PROC. ENTOMOL. SOC. WASH.
109(2), 2007, pp. 265–276

A NEW GALL-INDUCING TORTRICID (LEPIDOPTERA: TORTRICIDAE: OLETHREUTINAE) ON LIMA BEAN (*PHASEOLUS LUNATUS*; FABACEAE) FROM COSTA RICA

John W. Brown and Kenji Nishida

(JWB) Systematic Entomology Laboratory, PSI, Agricultural Research Service, U.S. Department of Agriculture, c/o National Museum of Natural History, Smithsonian Institution, P.O. Box 37012, MRC 168, Washington, DC 20013-7012, U.S.A. (e-mail: john.brown@ars.usda.gov); (KN) Sistema Estudios de Posgrado en Biología, Escuela de Biología, Universidad de Costa Rica, 2060 San José, Costa Rica (e-mail: kenji.nishida@gmail.com)

Abstract.—***Lusterala phaseolana*, new genus** and **new species**, is described and illustrated from Costa Rica. The new genus can be distinguished from all other Olethreutinae by its unusual male genitalia, with a digitate uncus covered with long hairs and the absence of socii, and its distinctive forewing maculation (i.e., dark brown with scattered iridescent scales). Assignment of the new genus to Grapholitini is provisional based on the general appearance and chaetotaxy of the larva and a feature of the wing venation (i.e., M_2 and M_3 parallel and widely separated at the base). The entire type series was reared from stem galls on lima bean, *Phaseolus lunatus* L. (Fabaceae).

Resumen.—Se describen e ilustran un **género y especie nuevos, *Lusterala phaseolana***, de Costa Rica. El nuevo género puede distinguirse de resto de Olethreutinae por el patrón de las alas anteriores, con escamas iridiscentes dispersas, y por la inusual genitalia del macho, sin socii y con un uncus grande, en forma de lóbulo y cubierto de pelos largos. La posición de este nuevo género en Grapholitini es provisional. Todos los especímenes de serie tipo fueron obtenidos a partir de agallas del tallo del frijol lima, *Phaseolus lunatus* L. (Fabaceae).

Key Words: gall, life history, neotropics, new genus, new species, taxonomy, *Cydia torostoma*, *Dolichogenidea*

Gall-inducing in Lepidoptera was reviewed by Miller (2005) who recognized 39 species of Tortricidae in 14 genera worldwide as gall-inducers, which is second only to Gelechiidae in the number of gall-inducing species in any family of microlepidoptera. Given that more than 9,100 species of tortricids have been described (Brown et al. 2005), and hosts have been documented for many (Robinson et al. 2006), gall-inducing by larvae of this family appears to be a relatively rare habit that has evolved independently numerous times in various lineages. Known gall-inducers are found primarily in three tribes, Cochylini (4 genera) (Nishida and Adamski 2004, Miller 2005 and references therein), Grapholitini (3 genera) (Miller 2005), and Eucosmini (6 genera) (Miller 2005);

single species are reported in Olethreutini (Miller 2005), Enarmoniini (Miller 2005), Euliini (Brown and Nishida 2003), and Hilarographini (Brown et al. 2004). The purposes of this paper are to describe and illustrate a new genus and species of Olethreutinae that induces galls on *Phaseolus lunatus* L. (Fabaceae: Papilionoideae) in Costa Rica and to provide comments on its biology. The new taxon is placed provisionally in Grapholitini.

Phaseolus lunatus, the larval host plant of the new tortricid, is known commonly as lima bean, sieva bean, or butter bean (Iziko Museums of Cape Town 2004). It is a vine that frequently grows in disturbed habitats and urban areas, climbing over adjacent vegetation (Fig. 8) and fences. The plant is common in tropical climates with distinct wet and dry seasons (Sauer 1993). Although Central and South American in origin (Sauer 1993), it has been domesticated for more than 8,500 years, and it now ranges in the New World from northwestern U.S. to Argentina; it also occurs in Europe, central Africa, Madagascar, and the Philippine Islands (Missouri Botanical Garden 2005). In Costa Rica, *P. lunatus* is known on the Pacific slope from sea level to about 1800 m elevation (INBio 1997, Missouri Botanical Garden 2005). The species has been targeted for conservation of plant genetic resources (Vargas et al. 2003).

Materials and Methods

Galls induced by Lepidoptera larvae were collected from *P. lunatus* between April 2000 and March 2002 in Quitirisí, Ciudad Colon (1050 m) and Aserrí Centro (1300 m), both in San José Province, Costa Rica. The climate at these two sites is considered ''tropical humid'' with three to six months of dry season annually (Herrera and Gómez 1993). Galls were placed in transparent plastic bags and taken to the entomological laboratory at Escuela de Biología, Universidad de Costa Rica (1150 m), San José, where they were maintained at ambient indoor temperature (23 to 24°C). To examine their contents, galls were split open longitudinally. A subset of larvae and pupae and reared parasitoid wasps were preserved in 75% EtOH. As adult moths emerged they were killed and pin-mounted.

Dissection methodology follows that presented in Brown and Powell (1991, 2000). Digital images of the life history were captured with a Nikon Coolpix© camera. Images of adults and genitalia were captured using a Microptics© digital camera system and enhanced using Adobe Photoshop© and Illustrator© software. Terminology for genitalia structures and wing venation follows Horak (1984). Terminology for larval chaetotaxy follows R. Brown (1987). Paratypes are deposited in The Natural History Museum, London, United Kingdom (BMNH); Instituto Nactional de Biodiversidad, Santo Domingo de Heredia, Costa Rica (INBio); National Museum of Natural History, Washington, D.C., U.S.A. (USNM); and Escuela de Biología, Universidad de Costa Rica, San José, Costa Rica (UCR). Vouchers of larvae are deposited in USNM.

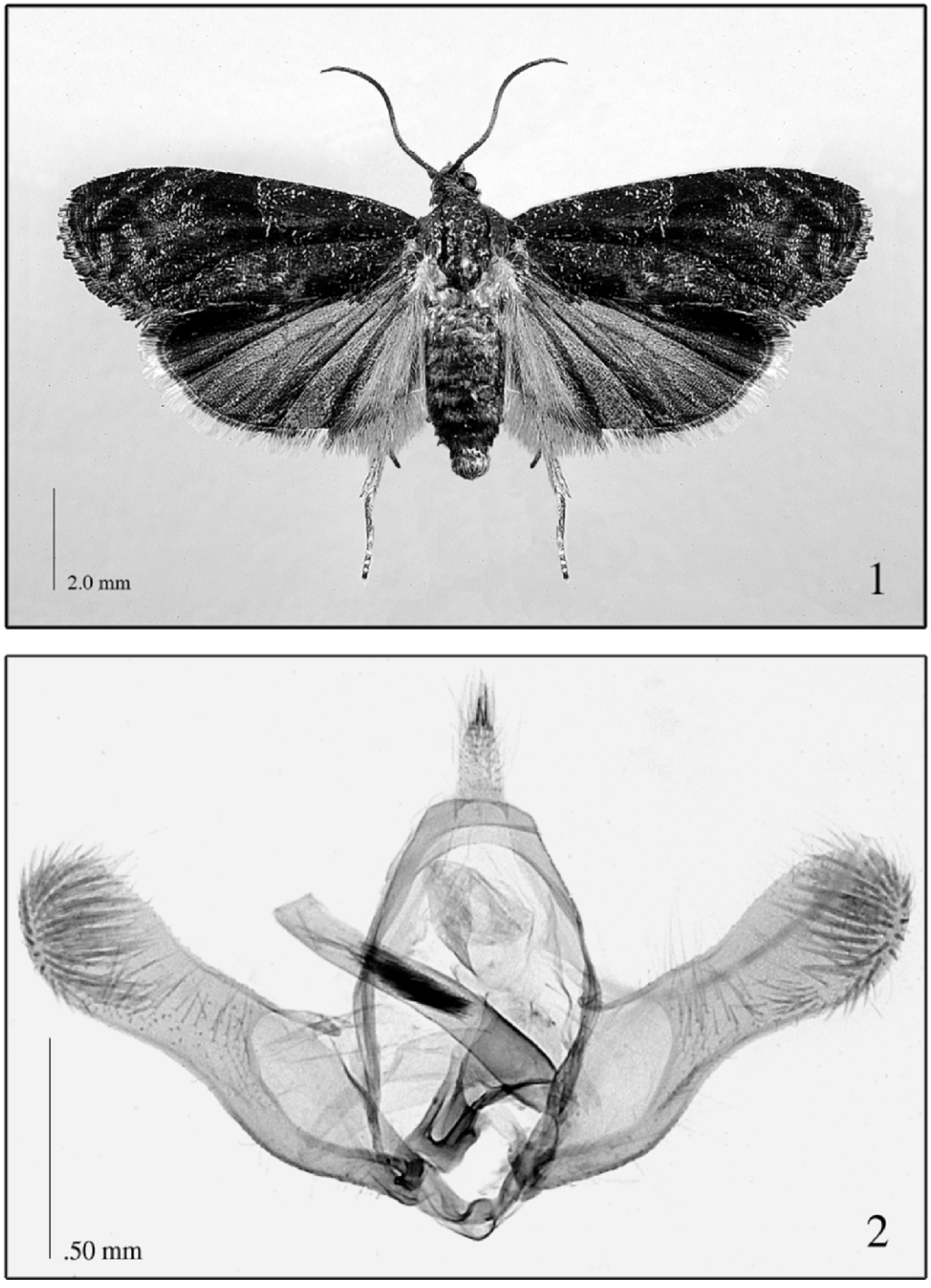
Systematics

Lusterala Brown and Nishida, new genus

Type species: *Lusterala phaseolana* Brown and Nishida, new species.

Diagnosis.—*Lusterala* can be distinguished morphologically from other genera of Olethreutinae by the somewhat digitate, weakly sclerotized uncus of the male genitalia combined with the absence of socii (Fig. 2), and superficially by the slightly upraised iridescent scales on an otherwise nearly uniform dark brown forewing (Figs. 1, 11).

Lusterala is assigned to Olethreutinae on the basis of the antenna with one ring of scales per flagellomere; the hindwing



Figs. 1–2. *Lusterala phaseolana*. 1, Holotype male (left side and mirror image). 2, Male genitalia of paratype, aedeagus in situ (USNM slide 84,931).

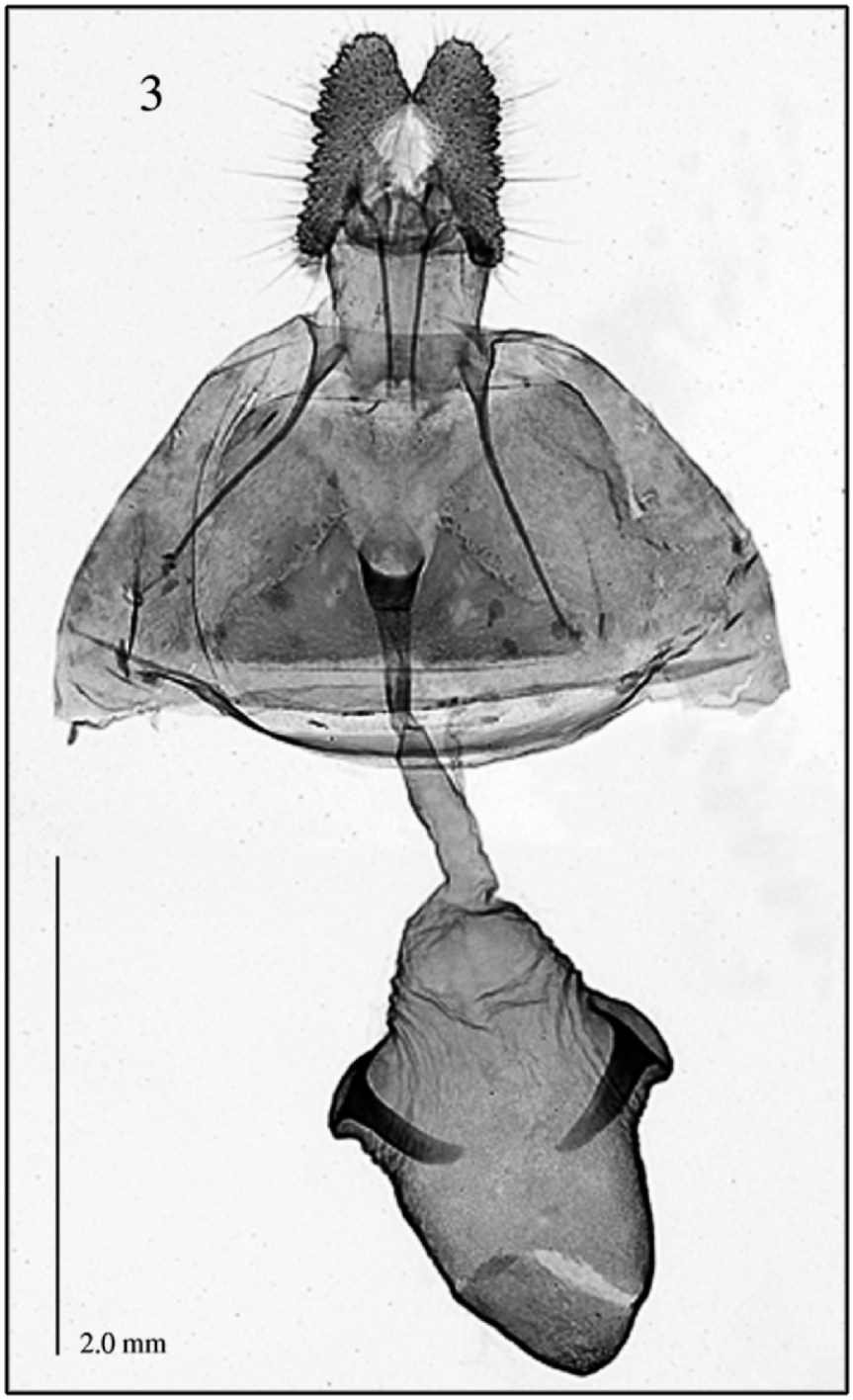


Fig. 3. Female genitalia of *Lusterala phaseolana* paratype (USNM slide 84,928).

with cubital pecten; the male genitalia with the transtilla and gnathos absent, the valva with a conspicuous basal excavation, and the aedeagus fused with the anellus and juxta (Fig. 2); and the female genitalia with two large hornlike signa (Fig. 3) (Horak 1998). Its tribal assignment is considerably more difficult. The large, paired, hornlike signa (Fig. 3) exclude it from Bactrini, Endotheniini, and Gatesclarkeanini, and combined with the general aspect of the male genitalia, from Olethreutini. *Lusterala* also lacks a modified anal region in the hindwing and modified scales of the basal portion of the patagia, which are characteristic of many male Olethreutini. The dark brown color of the forewing and the somewhat digitate uncus densely covered with hairs are highly reminiscent of those of *Cryptaspasma lugubris* (Felder) and some other Microcorsini (see Diakonoff 1959, Brown and Brown 2004), but *Lusterala* lacks virtually all of the characters that define that tribe. While the number and arrangement of the cornuti in the aedeagus are similar to those of *Ancylis* (Enarmoniini), other features typical of that tribe, e.g., falcate apex of forewing, valva usually with large basal excavation, a single or bifid thorn from the cucullus, and a pair of large angulate signa (Horak 2006), are lacking in *Lusterala*. The form of the aedeagus and cornuti, the presence of an uncus, the long ductus bursae, and the saberlike signa suggest an affinity with Eucosmini; however, the venation of the hindwing clearly contradicts this placement. *Lusterala* is superficially similar to some species of Grapholitini; the larvae are similar to many internal-feeding Grapholitini (e.g., *Cydia*); the overall aspect of the male and female genitalia are consistent with members of that tribe; and hindwing veins M_2 and M_3 are parallel and widely separated at the base—a character that has been used to define Grapholitini. On the basis of these characters, *Lusterala* is assigned provisionally to Grapholitini.

Within Grapholitini, *Lusterala* is superficially most similar to *Gymnandrosoma*, *Ecdytolopha*, *Thaumatotibia*, and relatives, characterized by a dark brown forewing with few distinct pattern elements. In addition, virtually all members of the *Gymnandrosoma* genus group are internal feeders. *Lusterala* can be distinguished from that group of genera by a more rounded forewing apex and the absence of a white or pale dot near the end of the discal cell characteristic of that group; also, males lack secondary sexual scales typical of the group (Adamski and Brown 2001). The larvae of *Lusterala* lack the large, sclerotized pinacula, including the distinctive enlarged L-pinaculum of the prothorax and the posteriorly displaced spiracle on A9 that are diagnostic for the *Gymnandrosoma* group (Adamski and Brown 2001).

According to Horak and Brown (1991), Grapholitini may represent a polyphyletic assemblage of genera in which features of the genitalia and wing venation reflect parallel reductions rather than synapomorphies. In contrast, Komai (1999) recognizes the shortened sternum 8 in the male with a straight posterior margin as a putative synapomorphy for the tribe. In *Lusterala* the sternum is not particularly short, and the margin is slightly convex.

Description.—*Adult: Head*: Frons weakly convex, with small appressed scales; vertex with forward projecting scales, approaching but not reaching base of labial palpus, each scale with a scalloped tip. Antenna ca. 0.5 as long as forewing length; setae less than 0.25 times width of flagellomere, much more dense in males than in females; one row of scales per flagellomere. Labial palpus short, ca. 1.2 times horizontal diameter of compound eye; first segment short, upcurved; second segment longest, densely scaled, ca. 6 times as long as

third segment, slightly upcurved; third segment short, barely extending beyond scaling of second. Maxillary palpus inconspicuous. Proboscis developed, naked. Ocelli large, chaetosemata well developed. A narrow band of long semierect scales from lateral posterior part of vertex to occiput and surrounding compound eyes. *Thorax*: Dorsum and tegula smooth scaled; posterior tuft weak, comprised of a patch of conspicuously broad, somewhat elongate-rectangular scales (worn and/or lacking in most specimens). Legs unmodified. Forewing with all veins present and separate beyond discal cell; discal cell ca. 0.65 times length of wing; M-stem weak, chorda present forming short accessory cell arising ca. midway between R_2 an R_3 and extending to base of R_5; base of R_5 closer to base of R_4 than to base of M_1; M_2, M_3, and CuA_1 nearly parallel, with bases nearly equidistant among them; CuP weak, present only at wing margin; anal loop ca. 0.35 times length of 1A+2A; male without costal fold. Hindwing with veins Sc+R straight, closely parallel to Rs in basal 0.5; M_1 parallel to Rs in basal 0.25; M_2 only slightly closer to M_3 than to M_1 at base; M_2 and M_3 parallel, widely separated at bases; M_3 and CuA_1 coincident at base; CuP present, but weak throughout; basal stem of CuP and 1A+2A setose. Frenulum in female with three bristles, male with one. *Abdomen*: Sternum 8 in male with slightly convex posterior margin; coremata absent in male; no specialized corythrogyne scales in female. Male genitalia (Fig. 2) (3 preparations) with tegumen simple, ovoid; uncus moderately large, somewhat digitate, rounded distally, weakly sclerotized, densely covered with long hairs somewhat thicker distally; socius and gnathos absent; anal tube poorly defined, represented by round, weakly sclerotized region; valva broadest in basal 2/5, slightly narrowed in middle, slightly dilated distally, rounded apically, costa very slightly undulate, cucullus well-developed in distal 1/4. Aedeagus simple, long, ca. 4/5 length of valva, vesica with 35–40 slender cornuti, sometimes in a dense, elongate patch and sometimes scattered throughout. Female genitalia (Fig. 3) (2 preparations) with ovipositor short; papillae anales simple with relatively short setae from papillate bases; apophyses long and slender, apophyses anteriores ca. 1.3 times the length of aphophyses posteriores; ostium ringlike; a small cup-shaped antrum between ostium and ductus bursae; sternite of seventh segment with a pair of irregularly triangular, lightly sclerotized areas antero-laterad to ostium; ductus bursae relatively straight, ca. 2/3 length of corpus bursae, slightly broadened in anterior 1/2, membranous; ductus seminalis from lateral right portion of ductus bursae ca. 2/3 distance from ostium to junction with corpus bursae; corpus bursae elongate-ovoid, without spicules; two large signa each consisting of a long, broad, straight, attenuate thorn, weakly curved apically, from a broad, round, invaginated, sclerotized pocket of the outer wall of corpus bursae.

Etymology.—The genus name is from the Latin "*luster*" (= illuminate), in reference to the iridescent scales of the forewing, and the Latin "*ala*" (= wing). The gender is masculine.

Lusterala phaseolana Brown and Nishida, new species

(Figs. 1–4, 11)

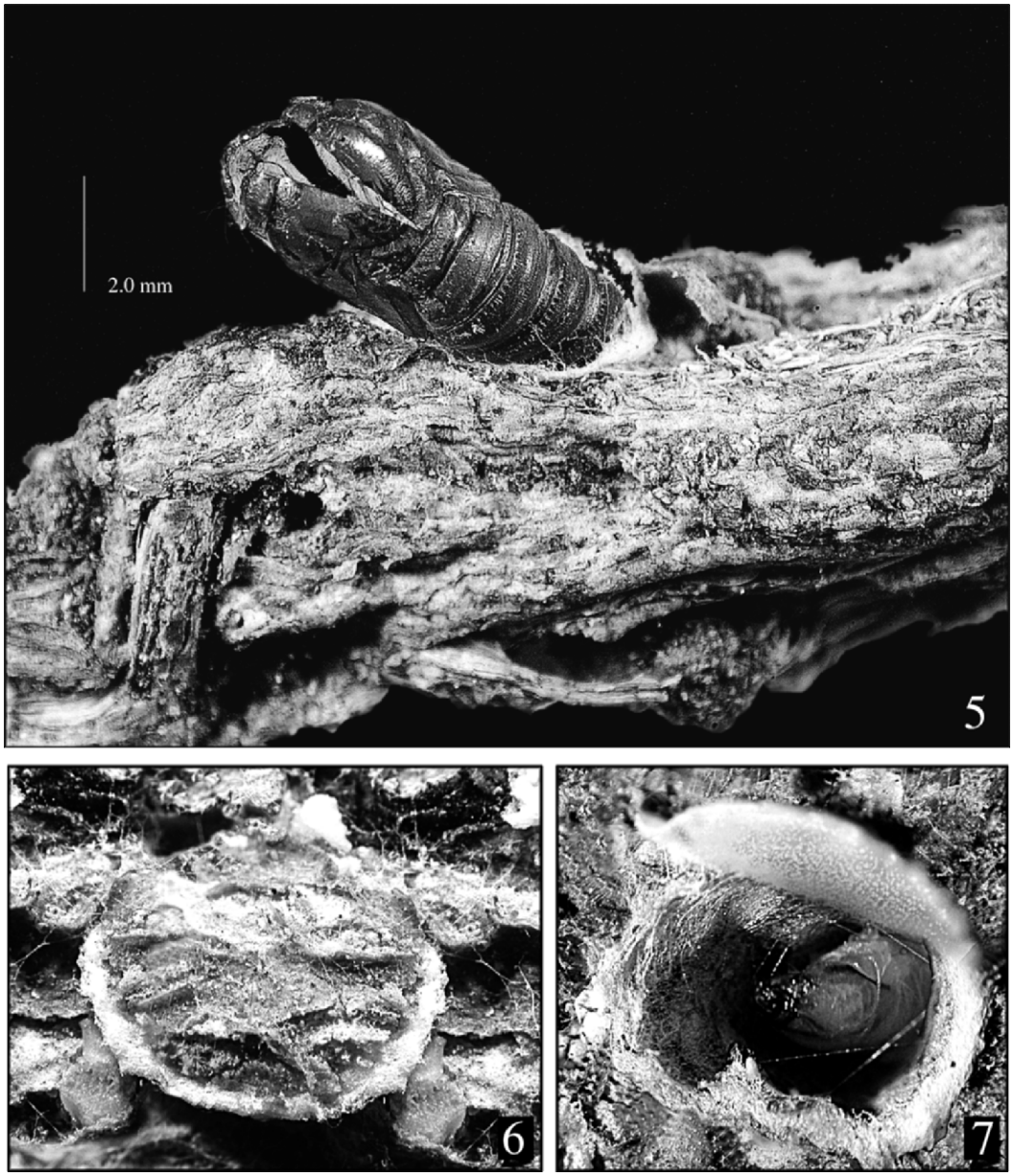
Diagnosis.—As presently defined, *Lusterala* is monotypic. The single included species can be distinguished superficially from all other Grapholitini by the sparse irregular lines and small patches of iridescent scales (slightly bluish) on the forewing and dorsum of the thorax. Distinctive morphological features include the digitate uncus in the male

Fig. 4. Pupal exuviae of *Lusterala phaseolana*; venter (on right) and dorsum (on left).

genitalia and the deeply invaginated, strongly sclerotized bases of the hornlike signa in the female genitalia. Females are conspicuously larger than males.

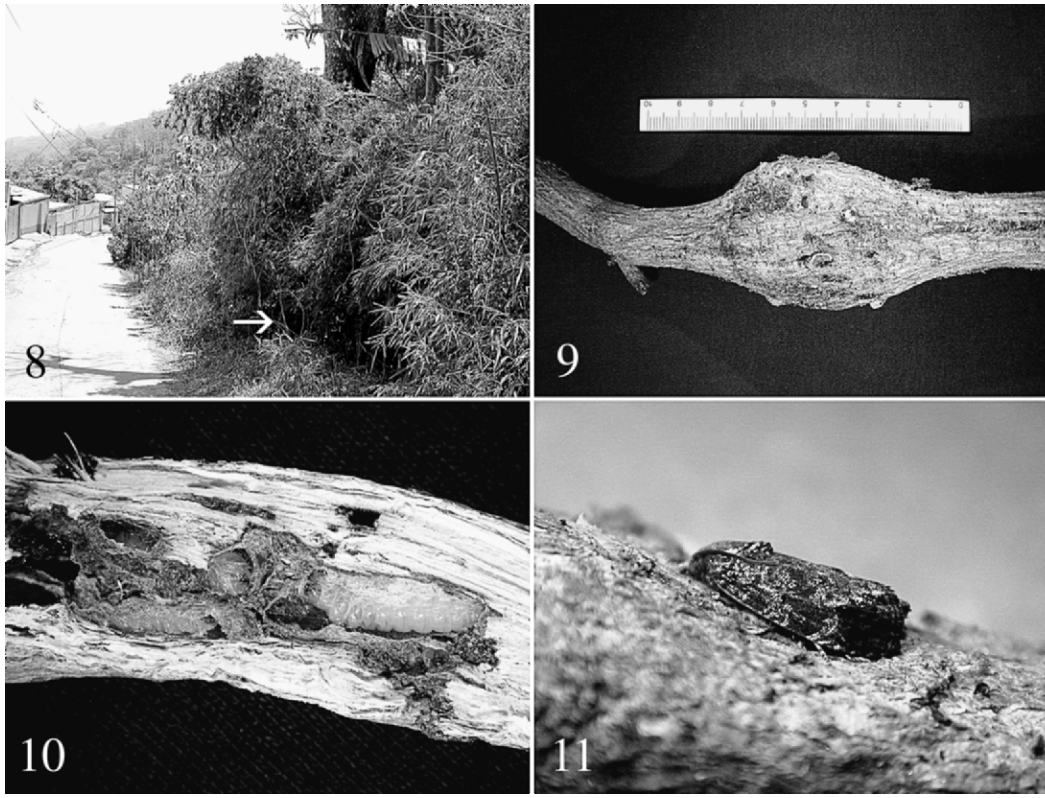
Description.—*Adult: Head:* Frons and vertex dark brown; labial palpus lighter brown with faint bluish iridescence. *Thorax*: Dark brown with scattered iridescent scales; posterior tuft a low, rounded patch of blackish brown scales. Forewing length 6.9–8.0 mm ($\bar{x}$ = 7.1; n = 10) in males, 8.5–9.5 mm ($\bar{x}$ = 9.2; n = 10) in females; dorsal surface entirely dark brown, with sparse irregular lines and small patches of slightly upraised, iridescent scales (reflecting slightly bluish), rarely with extremely sparse whitish striae; costal strigulae extremely weak, overscaled with brown; fringe dark brown. Undersurface uniform dark brown. Hindwing dorsal surface dark brown, concolorous with forewing; fringe pale cream; male without specialized scales. Undersurface uniform dark brown. *Abdomen*: Dark brown, outer surface of valva of male with sparse, fine, pale brown scales; no conspicuous specialized scales in male or female. Male genitalia (Fig. 2) as described above for genus. Female genitalia (Fig. 3) as described above for genus.

Larva: Based on four probable last instars. In general, the larva is short (8.0–8.5 mm in length), plump, and pale cream or pinkish; the pinacula lack distinct sclerotization; and the anal fork is absent, features typical of many internal-feeding Olethreutinae, especially Grapholitini (e.g., *Cydia* spp.). The spiracles are distinctly ovoid, the prothoracic spiracle is ca. 2.5 times the size of the others, and the spiracle on abdominal segment 9 is only slightly larger than those of other abdominal segments. The head is pale amber with an extremely faint genal bar. The prothoracic shield is ill-defined, represented by a pair of weakly sclerotized, triangular patches, one on each side of the dorsum. The L-group on the prothorax is bisetose, which is rare in Tortricidae. Although endophagous Tortricinae have a propensity for the loss of one of the L setae, this is seldom, if ever, the case in endophagous Olethreutinae (Dugdale pers. comm., Brown et al. 2004). The SV-group on thoracic segments 1, 2 and 3 is 2:1:1, typical of Tortricidae. The SV-group on abdominal segments 1, 2, 7, 8, 9 is 2:2:2:1:1 (variable within most tribes of Olethreutinae). On abdominal segment 8, seta SD1 is directly anterior to the spiracle. On abdominal segment 9, the D2 setae are on a shared, unsclerotized, dorsal pinaculum; setae D1 and SD1 are on a shared pinaculum; and the L-group is bisetose. The distance between the V setae on abdominal segment 9 is about two-thirds that between the V setae of abdominal segment 8. The setae of the anal shield are short. The prolegs of abdominal segments 3–6 bear 25–35 uniordinal crochets, the proleg of segment 10 bears 8–10.



Figs. 5–7. *Lusterala phaseolana* gall. 5, Pupal exuviae protruding from gall. 6, Exit cover of gall. 7, Larva within gall chamber with exit cover opened.

Pupa (Figs. 4, 5): Based on 15 exuviae. Typically tortricoid, without conspicuous sculpturing or cephalic prominence; length 8.0–10.0 mm in males, 11.5–12.0 mm in females. Dorsum of abdominal segment 1 without spines and with spiracle inconspicuous. Dorsum of abdominal segments 2–7 with two distinct rows of spines, anterior row on segment 2 with only 2–4 small spines, posterior row well developed; anterior row on segments 4–7 extending from spiracle to spiracle. Dorsum of abdominal segments 8–10 with a single row of large thorns



Figs. 8–11. Habitat, gall, and resting posture of *Lusterala phaseolana*. 8, Roadside habitat and host (arrow indicates position of gall). 9, Globose gall induced by *L. phaseolana* (scale bar in mm/cm). 10, Inside of elongate gall induced by *L. phaseolana* showing larvae in chambers. 11, Adult *L. phaseolana* resting on branch of host.

representing anterior row; no conspicuous hooked seta on abdominal segment 10. Cremaster absent.

Type material.—Holotype ♂, Costa Rica, Provincia San José, Aserrí Centro (site E43), 1400 m, 7 Jun 2000, r.f. *Phaseolus lunatus*, collected by M.-H. Kestemont, reared by K. Nishida. Deposited in USNM.

Paratypes: COSTA RICA: Provincia San José: Aserrí Centro (site E43), 1400 m, 8 May 2000 (1♂), 10 May 2000 (1♂, 3♀), 15 May 2000 (1♀), 16 May 2000 (3♂, 3♀), 23 May 2000 (2♂, 1♀), 3 Jun 2000 (2♂, 1♀), 7 Jun 2000 (1♂, 1♀), gregarious gall former on *Phaseolus lunatus*, collected by M.-H. Kestemont, reared by K. Nishida. Ciudad Colon, Quitirisí, De Quebrada Honda, 2 km hacia Quitirisí, 16 Apr 2000 (1♂, 1♀), K. Nishida. Site MH1, 18 Mar 2000 (1♂), 20 Mar 2000 (3♂), 31 Mar 2000 (1♀), gregarious gall former on *Phaseolus lunatus*, collected by M.-H. Kestemont, reared by K. Nishida.

Etymology.—The specific epithet is derived from the host plant genus, *Phaseolus*.

Biology

The galls of *Lusterala phaseolana* are variable from elongate spindle-shaped to globose (Figs. 5, 9, 10). They were discovered on old (lignified) stems of *Phaseolus lunatus* growing along roadsides (Fig. 8, arrow). The galls usually were located near the basal part of the plant close to the ground (Fig. 8). Gall-

induction usually caused wilting and eventual death of the plant (E. Castro, personal communication). A single large gall (ca. 10 cm × 1.6 cm; stem diameter of 8 mm) contained as many as 12 last instar larvae (unilocular, i.e., one larva per chamber). Apparently, swelling of the stem (i.e., gall) is the result of enlarged parenchyma tissue. Several galls had a purplish tint in tissue that surrounded the larvae or pupae. One gall collected in Aserrí Centro contained coexisting larvae of *Lusterala phaseolana* and *Carmenta mimosa* Eichlin and Passoa (Sesiidae). This gall was larger than galls occupied by *Lusterala* alone. Larvae of *C. mimosa*, erroneously cited as *Synanthedon* sp. by Saunders et al. (1998), are recorded as gall-inducers on some bean plants (Saunders et al. 1998) including *P. lunatus* in Costa Rica (K. Nishida, personal observation).

Each larval chamber of last instar *Lusterala* larvae (Fig. 10) was lined with silk, the chambers clustered together within the gall. Frass was present in spaces surrounding and between chambers and was more or less compacted. Some of it protruded from the gall surface through the exit holes. Some frass was exuded and attached along shallow longitudinal grooves of the gall surface (Fig. 9).

Last instar larvae reacted to gentle probing with forceps by regurgitating a translucent fluid. Agitated larvae kept their mandibles open after regurgitating and aggressively moved toward and bit at the source of agitation.

The pupal chamber in the gall is ca. 12 × 3 mm, cylindrical, and white to cream white. The outer surface of the cocoon is brown and covered with frass. The exit hole from the chamber (Figs. 6, 7, 9) is round, ca. 2.8 mm in diameter; each larva has its own exit hole. The exit "valve" is penelliptical, constructed by silk with the peridermal layer of the plant tissue on the outside (Figs. 6, 7). The pupa protrudes prior to adult emergence (Fig 5). Emerged adults perched on the host (Fig. 10), where they were highly camouflaged by their barklike appearance.

The galls of *Lusterala* are superficially similar to those described for *Cydia torostoma* (Clarke) (Clarke 1972), which is also a pest of beans in Costa Rica (Saunders et al. 1998). The adult of *C. torostoma* is somewhat similar to that of *Lusterala*; however, the similarity is merely the result of the shared absence of distinct forewing pattern elements; i.e., both species are mostly nondescript little brown moths; however, *C. torostoma* has considerably more whitish scaling on the forewing. The genitalia of the two species demonstrate that they are not closely related.

It is interesting that no specimens of *L. phaseolana* were discovered in the rather extensive Lepidoptera collection at INBio, suggesting that the species may be diurnal or possibly not attracted to ultraviolet light; the latter is the standard collecting method. Hence, the discovery of species related to *Lusterala phaseolana* may require the rearing of larvae.

A series of *Dolichogenidea* sp. (Hymenoptera: Braconidae: Microgastrinae) (determined by Alejandro Valerio) parasitoid wasps was reared from larvae of *L. phaseolana*. Several specimens of *Perilampus* sp. (Hymenoptera: Perilampidae) (identified by Paul Hanson) also were reared as a hyperparasitoid of *Dolichogenidea* sp.

Acknowledgments

We thank Marie-Helene Kestemont and Arnauld Thiry (Faculté des Sciences Agronomiques de Gembloux, Gembloux, Belgium) for sharing specimens and for providing collecting data; Tom Eichlin (California Department of Food and Agriculture, Sacramento, California, USA) for identifying the sesiid moth; Oscar Rocha (University of Costa Rica,

San José, Cost Rica) for sharing useful information on the host plant; Alejandro Valerio (Instituto Centroamericano de Investigación en Biología y Conservación, San José, Costa Rica) and Paul Hanson (University of Costa Rica, San José, Costa Rica) for identifying parasitoids; and Revista Biologia Tropical for providing copies of literature. Marie Metz (SEL, c/o National Museum of Natural History, Washington, DC, USA) captured the images of the adult and genitalia and prepared the plates of illustrations, except for the plate of figures 8–11 which was prepared by Nishida. The following provided helpful reviews of the manuscript: Sonja Scheffer (SEL, USDA, Beltsville, Maryland, USA), Thomas Henry (SEL, USDA, c/o National Museum of Natural History, Washington, DC, USA), William E. Miller (University of Minnesota, St. Paul, Minnesota, USA), Joaquin Baixeras (Universitat de Valencia, Valencia, Spain), and Richard Brown (Mississippi State, USA).

Literature Cited

Adamski, D. and J. Brown. 2001. Revision of the *Ecdytolopha* group of genera (Lepidoptera: Tortricidae: Grapholitini) in the New World. Entomologica Scandinavica Supplements 58: 1–86.

Brown, J. W. and R. L. Brown. 2004. A new species of *Cryptaspasma* (Lepidoptera: Tortricidae: Olethreutinae) from Central America, the Caribbean, and southeastern United States, with a catalog of the world fauna of Microcorsini. Proceedings of the Entomological Society of Washington 106: 288–297.

Brown, J. W. and K. Nishida. 2003. First record of larval endophagy in Euliini (Tortricidae: Euliini): A new species of *Seticosta* from Costa Rica. Journal of the Lepidopterists' Society 56: 113–120.

Brown, J. W. and J. A. Powell. 1991. Systematics of the *Chrysoxena* group of genera (Lepidoptera: Tortricidae: Euliini). University of California Publications in Entomology 111. 87 pp. + figs.

———. 2000. Systematics of *Anopina* Obraztsov (Lepidoptera: Tortricidae: Euliini). University of California Publications in Entomology 120. 128 pp. + figs.

Brown, J. W., et al. (2005). World catalogue of insects. Volume 5. Tortricidae (Lepidoptera). Apollo Books. 741 pp.

Brown, J. W., J. Baixeras, J. A. Solorzano-Filho, and J. E. Kraus. 2004. Description and life history of an unusual fern-feeding tortricid moth (Lepidoptera: Tortricidae) from Brazil. Annals of the Entomological Society of America 97: 865–871.

Brown, R. L. 1987. Tortricidae (Tortricoidea), pp. 419–433. *In* Stehr, F. W., ed. Immature Insects, volume 1. Kendall/Hunt, Dubuque, Iowa.

Clarke, J. F. G. 1972. Two pests of beans from tropical America. Proceedings of the Entomological Society of Washington 74: 467–471.

Diakonoff, A. 1959. Revision of *Cryptaspasma* Walsingham, 1900 (Lepidoptera, Tortricidae). Zoologische Verhandelingen, Leiden 43: 1–60.

Herrera, S. W. and L. D. Gómez. 1993. Mapa de Unidades Bióticas de Costa Rica. Escala 1: 685. U.S. Fish and Wildlife Service – TNC – INCAFO – CBCCR – INBio – Fundación Gómez-Dueñas, San José, Costa Rica.

Horak, M. 1984. Assessment of taxonomically significant structures in Tortricinae (Lep., Tortricidae). Mitteilungen der Schweizerischen Entomologischen Gesellschaft 57: 3–64.

———. 1998. Tortricoidea, pp. 199–215. *In* Kristensen, N., ed. Lepidoptera, moths and butterflies. Volume 1: Evolution, systematics, and biogeography. Handbook of Zoology 4 (35), Arthropoda: Insecta. Walter de Gruyter, Berlin & New York.

———. 2006. Olethreutinae moths of Australia (Lepidoptera: Tortricidae). Monographs on Australian Lepidoptera 10. 522 pp.

Horak, M. and R. L. Brown. 1991. 1.2 Taxonomy and phylogeny, pp. 23–48. *In* van der Geest, L. P. S. and H. H. Evenhuis, eds. Tortricid pests, their biology, natural enemies and control. Elsevier Science Publishers B. V., Amsterdam.

INBio. 1997. INBio Atta database. URL: http://www.inbio.ac.cr/bims/BIMS.html. (accessed 31 July 2005).

Iziko Museums of Cape Town. 2004. URL: http://www.museums.org.za/bio/plants/fabaceae/phaseolus_lunatus.htm. (accessed 31 July 2005).

Komai, F. 1999. A taxonomic review of the genus *Grapholita* and allied genera (Lepidoptera: Tortricidae) in the Palaearctic region. Entomologica Scandinavica Supplement 55: 1–226.

Miller, W. E. 2005. Gall-inducing Lepidoptera, pp. 431–465. *In* Raman, A., C. A. Schaefer, and T. Withers, eds. Biology, ecology, and evolution of gall-inducing arthropods. Science

Publishers, Inc., Enfield, New Hampshire, U.S.A. and Plymouth, U.K.

Missouri Botanical Garden. 2005. w3TROPICOS Nomenclatural Data Base. URL: http://mobot.mobot.org/cgi-bin/search_vast. (accessed 23 August 2005).

Nishida, K. and D. Adamski. 2004. Two new gall-inducing *Saphenista* Walsingham (Lepidoptera: Tortricidae: Cochylini) from Costa Rica. Proceedings of the Entomological Society of Washington 106: 133–139.

Robinson, G. S., P. R. Ackery, I. J. Kitching, G. W. Beccaloni, and L. M. Hernández. 2006. HOSTS - a database of the hostplants of the world's Lepidoptera. The Natural History Museum, London. URL: http://www.nhm.ac.uk/research-curation/projects/hostplants/#10 (accessed 15 April 2006).

Sauer, J. D. 1993. Historical geography of crop plants: a select roster. CRC Press, Boca Raton, Florida. 309 pp.

Saunders, J. L., D. T. Coto, and A. B. S. King. 1998. Plagas invertebradas de cultivos anuales alimenticios en américa central. Centro Agronómico Tropical de Investigación y Enseñanza (CATIE), Turrialba, Costa Rica. xiv + 305 pp.

Vargas, E. M., E. Castro, G. Macaya, and O. J. Rocha. 2003. Variación del tamaño de frutos y semillas en 38 poblaciones silvestres de *Phaseolus lunatus* L. del Valle Central de Costa Rica. Revista de Biología Tropical 51: 707–724.