

NICHE PARTITIONING, CO-EVOLUTION AND LIFE HISTORIES OF ERYTHRINA MOTHS, *TERASTIA METICULOSALIS* AND *AGATHODES DESIGNALIS* (LEPIDOPTERA: CRAMBIDAE)

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Abstract – The life histories of the erythrina leafroller, *Agathodes designalis*, and the erythrina stem-borer, *Terastia meticulosalis* from north central Florida are described and illustrated, complementing previous literature accounts. It is proposed that competition among larvae of these two crambid moths has resulted in ecological niche partitioning. In the studied populations, both species feed on the coral bean, *Erythrina herbacea*, and each species occupies different parts of the plant and different plants in the ecosystem. Larval behavior and morphology are consistent with adaptation for resource partitioning. Distribution, hostplant and life history information are compiled from the literature, with a special emphasis on the economic importance of *T. meticulosalis* throughout the tropical and subtropical regions of the world, where this species and its sister species, *T. subjectalis*, attack a variety of *Erythrina* species. In Florida, both species are multivoltine and their life history varies between generations, suggesting adaptation to changes in environmental and hostplant conditions. The co-evolution of these moths in association with the diverse, pan-tropical genus *Erythrina* is proposed and discussed.

Key words: Africa, *Agathodes ostentalis*, Asia, Central America, coral bean, *Erythrina variegata*, Neotropics, pest, speciation, Spilomelinae

INTRODUCTION

It has been noted by ecologists that if several species exploit the same limited resource to an extent where the individuals of the same species compete more than they do with individuals of a different species, the two species tend to partition the resource in order to reduce inter-species competition (Armstrong and McGehee 1980). According to Hutchinson (1959), the more similar the two competing species, the more precisely differentiated and balanced are the adaptations that they develop to their specific environments. In Lepidoptera, different species frequently utilize the same hostplant, which often constitutes a limited resource. In the present study, it is proposed that niche partitioning has occurred between two crambid moth species in the subfamily Spilomelinae: the erythrina borer, *Terastia meticulosalis* Guenée, 1854 (Fig. 1), and the erythrina leafroller, *Agathodes designalis* Guenée, 1854 (Figs. 2, 12). In north-central Florida these species share the coral bean, *Erythrina herbacea* L., as a hostplant, and study of their life histories reveals potential temporal, spatial, and morphological adaptations. Their life histories are therefore described and discussed here in an attempt to identify adaptations for coexistence, as a basis for potential more detailed experimental studies.

Distribution, hostplants, and economic importance of *Terastia meticulosalis*

Terastia meticulosalis is a serious pest of naturally-occurring and commercially grown *Erythrina* L. (Fabaceae) (Table 1), a genus valued for its many uses from agricultural and ornamental to medicinal and pest control (Powell & Westley 1993). Raven (1974) suggests that *T. meticulosalis* makes the cultivation of *Erythrina* in southern Florida almost impossible. *Terastia meticulosalis* is native to the Neotropics and the southern part of North America, including the southern United States, such as Florida and Arizona (Powell & Opler 2009). It is listed as occurring from Georgia through Florida by Adams (2011), but judging by the distribution of its Florida hostplant, *Erythrina herbacea* (USGS 2011), the moth could

be found at the very least in all southern states between Arizona and South Carolina. It has also been introduced to the Galápagos Islands (Ecuador) (Peck et al. 1988). Heppner (2003) lists *Erythrina fusca* Lour. as an additional hostplant for Florida. According to Swezey (1923), *Terastia meticulosalis* was possibly imported with *Erythrina variegata* L. to Hawaii, and was found by him there on a plant that he called ‘wiliwili’, or ‘*Erythrina monosperma*’. These two names in fact refer to two different species, wiliwili actually being the common name for *Erythrina sandwicensis* Degener, and ‘*E. monosperma*’ now treated as *Butea monosperma* (Lam.) Taub, whose common name is ‘parrot tree’. The correct identification of Swezey’s (1923) hostplant is presumably *E. sandwicensis*, since all other host records for *T. meticulosalis* are in the genus *Erythrina*. Curiously, despite the robust nature of larvae of *T. meticulosalis* (pers. obs.), the species has apparently not become established in Hawaii as it has not been found following Swezey’s report (Zimmerman 1958).

Hampson (1896) reported *Terastia meticulosalis* as occurring in St. Domingo (type locality of *T. meticulosalis* is listed as “Haiti”), Honduras, Sri Lanka, Indonesia (Java), and the Philippines. He listed *Terastia subjectalis* Lederer as a junior synonym of *T. meticulosalis*. However, this former name is currently widely used (e.g., Common 1990; Wakamura & Arakaki 2004) for SE Asian and Australian populations, with *T. meticulosalis* and *T. subjectalis* both used for the supposedly

Table 1. Hostplant records for *Terastia meticulosalis*.

Host Plant Species	Locality	Reference	Remarks
<i>Erythrina sandwicensis</i>	Hawaii	Swezey 1923	Likely extinct (Zimmerman 1958)
<i>Erythrina variegata</i>	Sri Lanka	Hutson 1920	Likely <i>T. subjectalis</i>
<i>Erythrina variegata</i>	Great Nicobar, India	Bhattacharya & Mandal 1976	Likely <i>T. subjectalis</i>
<i>Erythrina caffra</i>	South Africa	Taylor 1951	Moth taxonomy unclear
<i>Erythrina herbacea</i>	SE United States	Dyar 1901	
<i>Erythrina fusca</i>	Florida	Heppner 2003	
<i>Erythrina ×bidwillii</i>	N Florida	Eric Anderson pers. com.	Hybrid <i>E. herbacea</i> × <i>E. crista-galli</i>
<i>Erythrina crista-galli</i>	N Florida	Eric Anderson pers. com.	Sold by nurseries with <i>E. ×bidwillii</i>

introduced and now presumably extinct Hawaiian population. In the present paper, I regard accounts of *T. meticulosalis* as a pest of *Erythrina variegata* in Sri Lanka (Hutson 1920) and on the island of Great Nicobar (Bhattacharya & Mandal 1976), as well as records in collection databases from Asia as these presumably referring to *T. subjectalis*.

In Africa, *T. meticulosalis* has been recorded in Kenya from light-trapping (Taylor et al. 1979), and from Cape Province in South Africa (Taylor 1951), where it feeds on coastal coral tree, *Erythrina caffra* Thunb. Additionally, the species apparently occurs in Uganda and Sierra Leone (Goff 2011). It is likely that lack of records from the other countries in the region is due to limited collecting data. The taxonomic status of the African populations has not been re-examined; hence, the name *T. meticulosalis* is used in the present paper when referring to them.

Distribution and hostplants of *Agathodes designalis*

In Florida, *Terastia meticulosalis* shares *Erythrina herbacea* with *Agathodes designalis* as its larval hostplant. The distribution of *A. designalis* is also largely tropical, from the southeastern United States (Florida to Arizona) and southwards all the way to Argentina, including the West Indies (Powell & Opler 2009), and the Galápagos Islands where it was apparently introduced (Peck et al. 1988). In Florida, according to Heppner (2003), larvae of *A. designalis* have been recorded to feed on several other Fabaceae: *Erythrina crista-galli* L., *E. fusca*, *E. variegata* L. and *Inga vera* Mart, and on other plant families: *Citharexylum berlandieri* B. L. Rob., *C. spinosum* L. (Verbenaceae), *Kigelia africana* (Lam.) Benth. (Bignoniaceae) and *Nerium oleander* L. (Apocynaceae). In Costa Rica, *A. designalis* has been recorded on *Erythrina berteriana* Urban, *E. costaricensis* Micheli, *E. lanceolata* Standley, and on *Triumfetta lappula* L. (Tiliaceae) (Janzen & Hallwachs 2011).

Table 2. Hostplant records for *Agathodes designalis*.

Host Plant Species	Locality of Record	Reference
<i>Erythrina crista-galli</i>	Argentina N Florida	Bourquin 1932 Eric Anderson pers. com.
<i>Erythrina herbacea</i>	Florida	Dyar 1901
<i>Erythrina flabelliformis</i>	Arizona	Powell & Opler 2009
<i>Erythrina fusca</i>	Florida	Heppner 2003
<i>Erythrina variegata</i>	Florida	Heppner 2003
<i>Inga vera</i>	Florida	Heppner 2003
<i>Erythrina ×bidwillii</i>	N Florida	Eric Anderson pers. com.
<i>Citharexylum berlandieri</i>	Florida	Heppner 2003
<i>Citharexylum spinosum</i>	Florida	Heppner 2003
<i>Kigelia africana</i>	Florida	Heppner 2003
<i>Nerium oleander</i>	Florida	Heppner 2003
<i>Erythrina costaricensis</i>	Costa Rica, ACG	Janzen & Hallwachs 2011
<i>Erythrina lanceolata</i>	Costa Rica, ACG	Janzen & Hallwachs 2011
<i>Erythrina berteriana</i>	Costa Rica, ACG	Janzen & Hallwachs 2011
<i>Triumfetta lappula</i>	Costa Rica, ACG	Janzen & Hallwachs 2011

*The plant nomenclature found in Heppner (2003) and other references has been updated here to reflect the current classification as in the International Plant Names Index (www.ipni.org).

Terastia meticulosalis and *Agathodes designalis* in collections

Despite the wide distribution of species and numerous accounts of larval feeding in the literature, the presence of this species in collections is rather limited. Given the broad distribution and apparent abundance of the immature stages, the observed scarcity of adult specimens of both species is presumably due to the habits of the moths (some moths are known not to come to light or/and to be largely active during the day). Some of the easily-accessible collections data are presented below:

The McGuire Center for Lepidoptera and Biodiversity (MCGL) includes only a dozen specimens of *A. designalis* from Latin America, including rearing vouchers from Costa Rica, a couple of specimens from each of Honduras, Panama, Dominican Republic, Mexico and Ecuador, and 34 Florida specimens. A recent moth survey in and outside Gainesville, Florida conducted with black-light (Austin 2010), though resulting in over 30,000 specimens, included none of *A. designalis* or *T. meticulosalis*. The general MCGL collection includes five specimens of *T. meticulosalis* from Latin America (Guatemala, Dominican Republic, and Ecuador) and 35 Florida specimens, with a single specimen from Louisiana and Arizona. The California Academy of Sciences has eight *T. meticulosalis* specimens from Latin America (Colombia, Costa Rica, Mexico, Nicaragua, Panama, Peru, and Venezuela), and single specimens from Florida and Arizona (Calacademy Database 2011). A total of 19 records from 17 different countries are found in that database for *A. designalis*, four of which are likely misidentifications from Asia. Latin American records include Brazil, Costa Rican, Ecuador, El Salvador, Guatemala, Mexico, Panama, Peru, and Venezuela, and there is only a single U.S.A. record from Arizona. The Essig Museum contains a single specimen of *A. designalis* from Arizona and none of *T. meticulosalis* (Essig Museum Database 2011).



Fig. 1. Female of *Terastia meticulosalis* (ex larva, June 2011, Gainesville, FL).



Fig. 2. Male of *Agathodes designalis* (ex larva, June 2011, Gainesville, FL).

Previous life history studies

The observations and illustrations provided in this paper are intended to supplement existing descriptions of the immature stages in literature for these two species (Dyar 1901; Taylor 1951; Bourquin 1932, 1945), and to examine how these two species might coexist on the same hostplant through partitioning resources.

No illustrations in the lepidopterological literature for the life history of *Terastia meticulosalis* seem to be readily available despite the economic importance of this insect. While Dyar's (1901) descriptions of *T. meticulosalis* and *Agathodes designalis* in Florida are very general, Taylor's (1951) description of the life history of *T. meticulosalis* is more detailed. The larval biology in Taylor's description differs from the observations presented below, because in the Cape Province of S. Africa, where Taylor conducted his studies, the moth uses another hostplant, *Erythrina caffra*, and obviously develops in different seasons of the southern hemisphere. For instance, he describes the species as a defoliator, while in Florida the species has not been observed feeding on leaves of *E. herbacea*. Taylor's description of larval morphology is detailed and shows some differences to that provided here, since he cites the presence of lighter-colored lines and dark tubercles on each segment on "either side of the center." He describes the pupa as "pale yellow to almost white," which does not correspond to the observations presented below. Taylor provides data on parasitism by an unidentified *Brachymeria* Westwood (Chalcididae) species, which emerged from the pupae.

The mature larva of *Agathodes designalis* was illustrated by John Abbot during the period 1776-1840, but this illustration, which is located in the University of South Carolina library, appears to be unpublished (John Calhoun, pers. com), although it can be viewed on that library's website (USC 2011). Bourquin (1932) described the life history of *A. designalis* from Argentina and later repeated and illustrated this description in his book (Bourquin 1945). The description involved a different hostplant, *Erythrina crista-galli*, which probably explains why the biology he described, as well as the seasonality, is different from those described below. Bourquin observed oviposition in January and February, which are the hottest months in Argentina, probably equivalent to July and August in Florida. Therefore, not surprisingly, some of his observations of larval behavior are more similar to those presented here for the summer generation in July. He described oviposition of solitary eggs, and larvae that emerged eight days later and lived inside shelters constructed on the ventral side of the leaf by spinning a web tunnel and pulling the leaf edges together. Bourquin described larvae as pale green with cream subdorsal lines and warts, and listed parasitoids attacking *A. designalis*. Among these parasitoids were several species of tachinid flies, one of which, *Bourquinia deaurata* Blnch., was described using a specimen Bourquin reared from *A. designalis*. He also found a braconid wasp of the genus *Apanteles* Foerster parasitizing these larvae.

Finally, there are photographs of two mature caterpillars of *A. designalis* in Janzen & Hallwachs (2011). In this on-line database of caterpillars of NW Costa Rica, both specimens differ from the Florida population. One of these caterpillars

exhibits a complete row of dorsal spots, with subdorsal spots extending only in segments T1-T3. The other caterpillar exhibits dorsal and subdorsal spots only in T1-T3, with the rest of the spots reduced to mere dots. Hence this second caterpillar appears more cryptic than aposematic. Munroe (1995) listed two subspecies: *A. designalis monstrialis* Guenee with "North America" as a type locality, and the nominate subspecies with "Brazil" as a type locality. Larval coloration differences might therefore be indicative of subspecific or even specific status of the Costa Rican population, and more taxonomic research, perhaps involving DNA sequencing, is called for to answer these questions. Interestingly, the closely related coral tree moth, *Agathodes ostentalis* Geyer, known as pest of *Erythrina variegata* and *E. vespertilio* Benth. in Australia and throughout Southeast Asia, is very similar to *A. designalis* in its adult form, but is quite different in mature larvae, which are dark brown with yellow stripes (Mohn 2011).

MATERIALS AND METHODS

Erythrina herbacea is easily identifiable due to its beautiful flower and seed pods illustrated in numerous websites oriented towards landscapers (e. g., Brown 2011). A voucher specimen of the hostplant is deposited at MGCL. In the area in which the observations were made (Florida, Alachua Co., University of Florida, Natural Area Teaching Laboratory (NATL), 25m, 29°38'00" N, 82°22'10" W), *Erythrina herbacea* is one of the most common plants. The plant spreads through seeds and vegetatively through its massive root system, and, in the spring, some plants produce flowers, although the majority of plants are formed by young shoots that are non-flowering. This seems to be the pattern of growth for *E. herbacea* in north Florida, where hard freezes occur every year, killing off above-ground parts of the plant. Further south, where freezes are more sporadic, *Erythrina* tends to be shrub or tree-like (Brown 2011).

On 10 May 2011, a fourth instar larva of *Agathodes designalis* was found on an inflorescence of *Erythrina herbacea* (Fig. 3). On the same day in a different plot within NATL, a few pods of *E. herbacea* showing signs of infestation were collected (Fig. 4C). Some of these pods contained larvae of *T. meticulosalis* (Fig. 4A, B), which, within three weeks, resulted in adults. Larvae were continuously collected throughout the summer and fall, and were reared through to adult stage inside plastic bags placed indoors at ca. 20°C. New plant material (flowers, seed pods, or stems, depending on species and time of the year) was added every other day. Voucher specimens of adults and larvae were deposited at MCGCL. Identifications of adults were made using Powell and Opler (2009) and Brown (2011), and presented little problem since, in Florida, these are very distinctive moths. Photographs were made using Canon EOS Rebel T1i with a 60mm macro lens.

Table 3. Emergence dates of *T. meticulosalis* and *A. designalis* indicate presence of at least four generations per year.

<i>A. designalis</i>	31 May	1 Jul	3 Aug	14 Sep	
<i>T. meticulosalis</i>	9 Jun	6 Jul	15 Aug	14, 23 Sept	29, 31 Oct 15, 16 Nov



Fig. 3. Spring generation of *Agathodes designalis* feeding on *Erythrina herbarcea* flowers. (A) Infested plant; (B) Cryptic first and second instar larvae web the flower stalk; (C) Fourth instar larva; (D-F) Fifth instar larvae web over the inflorescence, or can be found inside individual flowers; (G) Prepupa, showing bright red aposematic coloration.

OBSERVATIONS

Spring generation

Despite their small size, both *Terastia meticulosalis* and *Agathodes designalis* require a substantial amount of plant material to develop to the adult stage. As a result, the health of their hostplants can be greatly affected and the whole plant, or at least its reproductive organs, are often destroyed. The two species were observed to exploit *Erythrina herbacea* plants simultaneously by apparently partitioning the resource, feeding on different parts of the plant and on different individual plants within the same habitat.

The first adult male of *Agathodes designalis* emerged at approximately the same time as the first *Terastia meticulosalis*. Continued collecting of larvae of all instars during late May – early June showed that the infestations of blooming and fruiting plants were becoming more extensive, and by June it was hard to find an uninfected flower or pod. Apparently, in the spring, female moths oviposit almost exclusively on plants which are in bloom, as no larvae were found on non-reproducing plants. No evidence of feeding damage to leaves and stems was found in the field, although some feeding by *A. designalis* occurred on young leaves in captivity when flowers were unavailable.

In the wild, the entire development of the spring generation of *Agathodes designalis* occurred while feeding on the inflorescences, which were covered with webs by both early and late instar larvae (Fig. 3), perhaps preventing or discouraging *Terastia meticulosalis* females from ovipositing on these plants. Young larvae of *A. designalis* are translucent, orange with six rows of short, black sclerotized tubercles, and are cryptic (Fig. 3B). The later instar larvae and prepupae appear aposematic: they develop cream-colored longitudinal stripes and the black tubercles become more prominent on the orange background. The head is bright red, which was also the color of the entire larva by the prepupal stage (Fig. 3G), but only in the spring generation that feeds on flowers (prepupae of summer and fall generation are cream-colored).

Young larvae of *T. meticulosalis* infest the tips of the stem and gradually kill off the upper part of the plant (Fig. 6A), from where, in the spring, they move into the pods to feed on seeds. In younger larvae, the dorsal prothoracic plate and the head are black and heavily sclerotized (Fig. 5). In older larvae, the prothoracic plate becomes cream-colored, slightly darker than the rest of the body, which is otherwise translucent, cream-colored (Fig. 7A). Prior to pupation, last instar larvae are able to consume large numbers of seeds and move from one pod to another. Larvae of *T. meticulosalis* sometimes accumulate red pigments prior to exiting pods to pupate on the forest floor (Fig. 4B). This however, was only observed in the spring generation that feeds on seeds.

Both *Terastia meticulosalis* and *Agathodes designalis* make loose double-layered cocoons and their pupae appear similar, though *T. meticulosalis* is typically larger, at least in the spring (Figs. 8H, 9). The adults of both species emerged within two weeks following pupation, with continued emergence taking place in the lab through the end of June until mid-July.



Fig. 4. Larvae of *Terastia meticulosalis* feeding on *Erythrina herbacea* seeds in the spring: (A) 3rd instar larva; (B) Prepupa; (C) Characteristic damage by *T. meticulosalis* to the *E. herbacea* seed pods.



Fig. 5. Second instar larva of *Terastia meticulosalis*.

Summer/fall generations

In the wild, larvae of the summer generation of both species developed in conditions that were quite different from those of May-June. With much higher temperatures and humidity than in May, no flowers or pods with edible seeds were present. By July, pods of *Erythrina herbacea* were dry and open, exposing red seeds, for which the plant has received its common name of coral bean (Fig. 6B). In the absence of flowers, the larvae of *A. designalis* were found feeding on leaves, making shelters by folding the leaf and building a loose nest inside (Fig. 8A, B). This second generation of *A. designalis* pupated by July 18 and the first adults of both species were obtained in captivity by early August. Recorded emergence dates of moth in captivity summarized in Table 3 suggest the presence of four *A. designalis* generations between May and September. During the summer, I was able to find only ten 4-5th instar larvae of *A. designalis*. Nevertheless, it appeared that the summer generations developed slower than the spring one, which also would indicate a higher nutritional value of their spring diet (flowers) vs. their summer

diet (leaves). Larvae of *A. designalis* collected in September, completed their feeding by mid October, and diapaused in a prepupal stage inside cocoons. Such a mode of diapause has previously been shown to be under photoperiodic control (Wu *et al.* 2006).

The young larvae of *T. meticulosalis* were found inside the stems of plants that had new growth, producing a characteristic dying-off of the tip (Fig. 6C). In comparison to the spring generation, the infestation rate by *T. meticulosalis* was still relatively high. A similar situation was found in September, when multiple new infestations of young *E. herbacea* stems by *T. meticulosalis* continued to be present, with larvae ranging from young to mature. As the availability of undamaged shoots of *E. herbacea* declined, neonate *T. meticulosalis* larvae were found boring and feeding inside the leaf stalks and later making their way inside the stems in this way. As found by rearing *T. meticulosalis* in the spring and in the summer, feeding on seeds must have nutritional benefits in addition to protection from predators and the large volume of edible material that they offer. Individuals from the spring generation of *T. meticulosalis* found in and raised on seed pods were larger when compared to the summer generation found and raised inside the stems under similar laboratory conditions (Fig. 7B). Fore-wing length in specimens of June vs. Aug-Sept generations formed non-overlapping ranges: 0.76 ± 0.05 vs. 0.61 ± 0.03 (SD) inches; $N=10$ ($P < 0.05$). By the end of October there were still a few larvae completing their development in the wild. In captivity, these



Fig. 6. (A) Larva of *Terastia meticulosalis* purges the hollow stem from frass by crawling backwards to the entrance when defecating; (B) Coral bean, *Erythrina herbacea*, a hostplant of *T. meticulosalis*, in July with pods open and seeds exposed; (C) *Erythrina herbacea* in July, showing a characteristic dying off of the stem as the larva of *T. meticulosalis* burrows downward.

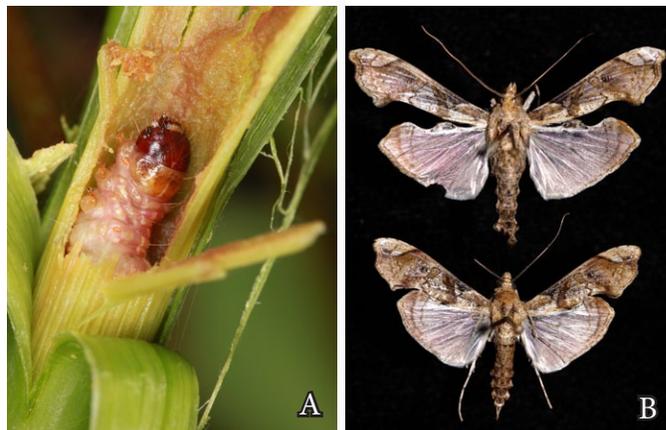


Fig. 7. (A) The larva of *Terastia meticulosalis* is capable of moving backwards within tight confines of the stem. (B) Spring generation adult of *T. meticulosalis* resulting from seed-feeding larvae (top) is 20% larger than late summer/fall generations resulting from stem-boring larvae.



Fig. 8. Summer and fall generations of *Agathodes designalis* feeding on *Erythrina herbacea* leaves. (A-B) Larvae of fourth-fifth instar were repeatedly found in shelters made either of a single folded leaf, or several leaves bound together; (C-F) Fifth instar larva; (G) Prepupa; (H) Pupa

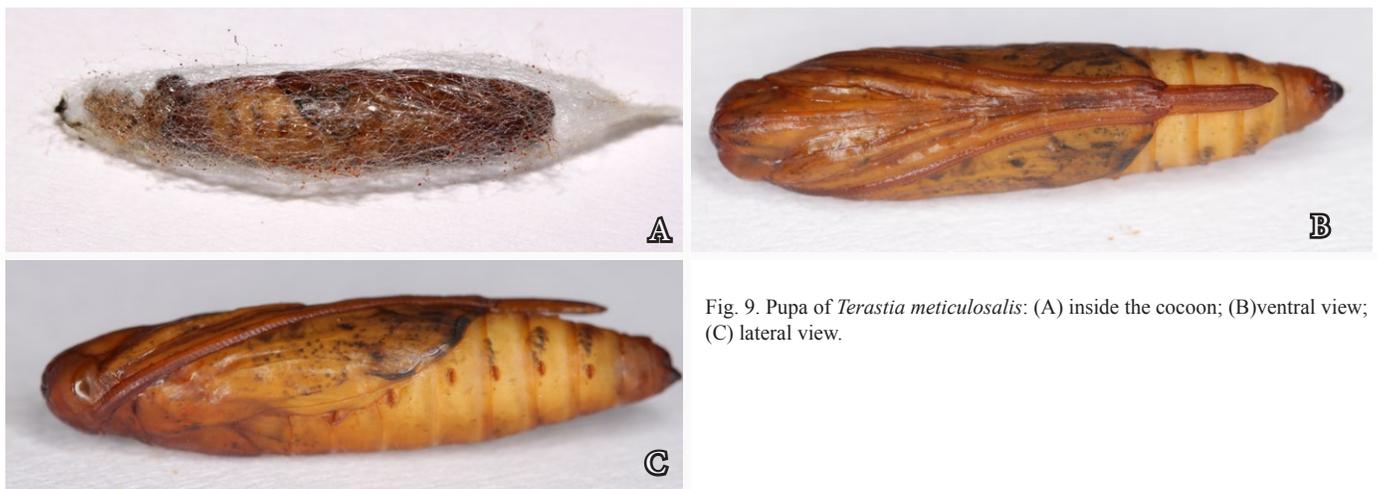


Fig. 9. Pupa of *Terastia meticulosalis*: (A) inside the cocoon; (B) ventral view; (C) lateral view.

larvae pupated and all of them emerged in October-November (Table 3), so the diapausing stage of *T. meticulosalis* in north-central Florida is yet to be determined.

Transgression of lifestyles

As additional evidence that niche partitioning has occurred between *Terastia meticulosalis* and *Agathodes designalis*, twice during the course of the present study each species was observed exhibiting behavior more typical of the other species. Specifically, following numerous observations of larvae of *A. designalis* building web shelters and feeding superficially on flowers and leaves, a single last instar larva was found boring inside a stem of *Erythrina herbacea* in a manner normally observed in *T. meticulosalis* (Fig. 10B). This was the sole record of such behavior despite over a hundred dissections of damaged stems, during which typically only *T. designalis* larvae were found. Likewise, in captivity, when unable to access the inside of the stem due, apparently, to its toughness, a mature larva of *T. meticulosalis* was observed feeding superficially, constructing a web shelter similar to that typical of *A. designalis* (Fig. 10A). Such “atavistic” behavior suggests that the common ancestor of both species may have had both boring and web-building lifestyles. Other crambid relatives of erythrina moths, such as *Glyphodes onychinalis* (Guenée), seem to be able to exercise

such “opportunism” as a norm, combining stem-boring and leaf-skeletonizing lifestyles (e. g. , Solis 2008), and I hypothesize that it is niche partitioning that has favored *T. meticulosalis* and *A. designalis* adopting the exclusively endophagous and exophagous lifestyles on *E. herbacea* in Florida.

DISCUSSION

Evolution of genus *Erythrina* (Fabaceae) and historical biogeography of erythrina moths

The erythrina moth system described above in Florida is replicated almost identically in Australia and the South Pacific, where respective sister species *Terastia subjectalis* and *Agathodes ostentalis* occur. Long considered a synonym of *T. meticulosalis* due to its phenotypic similarity, *T. subjectalis* was apparently resurrected by Eugene Munroe through personal communications and unpublished manuscripts (Hinckley 1964; Common 1990). It appears that the ranges of *T. meticulosalis* and *A. designalis* largely overlap and so do those of *T. subjectalis* and *A. ostentalis*. Considering that all four species feed on numerous species of *Erythrina* worldwide (Tables 1, 2), one might also suppose that this plant genus, which includes 112 species (Bruneau 1996), is the primary food source for this complex and has played a role in its evolution.



Fig. 10. Transgression of lifestyles: larvae of *Terastia meticulosalis* and *Agathodes designalis* exhibiting behavior typical of the other species.

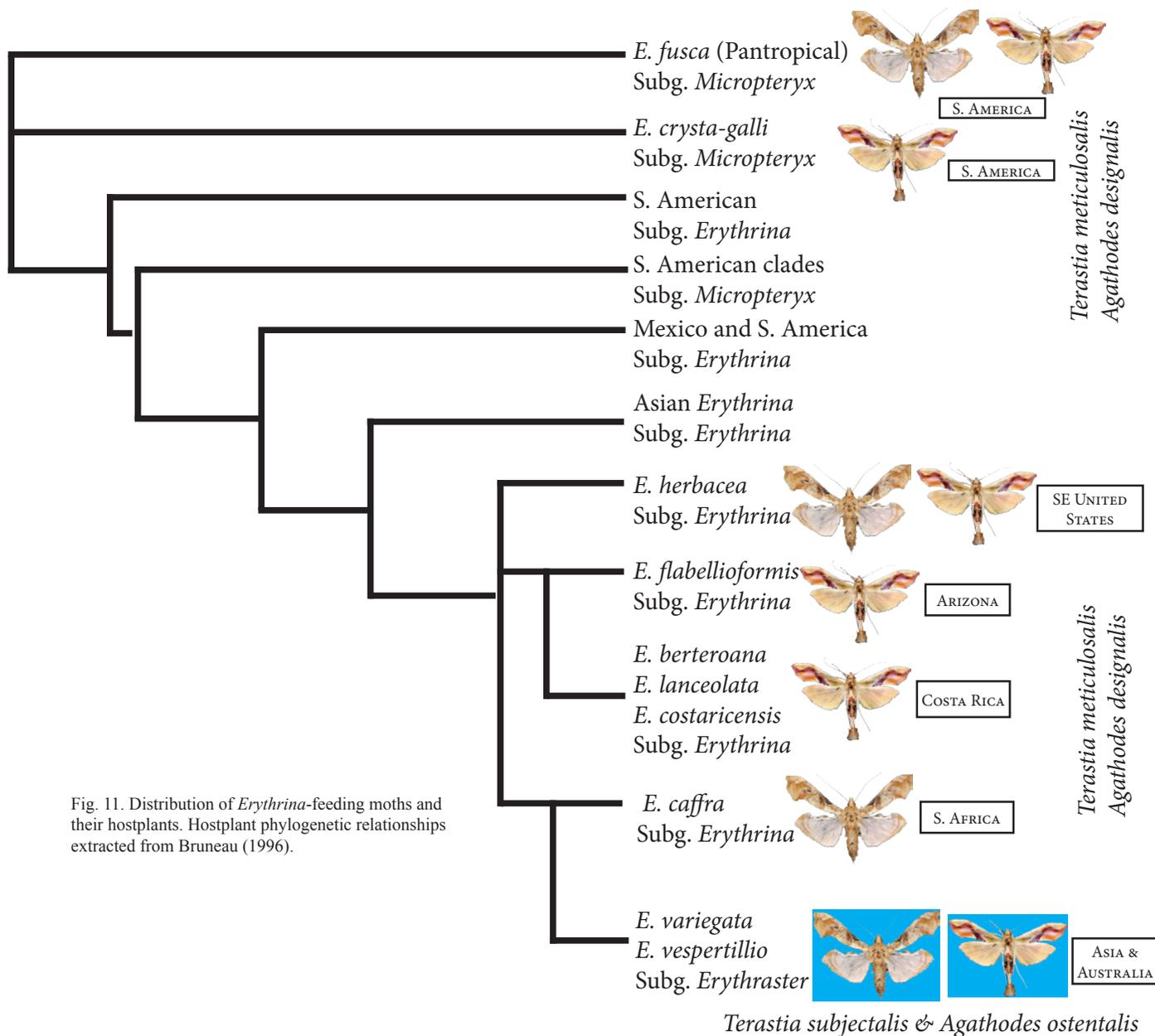


Fig. 11. Distribution of *Erythrina*-feeding moths and their hostplants. Hostplant phylogenetic relationships extracted from Bruneau (1996).

Bruneau (1996) states that “a paraphyletic assemblage of South American elements are basal in the genus.” She suggests that from this group derived a South American/Mexican clade and an Asian clade. The latter gave rise to a New World group and a primarily African clade. In Fig. 11, known hostplants of *Agathodes* and *Terastia* are presented in a form of a cladogram based on Bruneau’s analyses. The South American hostplants *Erythrina crista-galli* and pantropical *E. fusca* are in the subgenus *Micropteryx*, a basal clade in the genus. *Erythrina* (*sensu stricto*), to which *E. herbacea* and several other North and Central American hostplants belong, might have had, according to this evolutionary scenario, more prolonged association with erythrina moths than African *Erythrina* or the members of subgenus *Erythraster* in Asia/Australia. Given that modern *Terastia* and *Agathodes* are very phenotypically similar among regions, dispersal in which moths crossed oceans contemporaneously or following *Erythrina* species must have occurred. The plants themselves were most likely

dispersed by birds, which eat the seeds. The outer hard layer of the latter normally needs to be compromised either chemically or mechanically for them to germinate, which suggests that birds are required for dispersal of the plants. It is reasonable to conclude that when *Terastia* and *Agathodes* crossed water barriers in the past, they would readily have found established hostplants, such as *E. caffra* in Africa, *E. variegata* in Asia-Australia, *E. sandwicensis* in Hawaii, or *E. vespertilio* in Australia. Bruneau (1996) suggests an early Tertiary occurrence of *Erythrina* in North America based on the fossil record, with subsequent diversification in South America, Africa, and Asia, allowing many millions of years during which the hostplant associations described here could have been established and refined, including dispersal and the proposed niche partitioning. Future phylogenetic analyses of *Terastia* and *Agathodes* would be useful in determining how colonization of hostplants and co-evolution of these two genera occurred.

Niche partitioning and ecological cost of competition

The erythrina moth species discussed here have been occasionally described as defoliators. This indicates that they are capable of achieving a high density on any given hostplant. Both Taylor (1951) and Bourquin (1945) noted the presence of intraspecific competition in the populations they studied, which was expressed in territorial attacks and even cannibalism of larvae. This creates, according to Armstrong and McGehee (1980), an ideal scenario for niche partitioning, should these two species come into contact as they do in north-central Florida, when utilizing *Erythrina herbacea* as a host, and probably have done so historically on many other occasions.

Host damage by *Terastia meticulosalis*, which achieves higher density on *E. herbacea* and tends to destroy the inflorescences, is perhaps the driving force behind the success of *A. designalis* on alternative hostplants. As a result, at least four genera of plants other than *Erythrina* belonging to four different families (Table 2) have been utilized by *A. designalis*. Predator pressure and hostplant defenses such as alkaloids known from *Erythrina* (e. g., Powell & Westley 1993) are likely driving forces behind *T. meticulosalis* developing endophagous habits, and it is unclear how much *A. designalis* has contributed to this evolutionary shift in lifestyle. At the same time, it is apparent that *T. meticulosalis* has most likely been a factor in determining affinity of *A. designalis* for inflorescences and leaves - plant organs least affected by *T. meticulosalis*. Either of the species is capable of destroying or reducing the reproductive systems of plants, starting from the tip of the plant where the inflorescence is formed. It is perhaps not accidental that during the flowering of the plant in the spring, the habitat appeared to be partitioned by the moths: a patch of



Fig. 12. Live male of *Agathodes designalis* (ex larva, Gainesville, FL).



Fig. 13. *Erythrina x bidwillii* (a commercially sold hybrid between *E. herbacea* and *E. crista-galli*) attacked by *Terastia meticulosalis* (Gainesville, FL).

E. herbacea where *A. designalis* was found was devoid of *T. meticulosalis*, and vice versa. In the summer, *T. meticulosalis*, with its ability to avoid high temperatures by hiding inside the wet and secluded environment of the stem, was dominant, and was found throughout the habitat, while only occasional *A. designalis* larvae were found in leaf shelters and even inside a stem. Based on the observed population levels, *T. meticulosalis* proved to be the more successful competitor under summer conditions, though one can imagine a scenario where such high population levels can lead to collapse due to overexploitation of resources. Future studies might be designed to evaluate these populations with quantitative statistical analyses.

Hutchinson's (1959) suggestion that similarity between competing species leads to more precisely differentiated and balanced adaptations is consistent with the *Erythrina* moth system. The species are of similar size and are closely related, both belonging to the *Polygrammodes* group (Munroe 1995), so they probably derived from a common ancestor with very similar lifestyles to quite opposite ones. Since other species of Spilomelinae are known to be endophagous (e. g. Gibbs 1992) or to employ both stem-boring and leaf-skeletonizing strategies at once (e. g., Solis 2008), it is hard to say which of the feeding modes is ancestral for the erythrina moths. I hypothesize, with the hope in the future to acquire further experimental evidence, that webbing of the inflorescence by *A. designalis* larvae inhibits oviposition by *T. meticulosalis* and that the killing off the tips of the plant by young larvae of *T. meticulosalis* repels *A. designalis* females from oviposition. Other signals perhaps have evolved, including volatile chemistry, which help the two species partition resources without entering into costly competition on the same plant. For instance, their sister taxa in Asia, *T. subjectalis* and *A. ostentalis*, have been shown to have partitioned the "airspace" by evolving pheromones that are quite different and work only for attracting conspecifics (Wakamura & Arakaki 2004). Similar research is called for in North American *Terastia* and *Agathodes*.

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