## A NEW SPECIES OF *PYLA* GROTE AND REDESCRIPTION OF *PYLA AEQUIVOCA* HEINRICH (LEPIDOPTERA: PYRALIDAE: PHYCITINAE)

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Abstract.—A new species of phycitine pyralid, **Pyla arenaeola**, is described from sandy habitats in central North America. The female of this new species was previously associated with males of *Pyla aequivoca* Heinrich. *Pyla aequivoca* is redescribed, and *Pyla gaspeensis* McDunnough is placed as a synonym of *Pyla aequivoca* [new synonymy]. *Pyla arenaeola* is restricted to loose sandy soils, especially dunes of the Great Lakes shoreline. Its distribution appears to be associated with dunes formed since the last Wisconsin glaciation including fossil dunes on the shores of glacial Lake Agassiz. The larvae feed on bearberry, *Arctostapluylos uva-ursi* (L.) Sprengel (Ericaceae) while concealed in silk-lined sand tubes.

Key Words: Life history, dunes, Arctostaphylos uva-ursi, Ericaceae, Great Lakes, Pleistocene, Glacial Lake Agassiz

Heinrich (1956) grouped nine species of *Pyla* Grote based on the color of the forewings in the "Gray" section of the genus. Included were four new taxa described on the basis of well-defined genital characters. Shortly thereafter, McDunnough (1958) described *Pyla gaspeensis* from the Gaspé region of Québec and placed it in the same species group.

Recent collecting on the dunes of the Great Lakes shore has uncovered an additional species described in this paper. Based on distinct male genital characters, it is apparent that this moth is unlike any described *Pyla*. However, a female of this new species was previously described by Heinrich (1956: p.143, Fig. 855) based on a single specimen from Aweme, Manitoba, but incorrectly associated by him with the male type series of *Pyla aequivoca* Heinrich. This left *P. aequivoca* without a recognized female until examination of relevant primary types demonstrated that Mc-Dunnough's *P. gaspeensis* (McDunnough) is conspecific with *P. aequivoca*. We believe that when McDunnough described *P. gaspeensis* he was misled by both an incorrectly rendered illustration of the aedeagus of *P. aequivoca* (Heinrich, 1956, Fig. 366a; compare our Figs. 7, 10) and Heinrich's misassociated female. To clarify application of specific names we redescribe *P. aequivoca*.

The larva of the new species belongs to a guild of sand tube constructing Lepidoptera found on dunes and in other very sandy habitats. It feeds on the leaves of bearberry, *Arctostaphylos uva-ursi* (L.) Sprengel (Ericaceae). Despite the widespread distribution of its holarctic host, the new species is apparently restricted to habitats with loose, sandy soils. Documented localities include the dunes of the Great Lakes shoreline and one fossil Pleistocene dune complex in southern Manitoba. Specimens examined originated from the following institutions and personal collections:

AMNH	American Museum of Natural
	History, New York, NY (E.H.
	Rindge)
BGS	B. G. Scholtens, Charleston, SC
CNC	Canadian National Collection,
	Ottawa, ON, Canada (JF. Lan-
	dry)
EGV	E. G. Voss, Mackinaw City, Ml
GJB	G. J. Balogh, Portage, MI
JAB	J. A. Bess, Wanatah, IN
IHW	J. H. Wilterding, East Lansing,
	MI
JKM	J. K. Morton, Waterloo, Canada
LACM	Los Angeles County Museum,
	Los Angeles, CA (J. P. Dona-
	hue)
LAF	L. A. Ferge, Middleton, WI
MSU	Michigan State University, East
	Lansing, MI (F. W. Stehr)
NMNH	National Museum of Natural
	History, Smithsonian Institution,
	Washington, DC (M. A. Solis)
UCB	University of California, Berke-
	ley, CA (J. A. Powell)
UM	University of Minnesota, St.
	Paul, MN (P. J. Clausen)
UMDLB	University of Michigan Douglas
	Lake Biological Station, Pells-
	ton, MI (B. G. Scholtens)
UMMZ	University of Michigan Muse-
	um of Zoology, Ann Arbor, MI
	(M. F. O'Brien)
UZMH	Zoologiska Muset, Universitets
	Helsinki, Helsinki, Finland (J.
	Jalava, K. Mikkola)

Relevant types in the CNC and NMNH collections were examined during the course of this study.

# Pyla arenaeola Balogh and Wilterding, new species

(Figs. 1-5, 11-13, 17, 19-22)

Diagnosis.—Most *Pyla areuaeola* can be distinguished from other *Pyla* species by the broad blue-gray forewings and relative

absence of light scaling in the lower outer aspect of the median space (Figs. 19–21). A unique dark morph occurs in both sexes (Fig. 22). However, identification is only confirmed by genital features. The distal costal process of the valva in males (Fig. 2), and the elongate, triangular plates of the ostium bursae in females (Fig. 11) differentiate *Pyla arenaeola* from all other known *Pyla*. In addition, the new species is closely associated with loose sandy soils, especially dunes, and the larval host, bearberry (*Arctostaphylos uva-ursi.*).

Description.—Alar expanse: 23.0 to 28.7 mm (Mean = 25.3, n = 23). Vestiture: A mixture of dark gray, pale gray, whitish, and pale-tipped gray scales. Head: Frons convex, a conical tuft of gray or pale-tipped gray scales dorsally, whitish ventrally; male vertex shallowly concave with appressed central scaling; female vertex flat with loose central scaling; in both sexes anterior and posterior vertex scale tufts of gray or paletipped gray scales, midvertex usually paler; ocelli and chaetosemata well developed; labial palpus ascending to level of vertex, 2nd segment longest and broadest, male with medial maxillary palpal groove, 3rd segment thin and very short, less than ¼ length of 2nd, scaled with gray and pale scales, base and mesial aspect often nearly white, 3rd segment darker and sometimes pale at tip; male maxillary palpus extends nearly to 1/3 length 2nd segment labial palpus, 1st segment thin and elongate, 2nd bulbous distally, pale tufts of hairlike and elongate thin scales from 2nd and 3rd segments extend 1/2 to <sup>2</sup>/<sub>3</sub> length 2nd segment labial palpus, female maxillary palpus short, 1st segment reduced, scales shorter and broader; tongue well developed, covered proximally with gray and pale scales; antenna laminate, basal 5-6 segments of male flagellum modified forming a mesial sinus, first several segments of sinus may be fused or partially fused, each modified segment with distal spine, spines progressively larger distally, sinus bordered medially and laterally by rows of gray scales, inner row of scales

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Figs. 1–5. *Pyla arenaeola*, male genitalia. 1, Genital capsule, valves unspread and aedeagus removed, ventral view; telescoped figure illustrates patch of small spines on tegumen near junction with gnathos; arrow heads indicate pouches formed by anellar membrane. 2, Right valva, medial aspect. 3, Aedeagus, ventral view. 4, Juxta, ventral view. 5, 8th sternite, ventral view, without scale tufts.

forming medial border of sinus modified, thick, dark, each with curved central spinelike tooth, base female flagellum unmodified, unmodified segments of flagellum in both sexes scaled with fine bands of grav and pale scales, male scape with a patch or band of pale scales along posteromedial aspect, female scape pale distally. Thorax: Dorsum, tegula, and collar of thorax gray, scales sometimes faintly pale-tipped, small white patches on posterolateral aspect of dorsum, lateral and ventral thorax with mixture of gray and whitish scales, predominately white laterally; legs scaled with mixture of gray and whitish scales, white predominates on mesial aspect, mesotibia with dark band at two-thirds, tarsi contrastingly dark, each segment white-tipped distally, protibia with spine-tipped epiphysis from middle extending just distal to first tarsal joint, mesotibia with one and metatibia with two pair of spurs. Wings (Figs. 19-21): Forewing gray variably overscaled with white and white-tipped gray scales, in fresh individuals the forewing appears blue-gray; pale scaling fairly evenly distributed in basal and subterminal spaces; median space pale scaling denser in costal half and just distal to antemedial line and making the lower outer aspect of median space appear contrastingly dark: antemedial line white, oblique, indented and most sharply defined in lower third, margined proximally by dark gray band along lower third, and distally by dark band which is widest at costal half: a small white patch of scales often evident near inner margin just distal to antemedial line; postmedial line white, variably sinuate to dentate, often more sharply defined at costa and inner margin, indented opposite cell and in lower third, margined proximally and distally by weakly defined darker banding; terminal line a thin row of dark gray spots; discal spot dark gray, double, usually a thin connection along proximal aspect, lower component elongate along axis of wing; fringe pale gray white-tipped scales; underside gray, contrastingly pale at costal edge and along inner margin, vague

indication of pale postmedial and dark terminal lines; hindwing brownish gray, veins slightly darker; a thin slightly darker gray line at outer margin; fringe pale gray, a darker gray band proximal third; underside light gray, slightly darker at costal and outer margins. Dark morph (Fig. 22) occurs in both sexes (8% of material examined); forewing nearly uniform dark slate gray with at most a few scattered white scales: crosslines reduced to a vague, thin antemedial line, most contrasting at inner margin, and a faint white postmedial line which may be evident only at costal and inner margins; darker banding and discal spot often obscure; vague small patches of white scales may be evident along inner margin just distal to antemedial line and distal to position of discal spot. Abdomen: Scaled with gray and whitish scales forming lighter bands at posterior margin of segments.

Male genitalia (Figs. 1-5): Uncus subtriangular, slightly constricted near base; gnathos with a stout central hook; valva (Fig. 2) with tooth-like distal costal process, base of costa unmodified; clasper (sensu Heinrich) beyond middle of valva at junction of central membranous window and distal sclerotized portion, with setae and small spines; tegumen with weak cluster of small spines near junction with gnathos (see telescoped illustration Fig. 1); juxta (Fig. 4) with ventrally produced blind pockets and paired short blunt lateral processes that have fine distal setae; aedeagus (Fig. 3) divided distally, divisions symmetric, sclerotized, laterally outcurved, pointed, and without additional lateral spines below tips, cornuti absent; anellar membrane (arrows, Fig. 1) extensively developed into distinct membranous pouches extending onto valva; eighth abdominal sternite sclerotized as in Fig. 5 with prominent hair pencils.

*Female genitalia* [Figs. 11–13; Heinrich (1956): Fig. 855 (as *aequivoca*)]: Junction of ostium bursae and ductus bursae weakly convoluted, lightly sclerotized; triangular plates of ostium bursae, elongate, sclerotized, with fine spines; ductus bursae broad



Figs. 6–10. *Pyla aequivoca*, male genitalia. 6, Genital capsule, valves spread, aedeagus and juxta removed; note that the valves have partly separated from the vinculum along ventral margin (arrow). 7, Aedeagus, dorsal view (Mackinaw Co., Michigan). 8, 8th sternite, ventral view, without scale tufts. 9, Juxta, ventral view. 10, Aedeagus, ventral view, distal divisions spread out (vic. Schefferville, Québec).

with shallow lateral lobes, nearly continuous with corpus bursae but defined by its thickened membrane, with variably expressed minute median sclerotized patch and weakly developed paired sinuous lines of sclerotization laterally but without broad sclerotized patches or bands; corpus bursae membranous and subrectangular; ductus seminalis dorsal (Fig. 13), arising at posterior margin of corpus bursae, with slight sclerotized collar at junction; ovipositor telescoped, less than half length of genital capsule, ovipositor lobes rounded laterally (Fig. 12).

Holotype.— $\delta$  (Fig. 19), Michigan: Allegan Co., Saugatuck Dunes State Park,



Figs. 11–16. *Pyla arenaeola* and *P. acquivoca*, female genitalia. 11–13, *P. arenaeola*. 11, Genital capsule, ventral view, 12, Ovipositor lobes. 13, Ductus and corpus bursae, dorsal view, illustrating entrance of ductus seminalis. 14–16, *P. acquivoca*. 14, Genital capsule, ventral view. 15, Ovipositor lobes. 16, Ductus and corpus bursae, dorsal view, illustrating entrance of ductus seminalis.

42.39'18"N, 86.12'07"W, 7 August 1992, dunes, G. J. Balogh (NMNH).

Paratypes.—(157 ♂, 92 ♀). UNITED STATES. INDIANA: Porter Co.- 1 &, Ogden Dunes, 10 Sep 1996 (Bess)(JAB). MICHIGAN: Allegan Co.—1 d, Saugatuck State Park, 8 Aug 1992, dunes (Balogh)(GJB); 3 ♂, 6 ♀, Saugatuck State Park, 3 Jul 1994 (Balogh)(GJB); 4 ♂, 2 ♀, 42.39'18"N, 86.12'07"W, 1 Sep 1995, Saugatuck Dunes State Park, UV (Wilterding)(JHW); 6 ♂, 4 ♀, Saugatuck Dunes SP, 7-8 Aug 1992 (Balogh)(GJB); 1 8, 1 9, Saugatuck SP, dunes, 29 Jul 1995 (Balogh)(GJB); 12 ♂, 6 ♀, Saugatuck SP, dunes, 26 Aug 1995 (Balogh)(GJB); 1 9, Saugatuck SP, dunes, 16 Sep 1995 (Balogh)(GJB); 3 ♂, Saugatuck SP, [larva and pupae in silk/sand tubes under A. uva-ursi] collected 15 Jun 1995, em. 24 Jun [pupa], 16 Jul, and 17 Aug 1995 (Balogh)(GJB). Antrim Co.—1 9, T32N, R8W, sec 26, 21 Aug 1994 (Stehr)(MSU). Charlevoix Co.-2 9, Fisherman's Island State Park, dunes, 13 Aug 1988 (Balogh)(GJB); 1 9, High 1sland, 27 Jul 1923 (Moore)(UMMZ); 1 9, Beaver Island, 17 Jul 1925 (Moore) (UMMZ). Cheboygan Co.-6 d, T38N, R1W, NE¼ of sec 25, 5-18 Jul 1995 (Scholtens) (BGS); 1 &, Douglas Lake, Jul (NMNH); 1 8, Douglas Lake (UMMZ). Chippewa Co.—5 ♂, 6 ♀, 0.7 mi S Whitefish Point, Boat Launch, 3 Jul 1988 (Balogh)(GJB); 2 ♂, dunes and wetland on Lake Huron just E of Albany River, 22 Jun 1992 (Balogh)(GJB). Emmet Co.--3 ර, Wilderness SP, T38N, R5W, sec 8, 22 Jun 1992 (Balogh)(GJB); 1 d, Wilderness SP, base of Waugoshance Point, 19 Aug 1990 (Balogh)(GJB). Keweenaw Co.—6 ♂, 2 ♀, Great Sand Bay Dunes, W of Eagle Harbor, 18 Jul 1995 (Balogh)(GJB). Leelanau Co.-1 9, T32N, R11W, sec 13, 13 Aug 1988 (Balogh)(GJB). Mackinac Co.-4 3, 13 9, dunes 1 mi W of Brevoort Rd, 13 Aug 1993 (Balogh)(GJB); 1 3, 0.9 miles W of Brevoort Rd, dunes, ex. pupa in sand/ silk tube 1-2 inches under surface of sand, coll. 22 Jul 1995, emer. 25 Jul 1995 (Balogh)(GJB); 3 ♂, 2 ♀, Hog Island Point, dunes, 21 Aug 1990 (Balogh)(GJB); 1 &, 1 9, Pte. Aux Chenes, dunes/wetlands, 13 Aug 1993 (Balogh)(GJB); 3 &, Pte. Aux Chenes Bay, 2-3 Aug 1996 (Balogh)(GJB); 1 <sup>9</sup>, T41N, R5W, sec 22, dunes, larvae coll. 23 May 1996, ex. larvae in sand tubes under A. uva-ursi, issued 21 Jul 1996 (Balogh)(GJB); 6 ♂, 1 ♀, T41N, R5W, sec 22, 2 Aug 1996 (Balogh)(GJB). Mason Co.-15 8, 6 ♀, Ludington State Park, dunes, 26-27 Aug 1994 (Balogh)(GJB); 18 8, 15 ♀, Ludington SP, dunes, 11–12 Aug 1995 (Balogh)(GJB); 29 ♂, 10 ♀, Ludington SP, dunes, 26-27 Jul 1996 (Balogh)(GJB). Muskegon Co.—1 9, Muskegon SP, dunes, 18 Jun 1988 (Balogh)(GJB). Oceana Co.-1 9, Little Point Sable Light House, dunes, 27 Aug 1993 (Balogh)(GJB). Presque 1sle Co.—1 &, 1 º, Hoeft S. P., dunes, coll. 24 May 1996, ex. larvae in sand tubes under A. uva-ursi, 9 issued 28 Jun 1996, 8 issued 29 Jun to 21 Jul 1996 (Balogh)(GJB). W1S-CONSIN: Ashland Co.-3 &, T49N, R4W, sec 13, Long Island sand dunes, 21 Jul 1995 (Ferge)(LAF); 2 9, T49N, R4W, sec 13, Long Island sand dunes, 9 Aug, 1996 (Ferge)(LAF). Manitowoc Co.-3 さ, T20N, R25E, sec 16, 23 Aug 1992 (Ferge)(LAF). CANADA. MANITOBA: 1 9, Aweme, 26 Aug 1921 (Criddle)(CNC). ONTARIO [all localities are on islands in Lake Huron]: 2 ♂, Wagash Bay, Cockburn 1s., 9 Jun 1977 (Morton)(JKM); 2 &, Carter Bay, Manitoulin 1s., 9 Aug 1988 (Morton)(JKM); 1 3, 1 9, Dean's Bay, Manitoulin 1s., 19 Jun 1996 (Morton)(JKM); 3 δ, Dean's Bay, Manitoulin 1s., 8 Jul 1996 (Morton)(JKM); 1 &, Dominion Bay, Manitoulin 1s., 1 Sep 1990 (Morton)(JKM); 1 d, Michael Bay, Manitoulin 1s., 13 Jul 1989 (Morton)(JKM); 1 9, Providence Bay, Manitoulin 1s., 27 Aug 1977 (Morton)(JKM); 1 る, Square Bay, Manitoulin 1s., 18 Jun 1991 (Morton)(JKM); 2 3, 1 9, Mississagi 1s., North Channel, 7 Aug 1977 (Morton)(JKM); 1 8, West Duck Is., 3 Aug 1976 (Morton)(JKM).

Distribution.—(Fig. 17). All recently



Fig. 17. Known distribution of *Pyla arenaeola* in central North America (because of close proximity not all localities are represented with a dot).

documented localities are from the dunes of the Great Lakes shore extending from the Manitoulin Island region of Lake Huron west to the western portion of Lake Superior and south along the shores of Lake Michigan to northern Indiana. The species may range throughout the Great Lakes basin; appropriate dune habitat is found as far east as the eastern shore of Lake Ontario (J.K. Morton, personal communication, 1996).

Specimens labeled Douglas Lake, Michigan (NMNH, UMMZ) may have originated on the shores of that inland lake approximately ten miles from the nearest Great Lakes shoreline. However, it is possible these specimens are mislabeled since the locality label "Douglas Lake" has been used by students over the years to designate the general vicinity of the University of Michigan Biological Station. Also, there are no recently documented specimens from Douglas Lake despite intense collecting of pyraloids in the region (Scholtens 1996).

The Manitoba record, a single female collected at Aweme (August 26, 1921, Norman Criddle, CNC), is the specimen Heinrich (1956) misidentified as *P. aequivoca*. This is the only known record from outside the Great Lakes basin. The specimen originated from a region of fossil Pleistocene sand dunes which formed at the delta of the Assiniboine River where it entered glacial Lake Agassiz (Dubois 1976, Teller 1984).

Habits and life history (Figs. 29–34).— In the Great Lakes region *P. arenaeola* is often common on foredunes (partially stabilized dunes), dune ridges, and blowouts of the Great Lakes shoreline where the larval host, bearberry, *Artostaphylos uva-ursi*, grows in prostrate creeping mats (Figs. 29, 30). Here it is often in association with beach grass, *Ammophila breviligulata* Fern.; sand reed grass, *Calamovilfa longi-* *folia* (Hooker) Scribner var. *magna* Scribner & Merrill; jack pine, *Pinus banksiana* Lamb.; cottonwood, *Populus deltoides* Marshall; and mat-forming plants such as false heather, *Hudsonia tomentosa* Nutt.; common juniper, *Juniperus communis* L.; and creeping juniper, *Juniperus horizontalis* Moench.

Early instar larvae form short, thin tubes of silk and sand particles and skeletonize the lower leaf surfaces of the host (Fig. 32). Young larvae reared from eggs in the absence of sand form tubes of frass and silk (B.G. Scholtens, personal communication, 1996). Later instars form networks of larger tubes on and just beneath the sand surface and attached to the prostrate branches of the host (Fig. 33). Leaves and short branch segments are often incorporated into the tubes, and leaf segments are cut off and transported into the tube shelters where the larvae remain concealed. The sand tubes contain scattered frass, scattered leaf fragments, and occasional groups of leaf fragments which are apparently food caches (Fig. 34). Although the larval tubes of *P. arenaeola* are horizontal at or near the surface, pupation occurs in a vertical tube segment an inch or two under the sand surface.

Last instar larvae are gray green, lighter ventrally, and lack conspicuous longitudinal lines or markings. The head as well as the prothoracic and anal shields are heavily sclerotized, dark brown, and also lack conspicuous markings.

In spring (mid-May) and summer (late July), both early and late instars can be found on the dunes which correlates with the prolonged adult flight (June 9 to October 11—the latest date is not part of the type series). Based on spring collections which often include late instars, the larvae probably overwinter. Most adults were collected during July and August. Adults are nocturnal and strongly attracted to black-light, but occasionally are flushed from bearberry mats during the day (Fig. 31). It is uncertain if *P. arenaeola* is univoltine with asynchronous development, or perhaps

facultatively bivoltine with broadly overlapping broods. In view of relatively prolonged larval development the former is favored.

Comments.—Initial examination of the male genitalia of *Pyla arenaeola* collected on the Great Lakes dunes demonstrated that it was unlike any described species in the genus. Females have characteristic genitalia (Fig. 11) and agree well with a specimen collected at Aweme, Manitoba (Heinrich 1956, Fig. 855) and placed by Heinrich under *Pyla aequivoca*. Although Heinrich incorrectly associated this female with the male type series of *P. aequivoca*, he did so with reservation since he excluded it from the type series of *P. aequivoca*.

While P. arenaeola may be confused with a number of other Pyla species, the association with dune habitats containing the foodplant is strong evidence that the identity of a moth flying there will be P. arenaeola. Other than the widespread and well known Pyla fusca (Haworth), P. arenaeola is the most commonly encountered Pyla in Great Lakes sand dune habitat. Occasionally Pyla aenigmatica Heinrich and Pyla insinuatrix Heinrich are collected on dunes but they probably stray from other shoreline habitats. Both P. aenigmatica and P. aequivoca are typically associated with inland sandy habitats, however, P. insinuatrix is most often encountered in fens and sedgy wetlands in the Great Lakes region (in coastal bogs in Nova Scotia, D.C. Ferguson, personal communication, 1995).

Besides habitat preferences, subtle superficial characters that are best appreciated in a series of fresh specimens, also support the correct association of sexes for gray *Pyla* of the Great Lakes region. The forewings of *P. fusca* are usually dark gray and perceptibly narrower than other *Pyla* of the region. Great Lakes region *P. aequivoca* (Figs. 23, 24) can be very close to *P. fusca* in color but often the pale forewing scaling is more prominent and the forewings broader in *P. aequivoca*. Fresh *P. insinuatrix* demonstrate dense pale whitish-gray fore-



Fig. 18. Known distribution of *Pyla aequivoca* in North America (because of close proximity not all localities are represented with a dot).

wing scaling, with sharply contrasting dark maculation and the forewings of P. aenigmatica are medium gray with sharply defined dark maculation. The hindwings of the latter are contrastingly whitish, often lighter than other Pyla of the region. Finally, P. arenaeola has quite broad forewings, typical fresh individuals (Figs. 19-21) being bluish-gray with the pale scaling less dense in the lower-outer aspect of the medium space than elsewhere on the wing. The dark form, which occurs in both sexes (less than 10 percent of the population), is blackish-gray with pale scaling and maculation much reduced (Fig. 22), a combination not found in other North American Pyla.

*Pyla arenaeola* shows remarkably little variation in genital features; the character-

istic triangular plates of the ostium bursae show only minor variation in shape and width.

Etymology.—The specific epithet *arenaeola* is derived from *arena*, L. = sand, and *Aeolus*, L. (*Aiolos*, Gr.) = god of the winds, to designate the sandy wind-blown habitat. The Greek word *aiolos* also means shifting, changeable, or variable (Brown 1956) which describes the nature of dunes and also refers to the dimorphic appearance of the moth.

*Pyla aequivoca* Heinrich (Figs. 6–10, 14–16, 18, 23–28)

Pyla aequivoca Heinrich 1956: 143. Holotype ♂, Banff, Alberta, Canada (CNC). Type examined.

Pyla gaspeensis McDunnough 1958: 5. Ho-

lotype ♂, Mile 49, Cascapedia Road, Gaspé, Québec, Canada (CNC). Allotype ♀, Cascapedia Road, near Mt. Albert, Gaspé, Quebec, Canada (NMNH). Types examined. **New synonym.** 

Diagnosis.-Pyla aequivoca is a variable, broadly ranging species, best distinguished from other Pyla based on the following genital features. Aedeagus (Figs. 7, 10) with a variable number of asymmetrically developed stout lateral spine-like processes; valva (Fig. 6) with short clasper (sensu Heinrich) near base and lacking costal processes; juxta (Fig. 9) shield-like with a pair of symmetric, elongate and pointed lateral processes. Ostium bursae with lateral, ridged, finely spiculate, sclerotized plates that are roughly rectangular in shape; ductus bursae with distinct lateral outpouchings and lacking well developed sclerotizations at the junction of the ostium and ductus bursae or broad sclerotized patches or bands (Fig. 14).

Description.—Alar expanse: 20.5-27.5 mm (Mean = 24.0, n = 26); slightly larger in the southern Rocky Mountain region (UT, WY, CO: Mean = 26.1, n = 10). Vestiture, head, thorax, and abdomen as in Pyla arenaeola, except where indicated. Head: Anterior and posterior vertex scale tufts gray, pale-tipped, occasionally all vertex scales nearly white and contrasting; labial palpus with 3rd segment about 1/4 length of second; male maxillary palpus extends nearly to middle 2nd segment labial palpus and scale tufts extend to end segment labial palpus; scale tufts female maxillary palpus extend to <sup>2</sup>/<sub>3</sub> length 2nd segment labial palpus; male antenna with sinus bordered by gray, often pale-tipped scales, sinus including modified scales otherwise as in Pyla arenaeola, unmodified segments of flagellum in both sexes predominately scaled with gray, scape with a line of pale scales along posteromedial aspect. Thorax: Dorsum, tegula, and collar with pale-tipped gray scales, lateral and ventral thorax predominately white. Wings (Figs. 23-28): Forewing, individually and geographically variable, dark specimens can be very dark glossy gray with reduced pale scaling (Fig. 25); distribution of light and dark scales sometimes patchy giving the wing a mottled appearance (Fig. 26); in the southern Rocky Mountain region (Colorado, Wyoming) often light gray with more uniform distribution of pale whitish scales (Figs. 27, 28); antemedial line pale, variably sinuate, indented in lower third, margined proximally and distally by darker lines that are broadest and darkest proximally along lower third and distally along costal half of antemedial line; postmedial line pale, dentate, indented opposite cell and in lower third, margined proximally and distally by darker lines; discal spots dark, fused or separate; terminal line a thin row of dark spots; fringe overlapping rows of pale-tipped gray scales; underside gray, pale shade along inner margin and sometimes along costa, faint indication of postmedial and terminal lines; hindwing pale brownish gray, sometimes semitranslucent, darkened along outer margin, veins slightly darker; fringe paler with a gray band proximal third; underside pale gray, darker at costa and outer margin, vague indication of pale subterminal band.

Male genitalia (Figs. 6-10): Uncus hoodlike; gnathos with stout central hook; valva (Fig. 6) widest near basal third, tapering to apex, costa weakly convex centrally and without processes or other modifications; clasper short, angulate, near base of valva, with a variable number of small spines and setae; tegumen without spine clusters; juxta (Fig. 9) shield-like with elongate pointed caudal processes, the processes often with a few setae; aedeagus (Figs. 7, 10) divided distally, the divisions sclerotized laterally and asymmetrically spined, 1 to 8 posterolaterally directed spines on each division, usually more numerous on left, cornuti absent; eighth abdominal sternite sclerotized as in Fig. 8 with prominent hair pencils.

Female genitalia (Figs. 14–16): Junction of ostium and ductus bursae strongly con-



Figs. 19–22. *Pyla arenaeola*, adults. 19, Holotype, male, Saugatuck Dunes State Park, Allegan Co., Michigan. 20, Paratype, female, same locality. 21, Paratype, female, same locality. 22, Paratype, male, dark form, same locality.

voluted, wrinkled, and membranous; paired sclerotized plates of ostium bursae with irregular ridges and furrows, finely spiculate, without caudal extensions; ductus bursae broad with lateral lobe-like, partially sclerotized pouches, variable small sclerotized regions on lateral lobes but ductus bursae without broad strongly sclerotized patches or bands, junction ductus and corpus bursae only slightly constricted; corpus bursae membranous and subrectangular; ductus seminalis (Fig. 16) dorsal, arising on posterior margin of corpus bursa, without sclerotized collar at junction; ovipositor telescoped, about ½ length of entire genital capsule, ovipositor lobes (Fig. 15) taper to nipple-like tip.

Types examined.—*Pyla aequivoca* Heinrich. Holotype (CNC): "Banff, Alta., 30 VI 1922, C.B.D. Garrett, 6000 ft"; "genitalia slide PYR 133" [male symbol][green label]; "[male symbol] Genitalia Slide, 26 June 1937, C.H. #2"; "HOLOTYPE [male symbol] Pyla aequivoca Heinr. No. 7593" [red label].

Pyla gaspeensis McDunnough. Holotype

![](_page_12_Picture_2.jpeg)

Figs. 23–28. *Pyla acquivoca* adults. 23, male, Schoolcraft Co., Michigan. 24, male, Oneida Co., Wisconsin. 25, male, vic. Schefferville, Quebec. 26, female, Avalon Peninsula, Newfoundland. 27, male, Chaffee Co., Colorado. 28, female, Alamosa Co., Colorado.

(CNC): "49th Mile, Cascapedia Road, Gaspe, 15.VII.1950, D.C. Ferguson"; "Slide No. Pyla 6167C" [blue-green label]; "Photo No 11" [blue label]; "HoloTYPE Pyla gaspeensis McD No. 6812" [red label]; "Pyla gaspeensis McD Holotype" [red label]. Allotype (NMNH): "nr. Mt. Albert, Cascapedia Road, Gaspe, 13-VII-1950, D.C. Ferguson"; "SLIDE No. Pyla 6167C [female symbol]"; "Pyla gaspiensis [sic, handwritten] McD., Allotype" [red label].

Additional material examined.--(33 8, 34 ♀ and including 4 ♂ paratypes) UNITED STATES. ALASKA: 1 9, nr Fort Yukon (NMNH). COLORADO: Alamosa Co.---l 3, 3 9, Great Sand Dunes National Monument, 8200 ft., 22-28 Jun 1982 (Ferguson, Hodges)(NMNH). Chaffee Co.—1 ♂, Mc-Gee Gulch, 9100 ft., 5 miles E Buena Vista, 5 Jul 1982, Ponderosa Pine, Pinyon-Juniper, Douglas Fir-Willow (Ferguson)(NMNH). Hinsdale Co.—1 9, Lake City, 6 Jul 1957, 8684 ft. (Rindge)(AMNH). Jackson Co.-2 d, Gould, 18 Jul 1957, 9000 ft., (Rindge) (AMNH). Larimer Co.-7 3, 1 9, Rist Canvon, 10 mi W Bellvue, 10 Jul 1957, 7400 ft. (Rindge)(AMNH). San Juan Co.-2 9, Silverton, 16-23 (NMNH). MICHIGAN: Emmet Co.—1 9, Mackinaw City, 4 Aug 1949 (Voss)(EGV). Keweenaw Co-1 &, Ft. Wilkins S. P., 16 Jul 1995 (Balogh)(GJB). Mackinac Co.-1 9, 3 Aug 1936 (Dreisbach)(MSU). Schoolcraft Co.-1 3, T42N, R16W, sec 11 and 13, 4 Jul 1987 (Balogh) (GJB). UTAH: Garfield Co.-2 9, Blue Spruce Camp, 18 mi N Escalante, 30 Jul 1965, 8000 ft. (Rindge)(AMNH). WISCON-SIN: Oneida Co.-3 3, T38N, R5E, sec 13, 2 Jul 1987 (Ferge)(GJB). WYOMING: Crook Co.—1 ♂, 1 ♀, Reuter Canyon Camp, 5 mi N Sundance, 9 Jul 1962, 5900 ft (Rindge)(AMNH). Park Co.-6 9, Lake Creek Camp, 13 mi SE Cooke City MT, 24 Jul 1959 (Rindge)(AMNH). Sublette Co.-2 3, Lower Green River Lake, Wind River Range, 6 Aug 1959, 8000 ft. (Rindge) (AMNH). CANADA. ALBERTA: 1 3 paratype, "Banff, Alta., 6 VII 1922, C.B.D. GARRETT," "PARATYPE Pyla aequivoca Heinr., No. 7593" [yellow label], "JHW slide 97.1" (CNC); 1 & paratype, "Banff, Alta., 30. VI. 1922, C.B.D. Garrett, 6000 ft.," "[J symbol] genitalia on slide 10 Oct. 1950, C.H. #3855," "Genitalia Slide By 101, 092 NMNH" [green label], "PARATYPE" [blue label] (NMNH); 1 ♂ paratype, "Banff, Alta., 21 VI 1922, C. B. D. Garrett," "PARA-TYPE" [blue label] [specimen not dissected] (NMNH); 1 9, Nordegg, 24 Jul 1921 (McDunnough)(CNC); 1 9, Eisenhower Junction, 15 mi NW of Banff, 4800 ft, 12 Aug 1973 (Leuschner)(LACM). NEW-FOUNDLAND: 1 9, Hopedale, Labrador, 23 Jul 1924 (Perrett)(NMNH); 1 さ, St Anthony, 16 Jul 1951 (Moore)(CNC); 2 9, Avalon Peninsula, nr. Topsail, 23 Jul 1954 (Ferguson)(NMNH). NOVA SCOTIA: 1 &, Bog, Baddeck, Victoria County, 30 Jul 1970 (Wright)(NMNH); 1 3, Middle River, Cape Breton Island, 6 Jul 1968 (Wright)(NMNH). ONTARIO: 1 ♂ paratype, "June 8–15," "Hymers Ont.," "S. triplasiella Dyar comp. with Type Coll., very close, J McD." [red bordered label], "Barnes Collection" [label upside down], "[3 symbol] genitalia on slide 10 Oct. 1950 C.H. #3861", "Genitalia Slide By 101,091 NMNH" [green label] (NMNH); 1 ♂, 1 ♀, Black Sturgeon Lake, 23–28 Jun 1963 (CNC); 1 9, Black Sturgeon Lake, 20 Jul 1963 (CNC); 1 &, Neys Prov. Park, 7 Jul 1995 (D. Balogh)(GJB); 1 9, Minaki, 8 Jul 1928 (McDunnough)(CNC). QUÉBEC: 1 9, Knob Lake, 54.47' 66.47', 26 Jul 1948 (Munroe)(CNC); 1 る, vic. Schefferville, 55 N centr. Labrador, 23 Jul 1990 (Hensel)(CNC); 1 9, 30 km S Mistassini Post, fir/birch slope, at light, 20 Jul 1992 (Mikkola)(UZMH). NORTHWEST TERRITORIES: 1 ♂, Cameron Bay, Great Bear Lake, 8 Jul 1937 (Freeman)(CNC). YUKON TERRITORY: 1 3, Ross River, 132.30' 61.56', 21 Jun 1960, 3000' (Martin)(CNC); 1 8, km 155, Dempster Hwy., 4 Jul 1985, 950m (Lafontaine)(CNC); 2 9, 60.45N, 134.40W, 20 km SE Whitehorse, light trap, 16 Jul 1985 (Mikkola)(UZMH); 1 3, 1 9, 65.07N, 138.16W, Ogilvie Mtns., 1050 m, Dempster Hwy., km 155, at light, 8 Jul 1985 (Mikkola)(UZMH); 1 °, 62.55N, 136.30W, Klondike Hwy km 476, Pelly River bog, 15 Jul 1985 (Mikkola) (UZMH); 1 °, S. Yukon, Carcross sand dunes, ad. lnc., 12 Jul 1994 (M. Ahola and L. Kalia)(UZMH).

Distribution.—(Fig. 18). *Pyla aequivoca* is known from widely scattered localities across northern North America from the subarctic south to the boreal deciduous border of eastern Canada and the Great Lakes region. In the west, *Pyla aequivoca* ranges south in the Rocky Mountains to southern Colorado. There are also records of this species from the Black Hills region of Wyoming and the mountains of southern Utah.

Habits and life history.-The life history of P. aequivoca is unknown but larvae may feed on Ericaceae as do the larvae of Pyla arenaeola and Pvla fusca (Goater 1986, Palm 1986). The Great Lakes region localities of P. aequivoca (Fig. 18) are within the boreal and boreal deciduous border life zones (Danks and Foottit 1989). Specimens have been collected in relatively open, often early successional habitats with sandy or rocky soils including open pine woods and barrens where the ground cover includes bracken fern (Pteridium aquilinum (L.) Kuhn), blueberry (Vaccinium spp.), bearberry (Arctostaphylos uva-ursi), wintergreen (Gaultheria procumbens L.), trailing arbutus (Epigaea repens L.), and reindeer lichen (Cladina spp.). Where the water table is close to the surface such acid soil sites are often accompanied by boggy vegetation dominated by the mat-like growth of many ericads such as leatherleaf (Chamaedaphne calvculata (L.) Moench), Labrador tea (Ledum groenlandicum Oeder), sheep-laurel, bog-laurel (Kalmia angustifolia L. and K. polifolia Wangenh.), bog-rosemary (Andromeda glaucophylla Link), and blueberry and cranberry (Vaccinium spp.). Notable in the Great Lakes region is the apparent absence of P. aequivoca on lakeshore dunes and in the Manitoulin Island region of Ontario, the later dominated by calcareous limestone habitats. Both of these habitat types have been actively sampled for phycitines in recent years.

In Newfoundland, P. aequivoca has been collected on the Avalon Peninsula (near Topsail), a region of rocky topography with both forest and open heath vegetation including bogs and barrens. Localities in Nova Scotia include a bog (Baddeck), and a stream valley with nearby upland spruce and fir forest (Middle River, Cape Breton Island) (D.C. Ferguson, in litt., 1996). The types of P. gaspeensis were collected on the Gaspé Peninsula in boreal forest dominated by spruce (Ferguson and Rupert 1951, D.C. Ferguson, personal communication, 1996). In the far north, both boreal forest and tundra are rich in members of the Ericaceae. One dry tundra locality in the Yukon (km 155, Dempster Highway), as figured and described by Lafontaine and Wood (1988, Fig. 5), includes both rocky tundra and patches of spruce forest (J.D. Lafontaine, personal communication, 1996). Label data for specimens collected in the Yukon and northern Quebec (UZMH) indicates that P. aequivoca may be found in a variety of habitats in the far north including fir/birch forest, bog, and sand dunes although it is difficult to assign habitat preferences based on small samples taken at light. In the Rocky Mountain region, P. aequivoca has been recorded from 4800 ft. in Alberta to 9100 ft. in Colorado, but insufficient information is available to comment more specifically on habitat requirements.

*Pyla aequivoca* is apparently univoltine; dates of capture range from June 8 to August 12, but most records are for the month of July in all regions where it has been collected.

Comments.—When McDunnough (1958) described *P. gaspeensis*, he based his diagnosis on comparison with Heinrich's description of *P. aequivoca* and was misled by Heinrich's figure of the aedeagus (Heinrich 1956, Fig. 366a; aedeagus rotated into an off-lateral projection as on holotype slide) and the incorrectly associated female of *P. arenaeola*. Examination of the genitalia of the *P. gaspeensis* male holotype shows that it is conspecific with *P. aequivoca* McDunnough's illustration of the female genitalia of *P. gaspeensis* (McDunnough 1958, Fig. 5) does not

![](_page_15_Figure_1.jpeg)

Figs. 29–34. *Pyla arenaeola*, habitat and life history. 29, Dunes at type locality, Saugatuck Dunes State Park, Allegan Co., Michigan; bearberry (*Arctostaphylos uva-ursi*) mats and dune grasses in foreground. 30, Bearberry stems spreading over open sand, same locality. 31, Adult resting posture, same locality. 32, Early instar larval sand tubes dangling from bearberry stem that has been lifted from sand surface, same locality. 33, Late instar larval sand tube attached to bearberry stem that has been slightly elevated from the sand surface, Presque fsle Co., Michigan; arrow head points to the tube. 34, Late instar larval tubes on sand (reared in captivity and host material removed to view tubes); intact tube below; tube above opened exposing larva and food cache.

show the lateral pouches of the ductus bursae (our Fig. 14) which are only evident when the genitalia are well inflated and properly stained. Examination of the *P. gaspeensis* allotype slide revealed that the bursa is only weakly stained and not well inflated, but the characteristic sclerotized plates of the ostium bursae are easily seen (as illustrated and described by McDunnough) and in good agreement with other female *P. aequivoca* we have examined.

Superficial distinctions cannot be applied to all *Pyla* specimens, particularly those of *P. aequivoca*, and are totally unreliable for populations outside of the Great Lakes region. Over its wide geographic range, P. aequivoca shows considerable individual and geographic variation in color, size, and maculation. Light gray specimens with contrasting maculation (Fig. 26) resemble P. insinuatrix. Occasional northern specimens (Fig. 25) are dark glossy gray with reduced pale scaling and somewhat obscured maculation. In the Rocky Mountain region, and especially southward, P. aequivoca presents a considerably paler appearance, nearly ashy gray due to an even overlay of fine pale scales and less contrasting maculation (Fig. 27, 28). Specimens from the southern Rocky Mountain region are also slightly larger. In the western mountains, P. aequi*voca* is superficially indistinguishable from sympatric but genitalically distinct Pyla impostor Heinrich (Heinrich 1956) and the two species are frequently collected together. Despite superficial variation, genital characters allow identification of P. aequi*voca* in all portions of its range. Variation in number of lateral spines (1-8) on the divisions of the aedeagus (Fig. 7, 10) and in size and shape of the lateral lobes of the ductus bursae (Fig. 14) has been noted but without a detectable geographic pattern.

Etymology.-Four specific epithets applied to Pyla species by Heinrich (1956) illustrate the difficulty of relying on superficial characters to determine specimens of the genus. These names, readily linked to commonly used English words, probably came to mind as Heinrich discovered Pyla's hidden genitalic riches (or more likely the names were coined to leave a palpable record of frustration due to the inability to depend on maculation to determine specimens). These names include aenigmatica (enigma = something obscure, inexplicable, a riddle or mystery), *impostor* (= a person who practices deception under an assumed character, identity, or name), insin*uatrix* (insinuate = to suggest or hint slyly), and *aequivoca* (equivocal = allowing the possibility of several different meanings especially with intent to deceive). Ironically, Heinrich's *Pyla aequivoca* deceived two competent workers, both Heinrich and McDunnough, but allowed us the possibility of recognizing two very distinct *Pyla* species.

### DISCUSSION

Biogeography.—All known populations of *P. arenaeola* are found north of the Wisconsin glacial boundary (the Great Lakes shoreline and Manitoba). The Great Lakes developed during the interval 11,000-14,500 BP when repeated glacial retreats and readvances eventually gave way to the present shoreline dunes (Loveless and Hamrick 1988). The only Manitoba specimen examined was collected at Aweme in 1921. This locality is on the western edge of a large fossil sand deposit, the Carberry Sandhills (Carberry Desert or Bald Head Hills), and includes approximately 39 square kilometers of active sand dunes within a larger sand deposit now stabilized by vegetation. The fossil dunes near Aweme Manitoba were formed at the old delta of the Assiniboine River where it entered the southwestern aspect of Glacial Lake Agassiz. At about 10,000 BP this glacial lake that formed at the southern edge of the receding continental ice sheet was the largest lake in North America, extending from the eastern Dakotas and Minnesota well north into Canada. Due to fluctuations in depth and extent of Lake Agassiz during its existence, multiple fossil beaches formed (as many as 55 different lake levels can be identified) and considerable open dune habitat was likely available for colonization by P. arenaeola during the glacial and immediate postglacial periods. Coincident with climatic warming and northward spread of prairie grassland to its southern aspect (approximately 9,000 BP), Lake Agassiz drained southeastward into Lake Superior (Teller 1984). The southern shoreline of Lake Agassiz and this drainage corridor may have provided a biogeographic link between the dunes of the Assiniboine delta and those of the Great Lakes shoreline.

Species of the genus Pyla share a northern transcontinental and western montane distribution in North America. Almost the entire range of the genus east of the Rocky Mountains (an estimated 8 species of the grav Pyla group) lies north of the Wisconsin glacial boundary. There is no known southern relict population or obvious progenitor species to suggest the preglacial origin for P. arenaeola. Pyla arenaeola could have evolved during the Wisconsin glacial period as a result of vicariant events near the glacial margin. It is also possible that P. arenaeola evolved prior to Wisconsin glaciation, survived the Wisconsin period on unglaciated portions of the Atlantic coastal plain or on the pre-Wisconsin sand deposits of the central and western Great Plains, then migrated north with glacial recession. Lafontaine (1982), and Loveless and Hamrick (1988) summarized the relevant biogeographic history of the Wisconsin period and possible scenarios for speciation events. It is of note that the larval host, bearberry, is still extant on the northern Atlantic coast and in the central and western Great Plains (Ferris and Fisher 1973, Great Plains Flora Association 1977). Both regions should be searched for possible relict Pvla populations.

Life history.-To the best of our knowledge, P. arenaeola is the only species of Pyla other than the holarctic P. fusca, for which specific life history information is available. In Europe, larvae of P. fusca have not been recorded forming sand or soil tubes but construct webs on shoots and leaves of Ericaceae and perhaps other plants. Goater (1986) and Palm (1986) record the following hosts: Heather (Calluna vulgaris (L.) Hull), heath (Erica spp.), bilberry, blueberry and closely related plants (Vaccinium spp. including V. myrtillus L.) and perhaps willow (Salix spp.) and birch (Betula spp.). In Europe the larvae overwinter. Heinrich (1956) was unable to document reliable life history data for P. fusca in North America and we have not encountered reared specimens during the course of this study. It should be pointed out that based on genital characters, P. fusca may not be closely related to P. arenaeola or P. aequivoca. Males of P. fusca have a thin cornutus in the vesica and females have a simple ostium bursae. Other Pyla species (both gray and bronzy-brown species groups, and including P. arenaeola and P. aequivoca), lack a cornutus, and the females of many species share extensive modifications of the ostium bursae. Perhaps the larvae of most Pvla, like those of P. arenaeola, feed concealed, accounting for a paucity of life history information. Once better known, the habits and morphology of the immatures should shed further light on the relationships of Pyla.

Pyla arenaeola is a member of a guild of sand-tube constructing Lepidoptera which inhabit the Great Lakes dunes and other very sandy habitats. Included in this guild are the pyraloids Prionapteryx nebulifera Steph. (host: Sand cherry, Prunus pumila L.) (see also Daecke 1905); Loxocrambus awemensis McD., Thaumatopsis sp., and Anerastia lotella (Hbn.) (host: culms of dune grasses); also included are two gelechiids, a Chionodes sp. and an undescribed member of the tribe Teleiodini (host: False heather, Hudsonia tomentosa) (personal observations). In Florida, Habeck et al. (1995) reported eight species of sandtube constructing Lepidoptera from Florida scrub habitat, including four pyraloids and four gelechilds. Tube formation from leaves, plant debris, and even soil has been described for other phycitines (Doerksen and Neunzig 1976, Neunzig 1979), and may be more widespread in this subfamily.

The documented distribution of *P. aren-aeola* is limited, but recent collecting has shown that it is locally common on the dunes of the western Great Lakes where its future seems secure. Nevertheless, conservationists and land managers should be aware of *P. arenaeola* and other sand-tube Lepidoptera. The pressures of development and the invasion of dune habitat by exotic plants are of ongoing concern. For instance,

at the P. arenaeola type locality, Saugatuck Dunes State Park, Michigan, a large introduced population of black or Austrian pine (Pinus nigra Arnold) is a troublesome invasive tree. Efforts should be made to locate other populations of P. arenaeola both outside the Great Lakes basin, such as in southern Manitoba where habitat may be more restricted, as well as on the Great Lakes and especially in regions where the pressures of development, overuse, and habitat degradation are most intense. The moth likely ranges east into the basins of Lakes Erie and Ontario. Additional disjunct populations may persist on dunes associated with the many fossil beaches formed during the existence of glacial Lake Agassiz in central North America (Teller 1984). Adults are easily sampled at blacklight, and with patience, larvae can be located by carefully lifting bearberry stems from the sand and looking for attached tube shelters (Figs. 32, 33). It is noteworthy that a relatively large moth such as P. arenaeola (average wing expanse about 2.5 cm) has gone unrecognized for so long. Moreover, other endemic dune Lepidoptera may await discovery; all the more reason to protect and wisely manage the Great Lakes shoreline.

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Matteson translated life history information for Pyla fusca from the Danish as published by Palm (1986). Members of the Michigan State University Entomology Department including F.W. Stehr and M.O. Nielsen, provided equipment, work space, and encouragement. N. Krieger, R. Leschen, F.W. Stehr, J. Zablotny and J. Wallace reviewed all or part of this manuscript. We must not forget to credit the many individuals and land managers who over the years contributed to preservation and maintenance of Great Lakes shoreline ecosystems. Finally, we thank our families and others not specifically mentioned for encouragement and for tolerating two lepidopterists fond of dunes and little gray moths.

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