*. ●, *weethumpi*; ○, *sordidus*. Uniform circle indicates that only one species is documented at site, split circle that both taxa have been documented. Abbreviations as in Fig. 4.

uncertain, thus an identification had to be made from the remainder of the animal. The two species differ in that *P. sordidus* generally is somewhat bigger, and more tan coloured than the fruit feeder. The lectotype best matches the stalk borer, thus it should retain the name *sordidus*.

Prodoxus weethumpi Pellmyr, sp. n. (Fig. 11)

Wingspan. ♂ 8.75–10.6 mm, ♀ 9.2–13.6 mm. Integument medium brown.

Head. With light tan scales. Antenna with basal 50–65% portion with tan scales matching FW colour, then bare.

Thorax. With light tan scales. Legs with fore- and mid femora partly brown scaled, other segments light tan. FW length in male 4.2–5.0 mm, female 4.4–6.6 mm; width in male 1.2–1.4 mm, female 1.4–1.5 mm; dorsal surface uniform solid light tan, with concolorous fringe. FW more convex especially near base than in *sordidus*, with less drawn-out apex, creating appearance of more even breadth and straight outer edge. Underside drab light brown, with lighter scales on some distal veins; light linear scales near outer edge, concolorous with fringe. HW grey with brown tinge along front

edge, mostly above basal field, then white, lightly scaled on rest; underside greyish brown along front edge in area overlapping FW, rest sparsely set with white scales.

Abdomen. With thin dorsal scaling dark greyish brown, ventrally lighter. Abdominal brush and valval scales light tan and amber in colour.

Male genitalia (Fig. 2L). Vinculum-saccus 0.62–0.64 mm in length. Valvae with cucullus bending dorsad in outer section from a distinct rounded ventroapical lobe; edge with 6–8 stout spines, some tightly clustered around ventroapical corner and then spaced along lower outer margin. Aedeagus 0.78–0.84 mm long, 0.05 mm in diameter.

Female genitalia (Figs 3F and 5A,C). Apophyses posteriores 1.84–1.86 mm long; ovipositor 0.020–0.030 mm high, with a 0.18–0.21 mm long, 0.007–0.008 mm high, finely serrated dorsal ridge with 24–30 densely spaced teeth starting immediately behind tip; ductus bursae with rugose section of internal short points; corpus bursae 1.38–1.40 mm in length, 0.39–0.52 mm wide, with two 0.32–0.40 mm wide stellate signa with 12–19 spines each.

Type material. Holotype, ♂, USA: Utah. Washington Co. W Beaver Dam Mountains, 1 km SSW Castle Cliff. 1075 m. N37°03.214'–W113°53.683'. 21.iii.2000, emer. from dried *Y. brevifolia* fruit 28.iii.2000 (Pellmyr & Augenstein) (OP). Paratypes, 1♂ 7♀, same data.

Etymology. The species name is derived from 'weethump' of the Paiute language, meaning 'ancient ones', alluding to the longevity of *Y. brevifolia*.

Known host, oviposition site, and immature biology. In young fruits of *Y. brevifolia*. The larva feeds inside a superficial gallery in the thickening exocarp. This gallery is hollowed out to a few mm in diameter, and the gallery with its very hard walls then serves as the diapause and pupation site. The hardened tissue remains attached to the fruit, and may eventually fall to the ground and remain for several years. Diapause can last at least 2 years, and likely much longer, before pupation and emergence.

Flight period. March–early May.

Distribution (Fig. 6). Throughout the range of *Y. brevifolia*, including the south-western and north-eastern edges of the Mojave Desert in southern California and Nevada, north-western Arizona, and extreme south-western Utah. Elevational range 800–1540 m.

Comments. See discussion under *P. sordidus*. This species generally is somewhat greyer and often with shorter wings than *sordidus*. The genitalia readily distinguish the two species, with *weethumpi* having a shorter aedeagus in the male, and the female having shorter apophyses and possessing signa. Figure 142 in Davis (1967) shows the *weethumpi* ovipositor.

***Prodoxus tehuacanensis* Pellmyr & Balcázar-Lara, sp. n. (Fig. 1K–M)**

Wingspan. ♂ 8.3–11.25 mm, ♀ 9.2–11.6 mm. Integument medium brown.

Head. With white scales. Antenna with basal 50–60% section covered by white scales, then bare.

Thorax. White scales in male, in female dark brown dorsofrontally and mediodorsally in most individuals, white elsewhere. Underside white in both sexes. Legs with darker brown pretarsi than remainder, covered with white scales. FW length in male 3.9–5.3 mm, female 4.2–5.5 mm; width in male 1.4–1.6 mm, female 1.1–1.5 mm. Dorsal surface white; in male dark bands emerging as spots on costa, basal 1–3 ending before discal field, bands 4+5 fusing above discal field and then generally only present on back edge. Outer edge brown with ample white to create a fine-grained checker matrix. In female, 5 brown bands from costa to back edge, although 1 and 2 basal may not always reach edge; band 5 converges with 4 at edge, where it is touching outer edge which also is dark, more or less marbled. Underside light greyish brown in male, greyish brown in female, with upperside pattern mirrored. FW fringe greyish brown. HW white with grey area along front edge, the latter in female generally confined to apical third of edge. Underside thinly scaled, white with grey area along front edge. HW fringe white. Males much lighter than females, arguably the most sexually dimorphic species of the genus.

Abdomen. In male with white and light tan scales above, white below, including white abdominal brush and valvae; in female, all scales white.

Male genitalia (Fig. 2J). Vinculum-saccus 0.60–0.70 mm in length. Valvae with slightly tapering cucullus, with 3–6 stout spines in part clustered around ventrodorsal corner and then along lower outer margin. Aedeagus 0.76–0.84 mm long, 0.05–0.06 mm in diameter.

Female genitalia (Fig. 3L). Apophyses posteriores 1.63–1.90 mm long; ovipositor 0.015–0.020 mm high, with a 0.17–0.19 mm long, 0.015–0.025 mm high serrated dorsal ridge with 15–22 densely spaced teeth starting immediately behind tip; ductus bursae with rugose section of internal short points; corpus bursae 0.66–1.04 mm in length, 0.31–0.60 mm wide, with two 0.18–0.24 mm wide stellate signa with 10–12 spines each.

Type material. *Holotype*, ♂, MEXICO: Puebla. 6 km WSW Santiago Acantepec, rd-km 55 on Rte 125. 2000 m. N18°12.553'–W97°38.058', 29.iv.1999 (Pellmyr & Balcázar-Lara) (UNAM). *Paratypes*, 1♂ 1♀, same data.

Etymology. The species name refers to the Tehuacán-Cuicatlán region where all known collection sites are located.

Known hosts, oviposition site, and immature biology. In the flowering stalk of *Y. periculosa* Baker and the doubtfully distinct *Y. mixtecana* Garcia-Mendoza. The larva feeds superficially inside the stalk, and can diapause for at least 3 years before pupation and emergence.

Flight period. Late April.

Distribution (Fig. 7). So far known only from the Tehuacán-Cuicatlán region, in the states of Puebla and Oaxaca. Elevational range 1660–2250 m.

Comments. This is the smallest species among the generally checkerspot-patterned species, and it also one of the most sexually dimorphic species.

***Prodoxus californicus* Pellmyr, sp. n. (Fig. 1J)**

[*Prodoxus coloradensis* auct.]

Wingspan. ♂ 7.2–10.9 mm, ♀ 13.1–13.6 mm. Integument brown to dark brown.

Head. With white or, in female, sometimes light tan scales. Antenna with basal 50–60% section covered by white scales, then bare.

Thorax. With dark brown scales dorsally, near white below. Legs with darker brown pretarsi than remainder. FW length in male 3.3–5.2 mm, female 5.8–6.3 mm; width in male 1.6 mm, female 1.6–1.8 mm; dorsal surface white; dark brown pattern consists of basal spot that merges on costa with bands 2–3, the latter of which may be fused to create an inverse Y. Bands 4–5 create a Y that reaches tornum, then merges with band that runs along outer edge. Underside medium brown to tan, mirroring upperside pattern. FW fringe white, occasionally light brown at tornum. HW basally white to very light grey, with slightly darker apex that can extend as fine grey line along edge; underside very lightly scaled, mirroring upperside pattern. HW fringe white, occasionally light brown at apex.

Abdomen. With dorsal scaling brown, ventrally white. In male, linear erect light tan scales on final abdominal segment and valvae.

Male genitalia (Fig. 2H). Vinculum-saccus 0.72–0.74 mm in length. Valvae with slightly tapering cucullus, with 4–6 stout spines well spaced along ventrodorsal margin. Aedeagus 0.98 mm long, 0.06–0.07 mm in diameter.

Female genitalia (Fig. 3J). Apophyses posteriores 2.26–2.30 mm long; ovipositor 0.020–0.025 mm high, with a 0.19–0.23 mm long, 0.020–0.025 mm high serrated dorsal ridge with 15–20 densely spaced teeth starting immediately behind tip; ductus bursae with rugose section of internal short points;

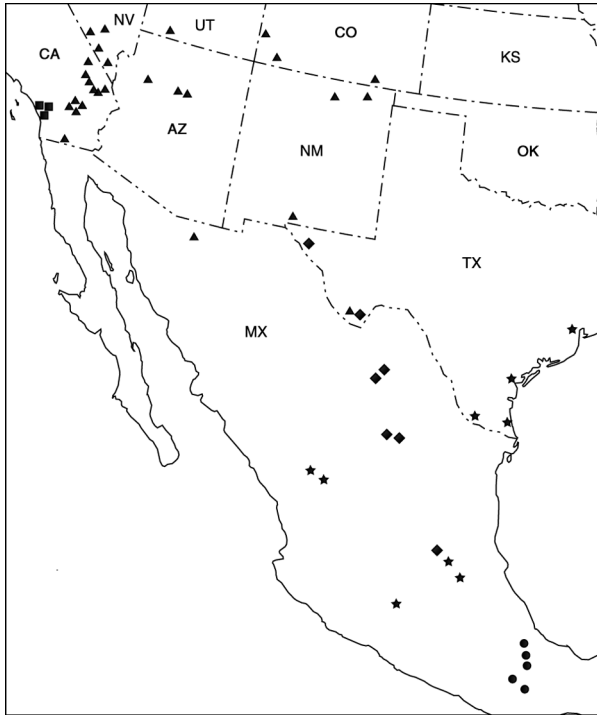


Fig. 7. Documented species for the five stalk-boring *Prodoxus* species with checkered FW pattern. ●, *tehuacanensis*; ★, *atascosanellus*; ◆, *mapimiensis*; ▲, *coloradensis*; ■, *californicus*. Abbreviations as in Fig. 4.

corpus bursae 1.50–1.60 mm in length, 0.52–0.60 mm wide, with two 0.38–0.40 mm stellate signa with 14–18 spines each.

Type material. *Holotype*, ♂, USA: California. San Diego Co. 5 km E Encenitas, elev. 15 m 27–28.iv.1967 (*D. Davis*) (USNM). *Paratypes*, 6♂ 9♀, same data as holotype (USNM, UCB).

Etymology. The species name refers to the known range, which is a coastal portion of the California cismontane floristic province (Raven & Axelrod, 1978).

Known hosts and oviposition site. In the flowering stalk of *Y. schidigera* Roetz ex Ortigas.

Flight period. April.

Distribution (Fig. 7). Known only from three coastal sites within 15 km of each other north of San Diego in southernmost California. It should be sought along the northeastern coast of Baja California, Mexico, as *Y. schidigera* and many associated species with similar distribution in California have ranges that extend south to the El Rosario area (30°N latitude) (Raven & Axelrod, 1978). Elevational range, near sea level.

Comments. The specimens from Encenitas previously were included with the similar, but smaller and lighter,

P. coloradensis. This is the largest and perhaps darkest member of the checkerspot-patterned members of the genus.

***Prodoxus coloradensis* Riley (1892) (Fig. 1N)**

Wingspan. ♂ 8.9–12.0 mm, ♀ 9.2–13.0 mm. Integument brown to dark brown.

Head. With white scales. Antenna with basal 50–60% section covered by white scales, then bare.

Thorax. With dark brown scales dorsally, near white below. Legs with darker brown pretarsi than remainder. FW length in male 4.1–5.8 mm, female 4.4–5.9 mm; width in male 1.4–1.7 mm, female 1.4–1.8 mm; dorsal surface white; five brown bands off costa, inner two sometimes connect mid-way to hind edge, 3 + 4 may create Y by fusing in mid wing or only 3 may reach back edge; outer edge usually complete brown band that merges with 4 at tornum. Female generally darker than male. Underside light to medium brown mirroring upperside pattern. FW fringe white. HW near white at base, then gradually becoming grey along outer edge, especially so by apex. Underside with dark edge along front. HW fringe white or sometimes light brownish grey.

Abdomen. With dorsal scaling brownish grey, ventrally lighter. Abdominal brush of linear scales in male very light tan.

Male genitalia (Fig. 2I). Vinculum-saccus 0.66–0.74 mm in length. Valvae with slightly tapering cucullus, with 4–6 stout spines in part clustered around ventrodorsal corner and then along lower outer margin. Aedeagus 0.86–0.94 mm long, 0.06 mm in diameter.

Female genitalia (Fig. 3I). Apophyses posteriores 2.00–2.18 mm long; ovipositor 0.022–0.027 mm high, with a 0.18–0.22 mm long, 0.022–0.027 mm high serrated dorsal ridge with 20–22 densely spaced teeth starting immediately behind tip; ductus bursae with rugose section of internal short points; corpus bursae 0.70–0.96 mm in length, 0.40–0.60 mm wide, with two 0.40 mm wide stellate signa with 14–16 spines each.

Type material. *Lectotype*, ♀, designated by Davis (1967).

Known hosts and oviposition site. The larva has been documented to feed in a gallery inside the flowering stalk of *Y. baccata* (Powell, 1984), including *Y. arizonica*, and *Y. schidigera*. It has been recorded to emerge after at least 5 years in diapause. Other historical host records refer to other *Prodoxus* species previously conflated under *P. coloradensis*.

Flight period. April–June.

Distribution (Fig. 7). Recorded from the Colorado Plateau in the north to northern Sonora in the south, eastward to the Big Bend region of Texas (where it is sympatric with *P. mapimiensis*) and westward to the coastal range of southern California. Elevational range, 1200–2160 m.

Comments. One of the early-described *Prodoxus* species, *P. coloradensis* has long been known to be highly variable in wing coloration, and some of this variation turns out to reflect separate, closely related species. Individuals from the Mojave Desert, at the western edge of the species as currently circumscribed, tend to be lighter and smaller than moths elsewhere in the range, but available molecular data do not support separate taxonomic status for them. Additional population-level genetic and morphological data will be needed to resolve this matter. Adults reported in Davis (1967) from *Y. treculeana* across south-central Texas reflect the scattered distribution of the species from the western desert to the mesic coastal grasslands and thornscrub where *P. atascosanellus* is found. Those specimens are not included here for two reasons. First, this area will include the contact zone (if any) of *P. coloradensis* and *P. atascosanellus*, and molecular data would be highly desirable to assign specimens from this area. Second, most of the material was collected by S. D. McKelvey, and prior studies have shown that her specimen labels are commonly in error (Pellmyr, 1999).

***Prodoxus mapimiensis* Pellmyr & Balcázar-Lara, sp. n. (Figs 10,P)**

[*Prodoxus coloradensis* auct.]

Wingspan. ♂ 7.3–10.9 mm, ♀ 8.8–12.0 mm. Integument medium brown.

Head. With white scales, occasionally with some light tan scales in female. Antenna with basal 40–50% section (male) or 50–65% (female) covered by white scales, then bare.

Thorax. With white scales, or occasionally light tan in female, dorsally; some females with a brown mediodorsal streak; white below. Legs light tan and darker brown pretarsi, with white scales. FW length in male 3.4–5.2 mm, female 4.1–5.8 mm; width in male 1.25 mm, female 1.0–1.3 mm; apex of wing drawn out to create an outer wing edge at about 45° angle. Dorsal surface white, with a few males being predominantly dark on balance; base of costa brown, then next band emerging from costa splits to create inverse Y at hind edge; next two bands off costa merge to create a Y that reaches tornum; brown outer edge that sometimes fuses with inner Y, even to create solid brown area. Underside light to medium brown, pattern mirroring upperside. HW white with light grey apex, sometimes extending along front edge. Underside lighter than top. Fringes of both wings white.

Abdomen. With dorsal scaling tan to light tan, ventrally white. Abdominal brush and scales on valvae white or light yellow.

Male genitalia (Fig. 2F). Vinculum-saccus 0.67–0.70 mm in length. Valvae with cucullus bending upward in outer section, creating ventroapical edge at 45° angle to remainder; edge with 5–6 stout spines, in part clustered around ventrodorsal corner and then along lower outer margin. Aedeagus 0.80–0.84 mm long, 0.06 mm in diameter.

Female genitalia (Figs 3H and 5E). Apophyses posteriores 1.84–1.96 mm long; ovipositor 0.020 mm high, with a 0.19–0.21 mm long, 0.020–0.025 mm high serrated dorsal ridge with 16–18 densely spaced teeth starting immediately behind tip; ductus bursae with rugose section of internal short points; corpus bursae 0.74–1.00 mm in length, 0.32–0.50 mm wide, with two 0.24–0.31 mm wide stellate signa with 12–13 spines each.

Type material. *Holotype*, ♂, USA: Texas. Brewster Co. Big Bend National Park. Dagger Flat Road, elev. 800 m, 16.iv.1995 in 1-year-old *Y. carnerosana* peduncle, emerged 20.ii–5.iii.1997. N29°31.50′–W103°02.89′ (*Pellmyr & Augenstein*) (USNM). *Paratypes*, 4♂ 5♀, Texas. Brewster Co., Big Bend National Park, Nine Point Draw and Green Gulch. 700–1425 m 16–17.iv.1995 (*Pellmyr*).

Etymology. The species name refers to its distribution in Bolson de Mapimi, the southern section of the main portion of the Chihuahuan desert. This was a glacial refugium for many taxa (Van Devender, 1990; Elias *et al.*, 1995), and like many others this species has a range that extends somewhat northward either as a result of postglacial recolonization or peak glacial persistence.

Known hosts, oviposition site, and immature biology. In the flowering stalk of *Y. carnerosana* (Trel.) McKelvey, *Y. linearifolia* Clary, *Y. filifera* Chab. and *Y. treculeana* Carrière in south-central Coahuila. Oviposition occurs during the flowering period, especially in the side branches of the inflorescence. The larva feeds superficially inside the stalk, and can diapause for at least 3 years before pupation and emergence.

Flight period. March–April.

Distribution (Fig. 7). Known from the main segment of the Chihuahuan desert, thus far from Saltillo-Torrón northward to the Big Bend region of west Texas. Elevational range 700–1920 m.

Comments. The drawn-out point of the FW, with an unusually inward-angled outer edge, lends a characteristic habitus to this species. In the Big Bend region of western Texas, the species overlaps with *P. coloradensis* that primarily or exclusively uses *Y. treculeana*. Some individuals reared from *Y. treculeana* from the Big Bend region of

Texas are phenetically similar to *P. mapimiensis*, and future study should focus on the possibility of range expansion and possible introgression between the species in this area.

***Prodoxus atascosanellus* Pellmyr & Balcázar-Lara, sp. n. (Fig. 1Q)**

Wingspan. ♂ 8.6–10.8 mm, ♀ 9.1–12.5 mm. Integument brown.

Head. With white scales, yellowish tinged in some females. Antenna with basal 50–60% section covered by white scales, then thinning brown scales toward bare tip.

Thorax. With white or light tan scales dorsally in male, light tan to light brown in female, white below in both sexes. Legs with darker brown pretarsi than remainder, with mixture of light and dark brown scales. FW length in male 3.9–5.0 mm, female 4.2–5.8 mm; width in male 1.1–1.4 mm, female 1.4–1.6 mm; dorsal surface white, but mostly dark brown coloration; basal dark brown streak on costa, then one dark band from costa branches to inverse Y at hind edge, next two bands off costa located near apex fuse to Y that reaches tornum. Outer edge brown, with occasional white scattering in some specimens. Underside light to medium brown mirroring upperside pattern. FW fringe white to grey in male, grey in female. HW light grey or grey at base, then gradually becoming grey along outer edge. Underside with light scaling, light grey at base with darker hues along front edge. HW fringe light grey. Female generally darker than male.

Abdomen. With dorsal scaling light to medium tan, ventrally lighter. Abdominal brush of linear scales and valval scales pale yellow.

Male genitalia (Fig. 2G). Vinculum-saccus 0.60–0.70 mm in length. Valvae with slightly tapering cucullus, with 3–5 stout spines along outer ventral and lower outer margin. Aedeagus 0.72–0.86 mm long, 0.04–0.05 mm in diameter.

Female genitalia (Fig. 3K). Apophyses posteriores 1.80–2.00 mm long; ovipositor 0.020 mm high, with a 0.16–0.20 mm long, 0.015–0.020 mm high serrated dorsal ridge with 19–22 densely spaced teeth starting immediately behind tip; ductus bursae with rugose section of internal short points; corpus bursae 0.70–1.04 mm in length, 0.34–0.44 mm wide, with two 0.24–0.27 mm wide stellate signa with 9–10 spines each.

Type material. *Holotype*, ♂, USA: Texas. Cameron Co. Laguna Atascosa National Wildlife Refuge, elev. 0–10 m. N26°15′–W97°21′. 8.iii.1995. (Pellmyr) (OP). *Paratypes*, 4♂ 5♀, same data except 8–10.iii.1995, 17–19.ii.1996.

Etymology. The species name refers to the type locality, Laguna Atascosa National Wildlife Refuge, in the Rio Grande/Rio Bravo river delta of southernmost Texas.

Known hosts, oviposition site, and immature biology. In the flowering stalk of *Y. treculeana*, *Y. filifera* and *Y. decipiens*. Oviposition in *Y. treculeana* occurs during the flowering period, especially in the branches inside the inflorescence. The larva feeds superficially inside the stalk.

Flight period. Mid-February–May, depending on elevation.

Distribution (Fig. 7). In the north from the Houston area of coastal Texas, southward to the Mexican state of Michoacan, and westward to the state of Durango. Elevation 0–2300 m.

Comments. This is one of the two darkest members of the checkerspot-patterned species. The broad geographical and elevational range of this species is noteworthy; further study, especially in the sparsely sampled interior portions of Mexico, will be needed to better understand the phylogeographical history of this species.

Phylogeny and life history evolution

The phylogenetic analyses provided a well-resolved and robust tree (Fig. 8), with parsimony-based analyses recovering the same topology as those based on maximum likelihood. The only polytomy in the tree involves the two *Y. brevifolia* feeding species and a clade containing all stalk-feeders except those of *H. whipplei*.

Formal comparison with previously proposed phylogenies (Davis, 1967; Frack, 1982) is complex because these studies included fewer than half of the currently known taxa, and were based on fewer than ten characters. Nonetheless, the present analysis largely is congruent with those previous studies, with the primary exception being *P. y-inversus* s.l., which was nested with the main group of stalk feeders in both prior analyses. In terms of ancestor reconstruction, Davis (1967) proposed that the basal *Prodoxus* was a fruit feeder, whereas fruit-feeding is a derived condition in the current analysis. In the current analysis, neither the outgroup, *Mesepiola*, nor the sister group genera *Tegeticula* and *Parategeticula*, feed on either of the three plant tissue types used by *Prodoxus*, and thus are not useful for reconstructing an ancestral state in the common *Prodoxus* ancestor. Fortunately, internal reconstruction based on a tree rooted using *Mesepiola* yields a statistically robust reconstruction.

The current data suggest a single, basal origin of stalk feeding within the *Prodoxus*, and three separate transitions to fruit feeding. These transitions represent independent origins onto the three major fruit types presented within yuccas, namely capsular, spongy, and fleshy fruits, although no fruit-feeders have been described from the most diverse

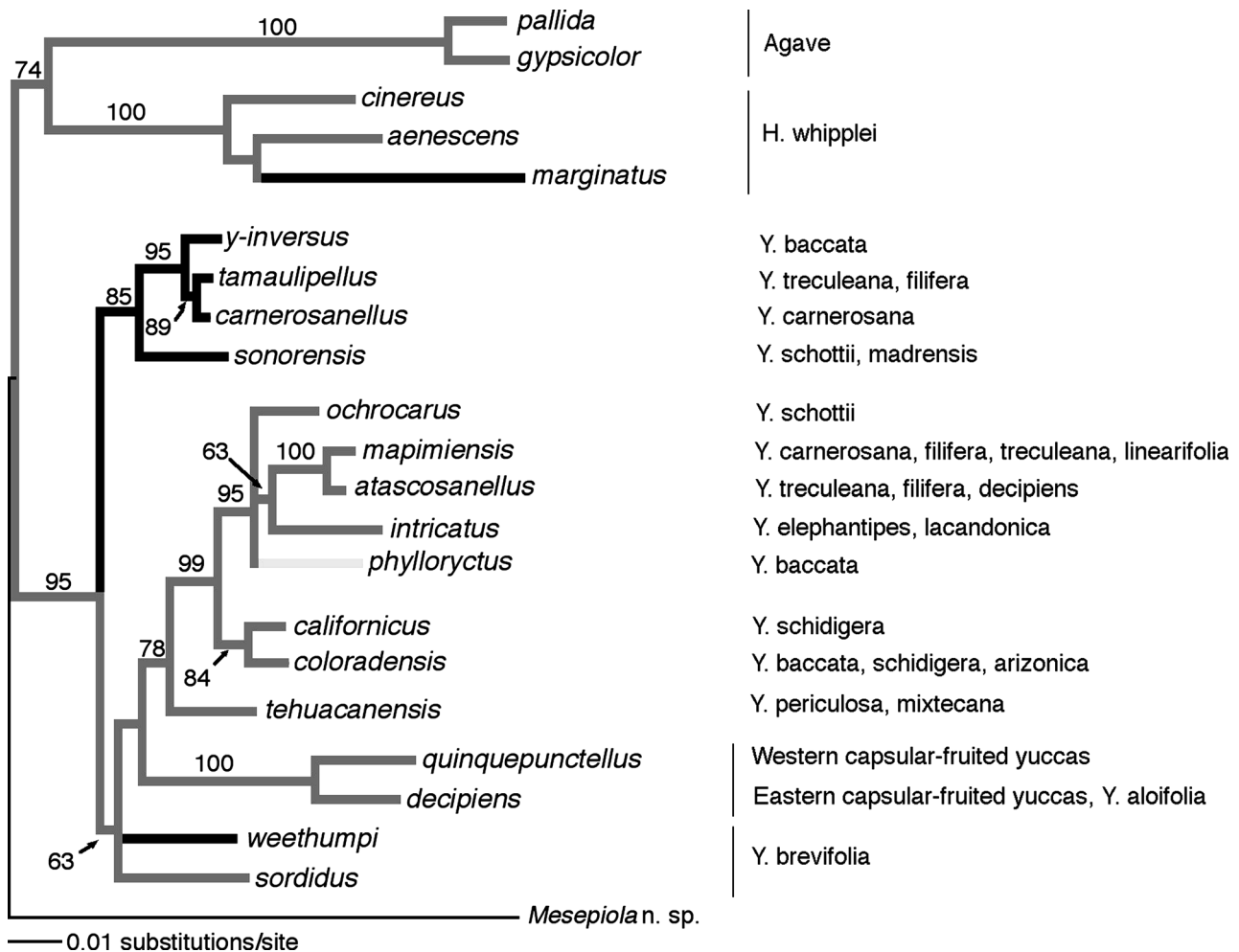


Fig. 8. Phylogram of *Prodoxus* based on maximum likelihood analyses. Numbers above branches are bootstrap values. Branches are coded for oviposition habit; black = oviposition into fruits, dark grey = oviposition into stalks, light grey = oviposition into leaves. Column on right gives known hosts for each taxon. Parametric bootstrap analyses rejected the hypothesis of monophyly for species ovipositing into fruit ($P=0.03$), but did not reject monophyly of *P. weethumpi* and *P. sordidus* that feed on *Yucca brevifolia* ($P=0.32$). See text for more detail.

lineage of capsular fruited yuccas, *Yucca* section Chaenocarpa. The three origins of fruit feeding were *P. marginatus* feeding in the thin walls of *H. whipplei* (Powell & Mackie, 1966), *P. weethumpi* on the spongy-fruited *Y. brevifolia*, and the clade of *P. y-inversus* and three others on fleshy-fruited yuccas (*Yucca* section Sarcocarpa). Parametric bootstrap analyses rejected the hypothesis of inclusion of *P. weethumpi* in the clade containing the fruit feeders *P. y-inversus*, *P. tamaulipellus*, *P. carnerosana* and *P. sonorensis* ($P=0.03$). Since this analysis specifically tests monophyly of the two fruit feeder groups that are least separated in the phylogeny, we can exclude the possibility that *P. marginatus* would group with either of them, thus the analysis supports three separate origins. It is worth noting that the thickened exocarp of the fruit, which is the feeding site of *P. weethumpi* larvae, has a very different, spongy structure, compared to the equivalent tissue of other yuccas that host fruit feeders. Further analyses may

clarify whether there are functional specializations among the moths in response to these substrate differences.

The only leaf-miner in the genus, *P. phylloryctus*, is also derived from a stalk-feeding ancestor. However, *P. phylloryctus* interestingly is not the sister taxon of its coexisting stalk feeder, *P. coloradensis*, which it resembles in gross morphology (Wagner & Powell, 1988). In fact, while coexisting species are common on yuccas, there are no coexisting species that are sister taxa, with the exception of those on *H. whipplei* and possibly *Y. brevifolia*, suggesting that ecological specialization within hosts may have played a limited role in diversification among the bogus yucca moths.

At the same time, closely related *Prodoxus* species tend to feed on related host species. The basal-most node in the *Prodoxus* phylogeny separates species feeding on *Agave* and on *Hesperoyucca*, part of the sister group of *Yucca* (Bogler *et al.*, 1995). Furthermore, species feeding on *Agave* (*P. pallida* and *P. gypsicolor*), *Hesperoyucca* (*P. cinereus*,

P. aenescens and *P. marginatus*) and *Yucca* section *Chaenocarpa* (*P. quinquepunctellus* and *P. decipiens*) form well-supported clades (Fig. 8). Some coastal populations of *P. decipiens* in the eastern U.S.A. do feed in the stalks of the fleshy-fruited *Y. aloifolia*, but this has been a recent expansion of host diet breadth (Groman & Pellmyr, 2000; Althoff *et al.*, 2001). The two *Prodoxus* species on *Y. brevifolia* are far removed genetically from the other *Prodoxus* species (3.00–7.71% uncorrected sequence divergence), perhaps reflecting the distinct reproductive morphology of the host from other yuccas (Simpson, 1975). These two moth species may indeed be sister taxa, as parameteric bootstrap analyses could not reject a hypothesis of monophyly ($P=0.32$). *Prodoxus* species on fleshy-fruited yuccas (*Yucca* section *Sarcocarpa*) fall into two distinct clades that correspond to plant part use. The hosts for all of the fruit-feeders in the clade including *P. y-inversus* are fleshy-fruited yuccas, as are the hosts of *P. phylloryctus* and the stalk-feeding species in the clade subtended by *P. tehaucanensis*. In conclusion, the phylogenetic patterns of plant part use and host affiliations suggest that both of these factors have influenced diversification within *Prodoxus*.

Supplementary material

Supplementary distributional data are available from: <http://www.blackwellpublishing.com/products/suppmat/SEN/SEN301/SEN301sm/htm>.

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Appendix

Samples used for the DNA analyses; locality, local host, and GenBank accession is given for each taxon.

Species	Locality and local host	GenBank
<i>Mesepiola</i> n. sp.	USA: Pima Co, AZ; <i>Nolina microcarpa</i> S. Watson	AF150914
<i>Prodoxus pallida</i>	USA: Riverside Co, CA; <i>Agave deserti</i> Engelm.	AF150919
<i>P. gypsicolor</i>	USA: San Bernardino Co, CA; <i>Agave utahensis</i> Engelm.	AF150920
<i>P. cinereus</i> Riley, 1881	USA: San Diego Co, CA; <i>Hesperaloe whipplei</i> Torrey (Trelease)	AY737258
<i>P. aenescens</i> Riley, 1881	USA: San Diego Co, CA; <i>H. whipplei</i>	AY737259
<i>P. marginatus</i> Riley, 1881	USA: San Diego Co, CA; <i>H. whipplei</i>	AY737260
<i>P. y-inversus</i>	USA: Clark Co, NV; <i>Yucca baccata</i> Torrey	AF150918
<i>P. sonorensis</i>	USA: Pima Co., AZ; <i>Yucca schottii</i> Engelm.	AY737262
<i>P. carnerosanellus</i>	USA: Brewster Co., TX; <i>Yucca carnerosana</i> (Trel.) McKelvey	AY737273

Appendix: Continued.

Species	Locality and local host	GenBank
<i>P. tamaulipellus</i>	USA: Cameron Co., TX; <i>Yucca treculeana</i> Carrière	AY737261
<i>P. sordidus</i>	USA: San Bernardino Co., CA; <i>Yucca brevifolia</i> Engelm.	AY737264
<i>P. weethumpi</i>	USA: San Bernardino Co., CA; <i>Y. brevifolia</i>	AY737265
<i>P. tehuacanensis</i>	MEXICO: Est. Puebla; <i>Yucca periculosa</i> Baker	AY737269
<i>P. californicus</i>	USA: San Diego Co., CA; <i>Y. schidigera</i> Roetzl ex Ortgies	AY737271
<i>P. coloradensis</i>	USA: Mohave Co, AZ; <i>Y. baccata</i>	AF150917
<i>P. ochrocarus</i> Davis (1967)	USA: Cochise Co., AZ; <i>Y. schottii</i>	AY737263
<i>P. mapimiensis</i>	USA: Brewster Co., TX; <i>Y. carnerosana</i>	AY737266
<i>P. atascosanellus</i>	USA: Cameron Co., TX; <i>Y. treculeana</i>	AY737270
<i>P. intricatus</i> Riley, 1893	MEXICO: Est. Veracruz; <i>Y. elephantipes</i> Regel	AY737274
<i>P. phylloryctus</i> Wagner & Powell (1988)	USA: Dolores Co., CO; <i>Yucca baccata</i> Torrey	AY737272
<i>P. quinquepunctellus</i> (Chambers, 1875)	USA: Coconino Co., AZ; <i>Y. baileyi</i> var. <i>intermedia</i> (McKelvey) Reveal	AY737267
<i>P. decipiens</i> Riley, 1880	USA: Wilson Co., TN; <i>Y. filamentosa</i> L.	AY737268