

Early stages of the enigmatic *Prodidactis mystica* (Meyrick) with comments on its new family assignment (Lepidoptera: Prodidactidae)

MARC E. EPSTEIN¹ & JOHN W. BROWN²

¹ Department of Systematic Biology, Entomology Section, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560-0105, USA

² Systematic Entomology Laboratory, Plant Sciences Institute, Agricultural Research Service, U.S. Department of Agriculture, National Museum of Natural History, Washington, D.C. 20560-0168, USA

Abstract

Prodidactis Meyrick is a monotypic genus restricted to southern Africa (South Africa, Zimbabwe, and Swaziland). The early stages of *P. mystica* (Meyrick) are described and illustrated for the first time; the larval host is *Nuxia congesta* (Loganiaceae). The genus previously has been assigned to Tortricidae, Yponomeutidae, and Limacodidae; however, an examination of larval, pupal, and adult characters contradict these placements. Although evidence from the larval stage places *Prodidactis* in Crambidae (Pyraloidea), features of the adults convincingly contradict this assignment. As an interim solution, we propose Prodidactidae, new family, to accommodate this unusual genus.

Key words: Africa, biology, Crambidae, Immidae, larvae, Limacodidae, morphology, chaetotaxy, phylogenetic relationships, Tortricidae, Yponomeutidae, Zygaenoidea

Introduction

Prodidactis Meyrick is a monotypic genus from southern Africa (South Africa, Zimbabwe, and Swaziland) that traditionally has defied confident familial placement. Historically assigned to Tortricidae (Meyrick 1918, 1921) and Yponomeutidae (Meyrick 1930), the genus has resided in Limacodidae for the last 39 years (Janse 1964). The current familial assignment of the genus fell into question in 1992 when Neville Duke (Swaziland), an experienced field lepidopterist, reared *Prodidactis* from field collected larvae. Upon emergence of the adults, Duke recognized that based on the larvae, *Prodidactis* did not belong in Limacodidae. While features of the early stages convincingly exclude *Prodidactis* from all previous familial assignments, the unique combination of larval and adult features con-

tinues to defy confident placement in currently defined families of ditrysiian Lepidoptera. The purposes of this paper are to propose a new family, Prodidactidae, as an interim solution to the problem, discuss the putative position of the family within Ditrysia, describe and illustrate the last instar larva, pupa, and adult of *Prodidactis mystica* (Meyrick), and briefly describe its life history.

Materials and methods

Larvae of *P. mystica* were collected by Neville Duke in Mbabane, Swaziland, in February 1992, and taken into the laboratory where they were reared under ambient temperature in a small plastic container. They were fed *Nuxia congesta* (Loganiaceae), the plant upon which they were discovered in the field. Three larvae were preserved in pyric acid for subsequent study, and the remaining three allowed to develop, resulting in two adults and one dead pupa.

Larvae, pupae, and adults were examined using a dissecting microscope. Terminology for characters of the larvae used in the description below follows Stehr (1987). Genitalic dissection methodology follows essentially that summarized in Brown and Powell (1991). Illustrations of genitalia were drawn with the aid of a microprojector. Terminology for wing venation and genitalic structures follows Epstein (1996). Electron micrographs of larval and pupal skins, cocoons, and adult pretarsus were taken using a Leica 440 Stereoscan Scanning Electron Microscope (SEM). Specimens studied by SEM were glued to a stub and were sputter coated with gold-palladium as described in Epstein (1996). Voucher specimens of larvae, pupae, and adults are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Prodidactidae, New Family

The following description is based on the single species, *Prodidactis mystica* (Meyrick) and is intended also to function as a redescription of the genus and species. Hence, it includes a combination of familial-, generic-, and species-level characters. The description includes the states for each of the 24 key characters listed in Heppner's (1998: Table 2) "Family Characters States." The importance of certain family-level characters are detailed in the discussion following the description; a comparison of these among the taxa discussed is outlined in Table 1. Choice of characters and definition of character states are based on Epstein (1996), Heppner (1998), and Kristensen (1999). Of the character states described below, the extremely reduced labial palpus and the elongate membranous lobe of the male hindcoxa appear to be of greatest significance, and both are considered autapomorphies for the family.

Adult. Head (Figs. 1-2, 5-7): Smooth scaled or only slightly roughened, frons red; vertex pale gray; ocellus absent; chaetosema absent; maxillary palpus well developed, 3-segmented, covered and tufted with large pale scales; labial palpus greatly reduced, 3-segmented, with crimson-red scales; haustellum well developed, unscaled. Area dorsad of haustellum base with a vertical row of pale scales. Antenna filiform, finely ciliated, not differentiated between sexes; antennal pecten absent.



FIGURES 1-4. Adult and larva of *Prodidactis mystica*. 1) Spread adult moth; 2) Adult in natural resting posture; 3-4) Last instar larva feeding on *Nuxia congesta* (photographs in Figures 2-4 by Neville Duke).



FIGURES 5-6. Adult head and thorax of *Prodidactis mystica*. 5) Frontal view of head (scales removed from frons) (pr=proboscis (haustellum), mp=maxillary palpus, lp=labial palpus); 6) Dorsal view of head and prothorax.

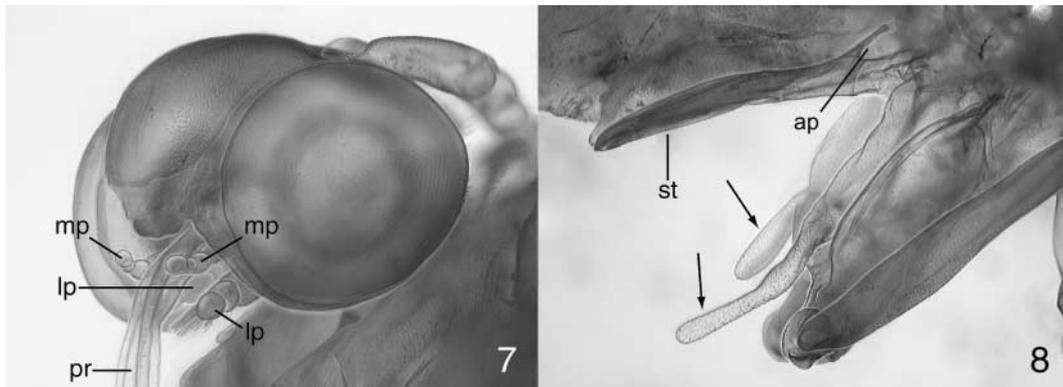
TABLE 1. Comparison of character states of egg, larva, pupa, and adult among families. [Where two states occur, the more common is listed first. * Differs from Heppner (1998)]

	Yponomeutidae	Tortricidae	Zygaenidae	Limacodidae	Immidae	Crambidae	Prodidactidae
EGG							
egg type	upright	flat	flat	flat	upright	upright	flat
LARVA							
L-group on T1	trisetose	trisetose	bisetose	bisetose*	trisetose	bisetose	bisetose
pinaculum w/ out seta	absent	absent	absent	absent	absent	absent/ present	present
crochets	multiserial rows	uni-triordinal circle	mesoserries	mesoserries	mesoserries	bi-triordinal circle	biordinal circle
prolegs	A3-6, 10	A3-6, 10	A3-6, 10	A2-7, 10*	A3-6, 10	A3-6, 10	A3-6, 10
L1 and L2 on abd	separate pinaculum	same pinaculum	same pinaculum	same pinaculum	separate pinac.	same pinaculum	same pinaculum
anal fork	absent	present	present	absent	absent	absent	absent
PUPA							
general form	fusiform	fusiform	compact	compact	fusiform	fusiform	compact
haustellum	present	present	present	present	present	present	present
labial palpus	small	small	small	small	small	small	small
maxillary pal- pus	absent	present	absent	absent	absent	absent	present
eye	unsculptured	unsculptured	sculptured	sculptured	unsculptured	unsculptured	unsculptured
dorsal spines	absent	present	present	present	absent	absent	absent
cremaster	absent	present/ absent	vestigial	absent/present	present	present/ absent	absent
cocoon	present	present/ absent	present	present	present	present	present
protrudes at em.	no	yes	yes	yes	?	no	no
ADULT							
vertex of head	smooth-scaled	rough-scaled	unmodified	rough-scaled	smooth- scaled	unmodified	smooth-scaled
labial palpus	3-segmented	3-segmented	3-segmented	2-3-segmented	3-segmented	3-segmented	3-segmented

TABLE 1 (continued)

	Yponomeutidae	Tortricidae	Zygaenidae	Limacodidae	Immidae	Crambidae	Prodidactidae
maxillary palpus	1-2-segmented	2-4-segmented	1-2-segmented	1-3-segmented	1-2-segmented	2-4-segmented	3-segmented
haustellum	naked	naked	naked	naked	naked	scaled	naked
male antenna	filiform	filiform/variable	bipectinate/filiform	bipectinate/filiform	filiform	variable	filiform
antennal pecten	absent/present	absent	absent	absent	absent	absent	absent
ocellus	absent	usually present	usually present	absent	absent/present	present/absent	absent
chaetosemata	absent	present	usually present	absent	usually present	present/absent	absent
venation	heteroneurous	heteroneurous	heteroneurous	heteroneurous	heteroneurous	heteroneurous	heteroneurous
wing coupling	frenulate	frenulate	frenulate	frenulate	frenulate	frenulate	frenulate
FW pterostigma	present/absent	absent	absent	absent	absent/present	absent	absent
FW chorda	present/absent	present/absent	absent	absent	absent	absent	present
FW anal veins	A1+2 stalked	A1+2 stalked	A1+2 stalked	A1+2 stalked	A1+2 stalked	A1+2 stalked	A1+2 stalked
FW cell vein	absent	present/absent	usually absent	present	absent	absent	absent
HW pterostigma	absent	absent	absent	absent	absent	absent	absent
HW anal veins	A1+2 A3 stalked	A1+2 A3 stalked	A1A2A3 stalked	A1+2 A3 stalked	A1+2 A3 stalked	A1+2 A3 stalked	A1+2 A3 stalked
HW cell vein	present	usually absent	present/absent	present	present	absent	absent
epiphysis	present	present	present/absent	absent	present	present	present
tibial spurs	0-2-4	0-2-4	variable	variable	0-2-4	0-2-4	0-2-4
pretarsal pulvillus	unmodified	unmodified	unmodified	unmodified	unmodified	setiform outgrowth	setiform outgrowth
abdominal tympana	absent	absent	absent	absent	absent	present	absent
abd. apodemes	tineoid-type	tortricoid-type	tortricoid-type	tortricoid-type	tortricoid-type	unmodified	tortricoid-type

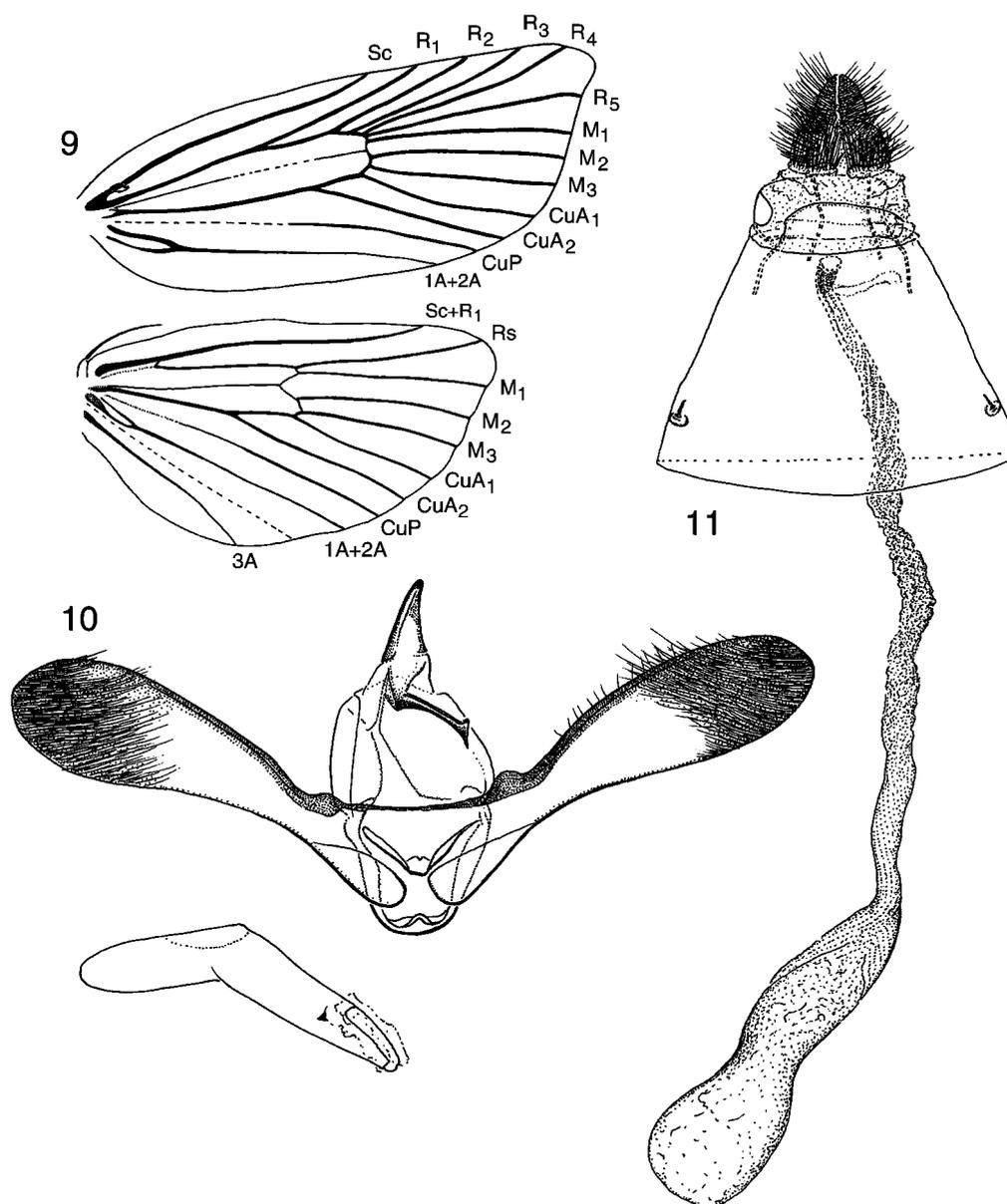
Thorax: Whitish gray (Fig. 6). Epiphysis well developed in both sexes. Distinct hair-pencils on posterior aspect of hind coxae of male associated with free, elongate, membranous, saclike lobes that are asymmetrical (Fig. 8); hindtibia with 4 spurs. Pulvillus of pretarsus with long setiform outgrowths on dorsal lobe (Fig. 21). Forewing (Figs. 1-2, 9) moderately broad; costa weakly arched throughout; apex slightly falcate. Length 17-28 mm (females larger). Upper surface buff to yellow buff, faintly rosy tinged in some specimens; anterior 0.66 of costal region suffused whitish, with a few scattered black specks, especially towards dorsal and terminal areas; costa crimson at base; an elongate orange spot near middle of costa; variably developed antemedial, medial, and postmedial zig-zag fasciae of pale orange. No costal fold, upraised scales, or other male secondary structures. Length of discal cell approximately 0.55 forewing length, closed; all veins present, free and separate basally; discal cell between M_1 and M_2 weak, angled inward; M-stem present, weak, ending between M_1 and M_2 ; accessory cell present at distal end of discal cell; CuP weak; 1A+2A forked at base; pterostigma absent. Hindwing uniform pale yellow or pale orange yellow. All veins present, separate; discal cell approximately 0.65 length of hindwing, closed; discal cell between M_1 and M_2 weak; CuP well developed; tuft of long scales arising near base of CuP; pterostigma absent. Wing coupling frenulate, 1 spine in male, 3 in female. Under surface pale yellow.



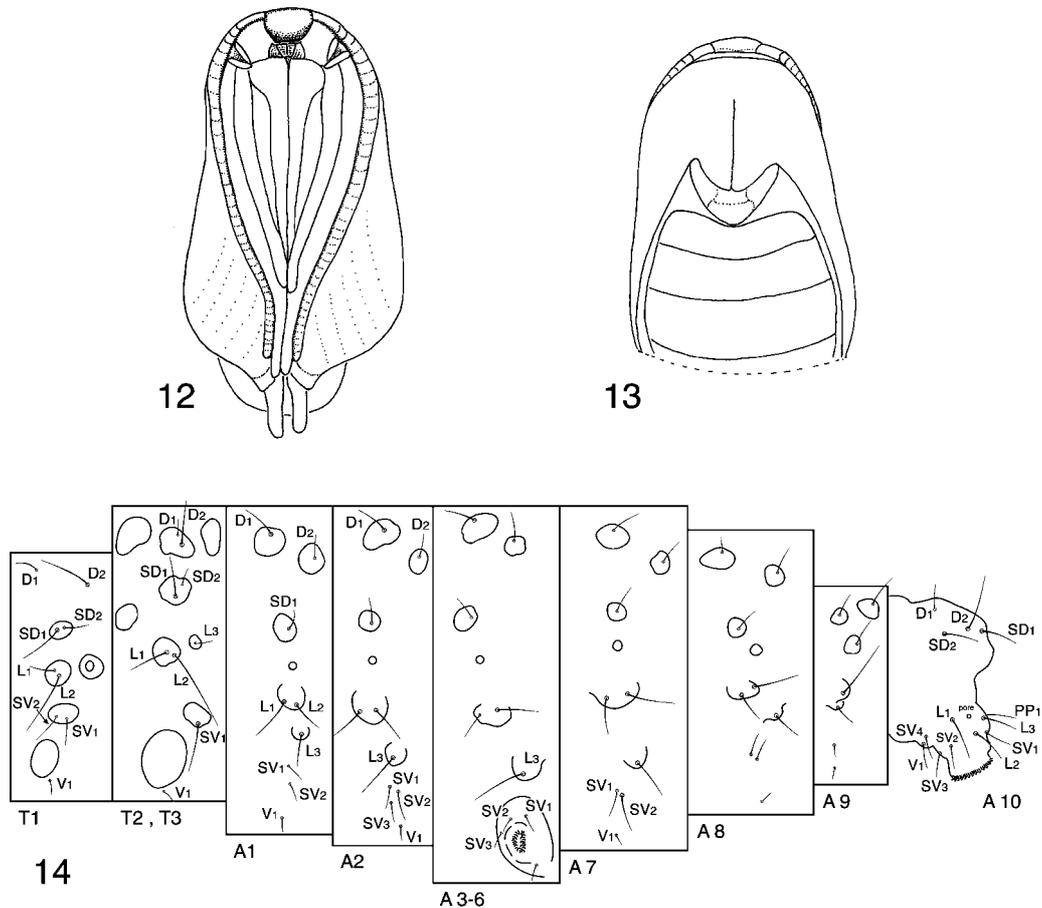
FIGURES 7-8. Adult head and hind coxa. 7) Laterofrontal view of cleared head (pr=proboscis (haustellum), mp=maxillary palpus, lp=labial palpus); 8) Hind coxa with saclike lobes (arrows point to lobes, st=sternum II of first abdominal segment, ap=apodeme).

Abdomen: Apodemes of tortricoid-type (Fig. 8); lacking tympanum. Pale orange buff. Male genitalia (Fig. 10) with uncus stout, as long as width of tergite, attenuate distally, tapering to a rounded point, densely covered with stout hairs directed anteriorly; attached to tegumen at a partially membranous point of articulation. Gnathos arms moderately broad, united into a single narrow, mesal process, strongly up-curved in distal 0.33, ending in a foot-shaped sclerite with pointed toe. Socius apparently absent. Valva long, with broad basal portion, slender central portion, and broad apical region; costa strongly sclerotized;

inner surface densely covered with long hairs. Aedeagus stout, bent near middle, slightly undulate; attenuate distally with short spine on left side near apex; cornuti absent. Female genitalia (Fig. 11) with papillae anales broad, rounded ventrally, moderately sclerotized, densely covered with long hairs; not fused dorsally. Apophyses moderately long, slender. Sterigma a simple plate, ostium bursae simple. Ductus bursae nearly as long as abdomen; corpus bursae small, rounded; signum absent.



FIGURES 9-11. Adult morphology of *Prodidactis mystica*. 9) Wing venation; 10) Male genitalia; 11) Female genitalia.



FIGURES 12-14. Pupa and larva of *Prodidactis mystica*. 12) Venter of pupa; 13) Dorsum of pupa (without caudal segments); 14) Chaetotaxy of larva of *Prodidactis mystica*.

Last Instar Larva ($n = 3$) (Figs. 3-4, 14, 17-19). General: Length 22-26 mm, rather stout. Head red brown with no conspicuous markings. Prothoracic shield dark greenish brown with dorsal separation of halves indicated by a yellow line. Body greenish yellow, with a narrow dark green longitudinal middorsal line and a broad, dark green longitudinal subdorsal line extending ventrad to dorsal edge of spiracles; pinacula conspicuous, yellow; non-setal bearing pinacula on meso- and metathorax red brown; secondary setae absent. Head: Frons extending about 0.7 to occipital foramen; stemmata arranged in an arc except for S5 (Fig. 19); spinneret moderate in length, rounded distally (Figs. 17-18); mandible with three large teeth, one smaller tooth, and a flattened region at inner portion (Fig. 18). Thorax (Fig. 14): Prothorax with bisetose L-group on common prespiracular pinaculum; SD2 seta approximately 0.4 times length of SD1; spiracle on prothorax surrounded by large, clear disk. SV-group bisetose on prothorax, unisetose on meso- and metathorax. Meso- and metathorax each with non-seta-bearing dorsal pinacula; mesothorax with three

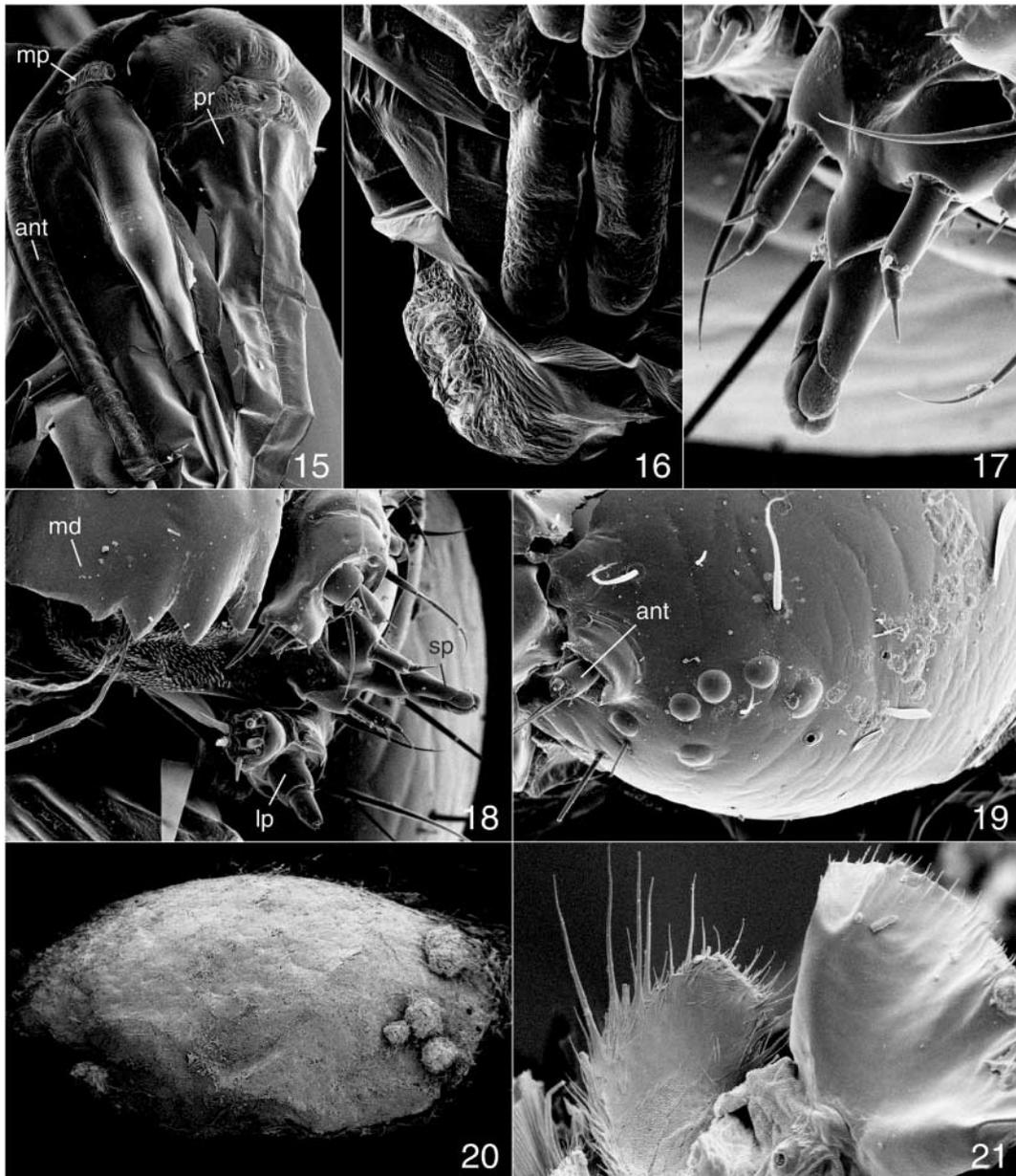
naked pinacula, two slightly dorsad of D pinaculum, one on each side, and a third anterad and slightly ventrad of SD pinaculum; metathorax similar, with hint of an additional naked pinaculum anterad and ventrad of first anterior pinaculum. Abdomen (Fig. 14): Spiracles surrounded by inconspicuous unsclerotized disk; spiracle on A8 slightly larger than those on A1-7; D2s on separate pinacula on A9; SD1 well dorsad and slightly anterad of spiracle on A1-7, conspicuously more anterad on A8; L1 and L2 together, in horizontal row, on large common lateral pinaculum below spiracle on A1-8; L1+L2 pinaculum on A9 nearly vertical; L3 absent on A9; SV group on 1,2,3-6,7,8,9 usually 2:3:3:2:2:1; anal fork absent. Crochets 70-75 in uniform biordinal circle on A3-6; crochets 50-55 in a semicircle on A10.

Pupa. General (Figs. 12-13, 15-16): Short and broad, compact, zygaeniform. Compound eye unsculptured; haustellum elongate, extending to distal end of front legs; maxillary palpi extending to near end of antennae; labial palpus a small triangle. Abdomen unmodified, without rows of spines on dorsum; spiracle not visible on A1; cremaster absent.

Cocoon. General (Fig. 20): Somewhat smooth on one surface and rough on opposite side; oval and flattened, 1.8 cm x 1.0 cm; opening along edge of narrow end, ca. 0.33 length of cocoon.

Life history. Eggs are flat and scalelike (N. Duke, pers. comm.), similar to those of many Tortricidae (Horak 1999) and Limacodidae (Epstein 1996), and are laid on the leaves of the host. Behavior of the early instars was not recorded. Fourth and fifth instars are solitary, apparently feeding from the upper surface on leaves of *Nuxia congesta*, as supported by photographic evidence (Figs. 3-4). The larvae form a shelter in a rolled leaf, but spend more time feeding exposed on the leaf than do tortricids (N. Duke, pers. comm.). Pupation occurs on the host in a dense, tough cocoon spun on or between leaves forming a shelter; overwintering is apparently accomplished in this stage. The pupa does not protrude from the cocoon prior to eclosion. Adults have been collected from October through March (Janse 1964: 22).

Geographic distribution. According to Janse (1964: 22), *P. mystica* is known from Durban Nggeleni (Pondoland), Nkandhla Forest (Zululand), Noordkaap, Barberton, Marieps Mountain, Graskop, Kowyn's Pass, Pretoria, Woodbush, Malta, and Zoutpansberg (all Transvaal). Specimens in the Transvaal Museum (M. Krüger, pers. comm.) provide the following distribution data: SOUTH AFRICA: TRANSVAAL: The Downs, Entabeni Forest, Kownyn's Pass, Pilgrim's Rest District, Uitsoek, Louis Trichardt, Piesangkop NE, Louis Trichardt Mariepskop Forestry, Malta Forest, Woodbush, Barbeton, De Hoek Forestry, Timbadiola Forestry, Pretoria North. NATAL: Ngoya Forest, Mtunzini District, Durban, Nkhandla Forest. EASTERN CAPE: Transkei, the Haven, Nggeleni. SWAZILAND: Mbabane. ZIMBABWE: Vumba Mountains, Lundi.



FIGURES 15-21. Scanning electron micrographs (SEMs) of various stages. 15) Pupal head and legs (mp=maxillary palpus, ant=antenna, pr=proboscis (haustellum)); 16) Ends of metathoracic tarsi and abdomen of pupa (note absence of cremaster); 17) Spinneret and maxillary palpi of larva; 18) Larval mouthparts (lp=labial palpus, md=mandible, sp=spinneret); 19) Configuration of stemmata and antenna of larva (=ant); 20) Cocoon (note opening along bottom right); 21) Dorsal aspect of adult pretarsus (pulvillus is on left, with long setiform outgrowths; arolium is on right).

Discussion

Although considered by Meyrick (1918: 163) to belong to Tortricidae, *Crothaema* Butler, 1880, the genus in which *mystica* was originally described (Meyrick 1918), now is considered a member of Limacodidae, where it was placed originally by Butler. Meyrick's assignment of *mystica* to *Crothaema* probably was based on its somewhat superficial similarity to *Crothaema sericea* (Butler), the type species of the genus. Its assignment to Tortricidae was based in part on Meyrick's misconception that *Crothaema* was "probably a development of *Epichorista* [Tortricidae: Archipini], of which species of very large size occur in the Kilimanjaro region..." and the assumption that the labial palpi were broken on the type (see below). In 1921, Meyrick (1921: 52) described the genus *Prodidactis* to accommodate *mystica*, apparently realizing that it was not congeneric with *C. sericea*, but continued to assign it to Tortricidae. Meyrick (1930: 563) later redescribed *Prodidactis*, transferring it to Yponomeutidae on the basis of information regarding the genitalia received from August Busck (Meyrick 1930); Meyrick, himself, did not examine genitalia. Janse (1964: 20) transferred *Prodidactis* to the Limacodidae where it has remained for the past 39 years.

The primary features suggesting that *Prodidactis* belongs to Tortricidae (see Table 1) are the flat, scalelike eggs (not previously reported), and in the adults, an unscaled haustellum, the "tortricoid-type" apodemes of the second abdominal segment, and the simple wing venation. The latter is virtually identical to the ground plan condition for Tortricidae - all veins present and separate. Characters that contradict this placement include the following: long maxillary palpus, extremely short labial palpus, absence of chaetosemata, and smooth scaled head of the adult; the general aspect of the male and female genitalia, in particular, the articulation of the uncus and tegumen, and the non-tortricoid papillae anales (Horak 1999); the bisetose L-group on the prothorax (almost always trisetose in Tortricidae, but see below), the dorsal position of SD2 on A8, and the separate D2 pinacula on A9 in the larva; and the absence of rows of spines on the dorsum of the abdominal segments (but see below) and the tiny labial palpus of the pupa. The reduction of the labial palpus in the adult is so remarkable that Meyrick (1918) originally thought they were nothing more than the broken base of the palps (Meyrick 1930), undoubtedly biasing his assignment of *Prodidactis* to Tortricidae. The external feeding habit of the larva also is somewhat inconsistent with most tortricids, which typically feed from shelters (most Tortricinae) or bore into stems, roots, or fruit (most Olethreutinae).

Although the L-group of the prothorax is almost always trisetose in larvae of Tortricidae, a bisetose L-group is known in at least three tortricids: *Thaumato-grapha eremnotorna* Diakonoff and Arita (Chlidanotinae: Hilarographini) (Diakonoff and Arita 1981), *Pammene tsugae* Issiki (Olethreutinae: Grapholitini) (Nasu and Komai 1997), and *Hendecaneura rhododenrophaga* Nasu and Komai (Olethreutinae: Eucosmini) (Nasu and Komai 1997). However, in each of these species, all other characters of the larvae, pupae, and adults are characteristically tortricoid. Although nearly all tortricids have two rows of

spines on the dorsum of abdominal segments 3-7 of the pupa, these are absent in members of the tribe Ceracini (Tortricinae) (Diakonoff 1964, 1970). But larvae and adults of Ceracini are typically tortricoid, although adult Ceracini are remarkably large tortricids and are active diurnally.

The morphology of the genitalia (Janse 1964: 22), the superficial similarity to *Crothaema* (Limacodidae), and the compact pupa and cocoon all suggest placement of *Prodidactis* in Limacodidae (see Table 1). However, these same characteristics also are common to Zygaenidae and related families of Zygaenoidea (*sensu* Epstein et al. 1999). Also consistent with placement in these families or superfamily are the flattened egg, the “tortricoid-type” apodemes, and a well developed haustellum in the pupa. The absence of stalking in the wing venation is similar to some Zygaenidae and Epipyropidae, and the presence of a well developed haustellum in the adult is similar to Zygaenidae. Contradicting placement in Zygaenoidea are the presence of well developed maxillary palpus in adults; the presence of biordinal crochets on abdominal segments A3-6 and absence of retractile head in the larva; the presence of maxillary palpi and absence of a visible spiracle on the first abdominal segment of the pupa; and the fact that the pupa does not protrude from the cocoon prior to eclosion. In Zygaenoidea crochets are uniordinal and, with the exception of the highly specialized Epipyropidae, occur only in mesoseries (Epstein et al. 1999). The ground plan condition for the limacodid group (*sensu* Epstein 1996) has crochets on A2-7 and A10. A bisetose L-group on the prothorax is common to many Zygaenoidea, however, a trisetose L-group also occurs within the superfamily in Dalceridae (Epstein 1996). The well developed haustellum in *Prodidactis* differs from all members of the limacodid-group families, including *Crothaema* (Epstein 1996).

When compared to Yponomeutidae (see Table 1), *Prodidactis* has somewhat similar genital morphology and is superficially similar (including size) to adults of *Nosymna* Walker from southeastern Asia. However, two characters of the adults, i.e., the “tortricoid-type” apodemes of the second abdominal segment of *Prodidactis* and the absence of lateral integumental flanges from abdominal segment 8, and one character of the larvae, i.e., the close association of L1 and L2 on abdominal segments 1-8, convincingly exclude *Prodidactis* from Yponomeutidae (see Carter & Kristensen 1999: 30). In addition, Janse (1964) did not agree with Busck (Meyrick 1930) that the genitalia are similar to Yponomeutidae. Details of the morphology of the larva contradict assignment to this family. The larvae of Yponomeutidae typically are moderately long and slender, with a trisetose L-group on the prothorax, setae L1 and L2 widely separated on the abdominal segments, and crochets in triserial to multiserial rows (Stehr 1987). None of these characters is consistent with *Prodidactis*.

Larval and some pupal characters of *Prodidactis* are similar to those of some Pyraloidea (see Table 1). Indeed, all keys we used placed the larva in this superfamily (e.g., Weisman 1986, Stehr 1987, Solis 1999, Kristensen 1999). Larval features consistent with Pyraloidea include the bisetose L-group on the prothorax, the non-seta-bearing, naked dor-

sal pinacula (= non-setal bearing plates) on the meso- and metathorax, and the distinctly biordinal circle of crochets. Similar to some *Pyrausta* species (Crambidae) (Solis 1999), *Prodidactis* larvae have a pair of non-seta-bearing plates posterior to the D and SD pinacula and a second pair anterior to D and SD pinacula, although they differ from *Pyrausta* in the absence of microscopic setae. Similar non-seta-bearing dorsal pinacula anterior to the D and SD pinacula on the mesothorax are present in specimens of the Australian pyraustine, *Pleuroptya balteata* (Fabricius); the feature is not mentioned by Solis (1999) because this species is not encountered in quarantine situations. The complete circle of crochets in *Prodidactis* fits more closely with Crambinae than Pyraustinae in Solis (1999); however, the presence of biordinal crochets throughout the complete circle does not match the examples for either subfamily. Pupal characters shared with Crambidae and many other Pyraloidea are the obtect pupa (first four abdominal segments fused to hind wings), presence of maxillary palpi, a long haustellum, the absence of dorsal abdominal spines, the presence of a silk cocoon within the larval shelter, and the fact that the pupa does not protrude from the cocoon at adult eclosion (Common 1990). Furthermore, the absence of a cremaster is not unusual in the superfamily (Common 1990).

However, placement of *Prodidactis* in Pyraloidea is problematic because adult features do not conform. Characters that contradict assignment of *Prodidactis* to Pyraloidea include the absence of scales at the base of the haustellum, the presence of a complete CuP vein, the unbranched R veins of the forewing, and the fact that Sc+R1 are not approximate or anastomosed to Rs beyond the base of the hindwing. The absence of an abdominal tympanum is rare in Pyraloidea; this condition is found only in *Michaelshaffera* (Solis 1998). The reduction of the labial palpus in both adults and pupae is unusual, though this would be true for many of the taxa discussed above.

It has been suggested (J. Heppner, pers. comm.) that *Prodidactis* may represent a new subfamily of Immidae. Unfortunately, according to Dugdale et al. (1999), autapomorphies have not yet been defined for this family. However, they identify the following as potentially significant features: ovipositor lobes fused dorsally into a single bent disc; male segment 9 with tergum and sternum fused, forming a slender, looped structure; and larva with uniordinal crochets in a meso-series. None of these characters is consistent with *Prodidactis*. Adults of Immidae are not similar superficially to those of *Prodidactis*; they are stout, noctuid-looking moths with well developed labial palpi and 1-2-segmented maxillary palpi. In contrast, *Prodidactis* has minute labial palpi and 3-segmented maxillary palpi. The trisetose L-group of the prothorax and widely separated L1 and L2 on abdominal segments 1-8 of the larva of Immidae also are not consistent with *Prodidactis*.

In the absence of characters that convincingly associate *Prodidactis* with any potential "candidate" family or superfamily, we evaluated its placement in the context of the higher phylogeny of the Ditrysia, relying on characters from Minet (1991). The short apodemes of the second sternite of the abdominal base of adults ("tortricoid apodemes") and the close approximation of setae L1 and L2 on abdominal segments 1-8 of the larva (Fig. 14)

both convincingly support the inclusion of *Prodidactis* in Apoditrysia (sensu Minet 1991). The pit (Pb) of the larval head does not appear to be dorsal of P2, but this feature is nearly impossible to assess with certainty. Scott (1986) and Minet (1991) indicate that this character state is a potential synapomorphy for the Cossoidea+Sesioidea (including Castniidae)+Zygaenoidea assemblage. A putative synapomorphy of *Prodidactis* with obtectomeran groups (sensu Minet 1991) is the setiform outgrowths on the dorsal lobe of the pulvillus (Fig. 21).

As demonstrated by the above discussion, the unique combination of characters possessed by *Prodidactis* prohibits its confident assignment to any currently recognized family or superfamily, which in some regards, represents a symptom of the problematic nature of ditrysiian classification at present. Hence, as an interim solution we propose the family Prodidactidae. We are concerned that if we keep the genus incorrectly in Limacodidae, return it incorrectly to Tortricidae, or treat it as “*insertae sedis*,” it will remain in obscurity. Based on the character evidence presented, *Prodidactis* could be considered either a “Pyraloid grade” superfamily (e.g., larval data) or as a non-obtectomeran Apoditrysia (e.g., wing venation). However, the relationships of neither of these grades is resolved, nor are these grades particularly well supported at present.

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Literature cited

- Brown, J.W. & Powell, J.A. (1991) Systematics of the *Chrysoxena* group of genera (Lepidoptera: Tortricidae: Euliini). *University of California Publications in Entomology*, 111, 1-87 + figs.
- Carter, D.J. & Kristensen, N.P. (1999) Classification and keys to higher taxa. In: Kristensen, N. (ed.), *Handbook of Zoology, volume 4, Arthropoda: Insecta, part 35. Lepidoptera, Butterflies and Moths, volume 1: Evolution, Systematics, and Biogeography*. Walter de Gruyter, Berlin, New York, pp. 27-40.
- Common, I.F.B. (1990) *Moths of Australia*. Melbourne University Press, Melbourne, Australia, 535 pp.
- Diakonoff, A. (1964) Early stages of the "Ceracidae" (Lepidoptera), with remarks on the true position of the group. *Zoologische Mededelingen*, 39, 59-66.
- Diakonoff, A. (1970) Notes on the Ceracini (Lepidoptera, Tortricidae). *Tijdschrift voor Entomologie*, 113, 91-103.
- Diakonoff, A. & Arita, Y. (1981) The early stages of *Thaumato-grapha eremnotorna* Diakonoff & Arita, with remarks on the status of the Hilarographini (Lepidoptera: Tortricoidea). *Entomologische Berichten*, 41, 56-60.
- Dugdale, J.S., Kristensen, N.P., Robinson, G.S. & Scoble, M.J. (1999) The smaller Microlepidoptera-Grade Superfamilies. In: Kristensen, N.P. (ed.), *Handbook of Zoology, volume 4, Arthropoda: Insecta, part 35. Lepidoptera, moths and butterflies, volume 1: Evolution, Systematics, and Biogeography*. Walter de Gruyter, Berlin. New York, pp. 232
- Epstein, M.E. (1996) Revision and phylogeny of the limacodid-group families, with evolutionary studies on slug caterpillars (Lepidoptera: Zygaenoidea). *Smithsonian Contributions in Zoology*, 582, 1-102.
- Epstein, M., Geertsema, H., Naumann, C. & Tarmann, G. (1999) The Zygaenoidea. In: Kristensen, N. P. (ed.), *Handbook of Zoology, volume 4, Arthropoda: Insecta, part 35. Lepidoptera, moths and butterflies, volume 1: Evolution, Systematics, and Biogeography*. Walter de Gruyter, Berlin. New York, pp. 159-180.
- Heppner, J.B. (1998) Classification of Lepidoptera. Part 1. Introduction. *Holarctic Lepidoptera*, 5 (supplement 1), 1-148.
- Horak, M. (1999) The Tortricoidea. In: Kristensen, N. (ed.), *Handbook of Zoology, volume 4, Arthropoda: Insecta, part 35. Lepidoptera, moths and butterflies, volume 1: Evolution, Systematics, and Biogeography*. Walter de Gruyter, Berlin. New York, pp. 199-216.
- Janse, A. J. T. (1964) *The moths of South Africa, volume 7, Limacodidae*. Transvaal Museum, Pretoria, 136 pp.
- Kristensen, N. P. (ed.) (1999) *Handbook of Zoology, volume 4, Arthropoda: Insecta, part 35. Lepidoptera, moths and butterflies, volume 1: Evolution, Systematics, and Biogeography*. Walter de Gruyter, Berlin. New York, 491 pp.
- Meyrick, E. (1918) *Exotic Microlepidoptera*, 2(6), 161-192.
- Meyrick, E. (1921) Descriptions of South African Lepidoptera. *Annals of the Transvaal Museum*, 8, 49-148.
- Meyrick, E. (1930) *Exotic Microlepidoptera*, 3(18), 545-576.
- Minet, J. (1991) Tentative reconstruction of the ditrysian phylogeny (Lepidoptera: Glossata). *Entomologica Scandinavica*, 22, 69-95.
- Nasu, Y. & Komai, F. (1997) A new species of the genus *Hendecaneura* Walsingham (Lepidoptera, Tortricidae) injurious to the twigs of Hirado azelea hybrids from Japan. *Japan Journal of Entomology*, 65, 413-420.
- Scott, J. (1986) On the monophyly of the Macrolepidoptera, including a reassessment of their relationship to Cossioidea and Castnioidea, and a reassignment of Mimallonidae to Pyraloidea. *Journal of Research on the Lepidoptera*, 25, 30-38.

- Solis, M.A. (1998) *Michaelshaffera* gen. n. - a pyraloid taxon lacking an abdominal tympanal organ (Lepidoptera: Pyralidae). *Entomologica Scandinavica*, 28(4), 391-402.
- Solis, M.A. (1999) Key to selected Pyraloidea (Lepidoptera) larvae intercepted at U.S. ports of entry: revision of Pyraloidea in "Keys to some frequently intercepted lepidopterous larvae" by D.M. Weisman 1986. *Proceedings of the Entomological Society of Washington*, 101, 645-686.
- Stehr, F. (ed.). (1987) *Immature Insects*. Kendall/Hunt Publishing Company, Dubuque, Iowa, 754 pp.
- Weisman, D. M. (1986) Keys for the identification of some frequently intercepted lepidopterous larvae. USDA, APHIS-PPQ, APHIS 81-47 (unpublished).