

THE SPECIES OF *PSEUDEXENTERA* (TORTRICIDAE)

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ABSTRACT. Seventeen species of the nearctic genus *Pseudexentera* are recognized based on sometimes subtle differences in forewing pattern, and on one or more corroborative differences in structure or larval host. Seventeen characters were examined, and study material consisted of more than 1200 pinned adults, 450 genital preparations, and 500 wing preparations. Thirteen species occur only east of the Great Plains, three only westward, and one transcontinentally. Identities are revised for *P. cressoniana* (Clemens), the type species; also for *P. faracana* (Kearfott) and *P. spoliata* (Clemens). *Pseudexentera caryana* McDunnough proved to be a junior synonym of *P. cressoniana*. New species and their type localities are *P. sepia* (Cincinnati, Ohio), *P. hodsoni* (Oak Station, Pa.), *P. knudsoni* (Riviera Beach, Tex.), *P. oreios* (Rustler Park, Ariz.), and *P. vaccinii* (S. March, Ont.). Lectotypes are designated for *P. bipustulana* (Walker) (a junior synonym of *P. costomaculana* (Clemens)), and for *P. oregonana* (Walsingham).

Pseudexentera is a nearctic genus of the tribe Eucosmini. The known larvae appear to be monophagous or stenophagous on woody plant foliage. The adults are among the earliest spring-flying insects. Life history data and adult capture records suggest that all species of *Pseudexentera* are univoltine. At least three species are of economic interest: *P. mali* is a pest of apple, and *P. spoliata* and *P. oregonana* reach conspicuous numbers on oak and aspen, respectively.

Grote (1877) proposed the new genus and species *Exentera aprilana*, and Heinrich (1923) characterized the genus by male genital and other characters without having examined the type specimen. When he discovered that *E. aprilana* is a species of *Eucosma*, Heinrich (1940) proposed the name *Pseudexentera* for the genus, designating *Hedya cressoniana* Clemens as type species, and indicating his earlier belief (Heinrich 1923) that *H. cressoniana* was a junior synonym of *Sciaphila improbana* Walker. McDunnough (1959) discovered that *S. improbana* is a species of *Zeiraphera*. He regarded *Hedya cressoniana* as the type species of *Pseudexentera*, but likewise misidentified it. Thus the genus does not now have a correctly identified type species. The case is being referred to the International Commission on Zoological Nomenclature as called for by Art. 70b of the International Code of Zoological Nomenclature (3rd ed.).

There are two main forewing patterns in the genus, excluding the striped form of some *P. faracana* (Fig. 2). The main patterns are exemplified by *P. cressoniana* (Fig. 1) and *P. costomaculana* (Fig. 22). When forewing pattern varies within species, it ranges between distinct and less distinct or diffuse. Although adults can be identified by external appearance once their variation is understood, the species in each

of the two main wing-pattern groups are confusingly similar. This similarity has thwarted taxonomic progress and fostered confusion, especially with two of the earliest named species, *P. cressoniana* and *P. spoliata*, whose types remained incorrectly identified for more than a century.

METHODS

Pinned adults first were segregated by differences in forewing pattern, sometimes subtle ones. The resulting groups were then examined for differences in structure, larval host, adult phenology, and geography. The number of characters totaled 17. Structure refers to wing venation, genitalia, and body size. Either individual or statistical differences in structure were admissible. One distinguishing character state in structure or larval host was deemed sufficient to confirm specific distinction. Such differences are not always explicitly cited in the text except for new species. If differences beyond forewing pattern were not found, the group in question was combined with the next most similar one. Final groupings thought to comprise species were then assigned names based on their similarity to types.

The following structural characters and states or ranges proved useful in sorting and diagnosing the species. **Both sexes:** origin of forewing veins R_4 and R_5 : separate (like M_2 and M_3 in fig. 2 of Heinrich 1923), approximate (like R_s and M_1 in fig. 1 of Heinrich), connate (like M_3 and CuA_1 in fig. 1 of Heinrich), stalked (like M_3 and CuA_1 in fig. 2 of Heinrich). **Males:** position of valval constriction: $\frac{1}{2}$, $\frac{3}{5}$, $\frac{3}{4}$ distance between valval base and apex; maximal valval length/maximal cucullus length ratio, the latter distance measured between upper and lower edges: 1.6 to 3.4; position of anal spine on cucullus: near middle, near lower edge; projections from lower edge of cucullus: absent, one small but conspicuous curved spine present, one or more inconspicuous spinelets or bumps present; radius of curvature of lower edge of cucullus: greater or less than cucullus height; apex of aedeagus: unmodified, falcate, snoutlike and thin, snoutlike and thick; length of forewing: 5.0 to 10.0 mm. **Females:** position of ostium bursae: starting $\frac{1}{10}$ to $1\frac{1}{5}$ width of ostium bursae behind front edge of sternum 7; taper of forward end of sterigma: gradual if any, sharp; lightly sclerotized patch on corpus bursae: present, absent; size of signa: equal or subequal, unequal; symmetry of forward and rear halves of papillae anales: sub-symmetrical, asymmetrical; length \times width at maxima of one papilla analis: 0.08 to 0.16 mm²; length of forewing: 5.5 to 10.0 mm.

Genitalia were prepared as described by Clarke (1941). Position of the ostium bursae was estimated by eye at 45 \times nominal magnification. Measurements of papillae anales are to the nearest 0.03 mm, and were

made from microprojections. Valval length/cucullus length ratios were also determined from microprojections. Some wing venation preparations were permanent, but most were temporary. The latter were prepared by touching a capillary tube of xylol to a wing in a microscope field illuminated from below. Subsamples for venation study consisted of equal or nearly equal numbers of males and females when 20 or more adults of a species were available. When fewer adults were available, all were used regardless of the sex ratio. Wing length includes tegula and fringe, and was measured without magnification to the nearest 0.5 mm.

The letter n after a number denotes number of specimens underlying a statement. A parenthetical number after a color name refers to a color in Smithe (1975). Colors were estimated in natural light entering a window. Plant names follow Little (1979).

I examined 1234 pinned adults, 479 genitalia preparations, and 544 wing preparations from 20 sources. All nontypes bear the label "Voucher, W. E. Miller, 1986," and those illustrated here are also marked. The sources, with abbreviations used in the text, are: AMNH, American Museum of Natural History, New York; ANSP, Academy of Natural Sciences of Philadelphia; BMNH, British Museum (Natural History), London; CNC, Canadian National Collections of Insects, Arachnids and Nematodes, Ottawa; Craig, W. S. Craig, Columbia, Mo.; CU, Cornell University, Ithaca, N.Y.; FMNH, Field Museum of Natural History, Chicago; Heitzman, J. R. Heitzman, Independence, Mo.; INHS, Illinois Natural History Survey, Urbana; Knudson, E. C. Knudson, Belaire, Tex.; LACM, Natural History Museum of Los Angeles County, Los Angeles; Leuschner, Ronald Leuschner, Manhattan Beach, Cal.; Mather, Bryant Mather, Clinton, Miss.; MSUE, Michigan State University Entomology Museum, East Lansing; NSM, Nova Scotia Museum, Halifax; UCB, University of California, Berkeley; UMMZ, University of Michigan Museum of Zoology, Ann Arbor; UMSP, University of Minnesota, St. Paul; USNM, National Museum of Natural History, Washington, D.C.; UWM, University of Wisconsin, Madison.

Nomenclatural summaries consist mostly of primary works. Check lists are omitted except where they introduced new name combinations. Keys to species are omitted in the belief that matching specimens to diagnoses and illustrations is a suitable user alternative that saves space.

Pseudexentera Heinrich (1940:243)

Exentera (not Grote 1877:227); Heinrich (1923:172).

Diagnosis. The genus has been characterized by Heinrich (1923) and Brown (1982).
Both sexes: forewing lacking raised scale tufts, termen notched between veins CuA₁ and

M. **Males:** lacking forewing costal fold; socii densely setose, fused basally, articulating with tegumen on a stem; valval neck partly clothed with dense spinelike setae, a tiny anal spine on cucullus. **Females:** sternum 7 deeply emarginate around ostium bursae; sterigma consisting of lamella postvaginalis; lamella antevaginalis absent; tergum 9 with two to four tiny backwardly projected spinelets, a trait not previously known; anterior apophyses longer than posterior apophyses; ductus bursae partly sclerotized in an elbow shape near middle; corpus bursae with two finlike signa.

The genus appears to be monophyletic, the stemmed socii constituting a shared and perhaps derived character.

Pseudexentera cressoniana (Clemens)

(Figs. 1, 24, 41)

Hedya cressoniana Clemens (1865:514) (lectotype: Virginia, no date, abdomen missing, forewing length 8.5 mm, Type . . . 7222, designated by Darlington 1947, wings illustrated by Miller 1973a, in ANSP).

Exentera improbana (not Walker 1863:337); Heinrich (1923:174) (part).

Pseudexentera caryana McDunnough (1940:243) (holotype: female, St. David's, Ont., 14 April 1938, No. 5105, genitalia illustrated by McDunnough 1940, in CNC). NEW SYNONYMY.

Diagnosis. Forewing pattern (Fig. 1) varying little between or within sexes, but females averaging slightly higher in contrast (90n). Forewing veins R_1 and R_5 usually (92%) stalked at origin, sometimes (8%) connate (48n). In males, valva constricted at $\frac{1}{2}$ distance between base and apex, valval length/cucullus length ratio (spine included) 2.0 to 2.2, anal spine near lower edge of cucullus, aedeagus has a falcate apex (10n), a small curved spine projects from lower edge of cucullus (40n) (Fig. 24). The last is readily revealed without dissection by brushing away valval scales. In females, ostium bursae begins $\frac{1}{6}$ to $\frac{1}{2}$ its width behind front edge of sternum, forward end of sterigma tapers gradually if at all, corpus bursae spicule bases usually (94%) nowhere fused into a sclerotized patch, and signa unequal in size (Fig. 41) (18n). Forewing length of males 8.5 to 10.0 mm (40n), of females 8.0 to 10.0 mm (45n).

Comments. This species was known most recently as *P. caryana* McDunnough. Heinrich (1923) misidentified it, considering it to be a junior synonym of *Sciaphila improbana* Walker, which he also misidentified. When McDunnough (1959) discovered that the latter represented a species of *Zeiraphera*, he perpetuated Heinrich's misidentification of *P. cressoniana*, apparently unaware that Darlington (1947) had designated a lectotype for the species. Although the lectotype lacks an abdomen, its well preserved forewing pattern (Miller 1973a: fig. 10) is diagnostic. The pattern of *P. caryana* matches it well. This species accounts for the fifth of six known misidentifications of Clemens olethreutine types (Miller 1973a, 1973b, 1974, 1979, 1985).

I examined adults from Connecticut, Illinois, Iowa, Michigan, Mississippi, Missouri, New York, Pennsylvania, Texas, Virginia, and Wisconsin (AMNH, ANSP, Craig, Heitzman, Knudson, Mather, MSUE, NSM, UCB, UMMZ, USNM, UWM). The study sample included the *P. cressoniana* lectotype and a *P. caryana* paratype.

Biology. The larval host is *Carya ovata* (Mill.) K. Koch (McDunnough 1940). Adult capture dates range from 25 February to 16 May (90n).

Pseudexentera faracana (Kearfott)

(Figs. 2-4, 25, 42)

Proteopteryx faracana Kearfott (1907:47) (lectotype male: Scranton, Pa., 21 April 1906, A. E. Lister, genit. prep. CH 15 Dec. 1919, designated by Heinrich 1923, forewing length 9.0 mm, in AMNH).

Exentera faracana; Heinrich (1923:177).

Pseudexentera faracana; Powell (1983:36).

Eucosma haracana (not Kearfott 1907:46); Busck (1914:150).

Exentera spoliata (not Clemens 1865:513) (part); Heinrich (1923:175).

Pseudexentera spoliata (not Clemens 1865:513); MacKay (1959:123), Brown (1982:595).

Diagnosis. Forewing pattern of three slightly intergrading kinds, varying greatly between and within sexes, females possibly averaging higher in contrast. Kinds of pattern are striped (Fig. 2) (7n), thick banded (Fig. 3) (8n), and thin banded (Fig. 4) (35n). Forewing veins R_4 and R_5 usually (73%) approximate or connate at origin, sometimes (27%) stalked or separate (52n). In males, valva constricted at $\frac{3}{8}$ distance between base and apex, valval length/cucullus length ratio 2.3 to 2.7, anal spine near lower edge of cucullus, radius of curvature of lower edge of cucullus less than cucullus height, lower edge of cucullus may have up to four inconspicuous projections ranging in shape from bumps to spinelets, aedeagus has thin snoutlike apex (Fig. 25) (16n). In females, ostium bursae begins $\frac{1}{8}$ to $\frac{1}{2}$ its width behind front edge of sternum, forward end of sterigma tapers gradually if at all, corpus bursae spicule bases fused on one side near ductus bursae into a lightly sclerotized patch, signa unequal in size (Fig. 42) (25n). Forewing length of males 7.5 to 9.0 mm (19n), of females 7.0 to 8.5 mm (31n).

Comments. This species was most recently known partly as *P. spoliata* and partly as *P. faracana*. The former reflects Heinrich's (1923) misidentification of *P. spoliata*, which has a forewing pattern different from the three *P. faracana* patterns. Kearfott (1907) and Heinrich (1923) mused that one species with variable forewing pattern might be involved. Heinrich kept them separate because there were so few typelike examples of *P. faracana* at the time, the lectotype having the striped pattern. The three patterns here might indeed represent more than one species, but the information available now does not permit more than one to be recognized. Larval hosts are unknown for the striped and thick-banded adults. The larva of the thin-banded adult was described by MacKay (1959).

I examined adults from Connecticut, Illinois, Michigan, Mississippi, Missouri, New York, Ohio, Pennsylvania, Virginia, West Virginia, and Wisconsin (AMNH, ANSP, CNC, CU, FMNH, Heitzman, INHS, LACM, Mather, MSUE, UCB, USNM, UWM). The study sample included the *P. faracana* lectotype and a paralectotype, the pinned adult and genit. prep. No. 252 of Brown (1982), and thin-banded adults reared from *Castanea dentata* (Marsh.) Borkh. (Hopk. U. S. 1134) (4n).

Biology. The larva rolls the leaves of *Castanea dentata*, American chestnut, and the pupa overwinters on the ground (Busck 1914, MacKay 1959). There is one generation per year. Adult capture dates range from 25 February to 10 May (45n).

Although American chestnut was nearly exterminated by the blight fungus *Endothia parasitica* (Murr.) Anders. and Anders. early in this century, the host persists as stump sprouts and occasional disfigured trees. These host remnants could explain how $\frac{1}{3}$ of the study sample originated since 1950, two adults as recently as 1982. I captured an adult at stump sprouts. Alternate *Castanea* hosts could also be involved.

Pseudexentera sepia Miller, new species

(Figs. 5, 26, 43)

Exentera spoliata (not Clemens 1865:513) (part); Heinrich (1923:175).

Diagnosis and description. Forewing pattern (Fig. 5) varying little between or within sexes, females possibly averaging higher in contrast (22n). Forewing veins R_4 and R_5 usually (81%) approximate or connate at origin, sometimes (19%) separate or stalked (21n). In males, valva constricted at $\frac{3}{8}$ distance between base and apex, valval length/cucullus length ratio 2.2 to 2.6, anal spine near lower edge of cucullus, lower edge of cucullus has one or more inconspicuous projections ranging in shape from bumps to spinelets, aedeagus has thin snoutlike apex (Fig. 26) (7n). In females, ostium bursae begins $\frac{1}{8}$ to $\frac{1}{2}$ its width behind front edge of sternum, forward end of sterigma tapers gradually if at all, corpus bursae spicule bases fused on one side near ductus bursae into a lightly sclerotized patch, signa unequal in size (Fig. 43) (11n). Forewing length of males 7.0 to 8.5 mm (8n), of females 7.0 to 8.5 mm (14n) (holotype 7.5 mm). **Head.** Labial palpus mixed white and brown, second segment subequal in length to eye diameter, apical

segment $\frac{1}{3}$ length of second segment; front and crown mixed white and brown. *Thorax*. Mixed white and brown dorsally, shiny white ventrally; front and middle legs mixed white and brown, hind legs paler, tarsi of all legs banded; forewing upper-side dark markings near burnt umber (22) and raw umber (23), underside pale brown; hindwing upper side pale brown, underside paler. *Abdomen*. Mixed white and brown dorsally, paler ventrally. *Male Genitalia*. Vesica with 14 to 29 deciduous cornuti (5n).

Type data. Holotype female: Cincinnati, OHIO, A. F. Braun, 7 April 1906, genit. prep. DH 813813 (AMNH). Nineteen paratypes (AMNH, CNC, LACM, UCB, UMSP, INHS, Mather, Heitzman, USNM): ILLINOIS: Putnam Co., 31 March 1940, M. O. Glenn, ♀ genit. prep. DH 630812 (Fig. 43); MISSISSIPPI: Vicksburg, 19 Feb. 1982, B. Mather, ♀ genit. prep. WEM 510841; MISSOURI: Kansas City, 19 April 1971, J. R. Heitzman, ♀ genit. prep. SMG 905823; same data except ♂ genit. prep. SMG 907824 (this and preceding captured *in copula*); same data except 18 April 1973 (Fig. 5), wing prep. MGP 24, ♀ genit. prep. WEM 107844; same data except 13 April, ♂ genit. prep. SMG 905822 (Fig. 26); Grundy Co., 5 April 1980, J. R. Heitzman, ♂ genit. prep. SMG 1108828; same data except ♀ genit. prep. SMG 1108827; PENNSYLVANIA: New Brighton, 16 March 1903, H. D. Merrick, ♂, *Proteopteryx spoliata* Clem. AB 1920; same data except ♂ genit. prep. CH 3, 30 Jan. 1920, *Exentera spoliata* Clem. var.; same data except 18 March 1903, ♂, *Exentera spoliata* Clem. AB; same data except 30 April 1907, ♀; Pittsburgh, 22 April 1906, H. Engel, ♀ genit. prep. WEM 175854; QUEBEC: Ottawa Co., 1-7 April, ♀ genit. prep. LKM 824761; Old Chelsea, 30 April 1937, T. N. Freeman, ♀ genit. prep. WEM 107843; same data except 25 April 1935, W. J. Brown, wing prep. MGP 20, ♂ genit. prep. Exen 4A; Aylmer, 9 May 1932, G. S. Walley, ♀ genit. prep. Exen 4A, wing prep. MGP 19; WISCONSIN: Milwaukee, 25 April 1915, H. M. Bower, ♀ genit. prep. WEM 175853; Oneida Co., 20 May 1961, H. M. Bower, ♂ genit. prep. PB 221.

Comments. Heinrich (1923) included this species in what is here considered *P. faracana*, sometimes adding "var." to determinations. The new species most resembles thin-banded *P. faracana*. Among departures in forewing pattern, the basal patch is obscure, unlike that of *P. faracana* (Figs. 4, 5). Also, it is a smaller-bodied insect, based on forewing length. Forewing length of females, the more abundant sex in the study sample, averages 7.6 mm (11n) compared to 8.2 mm (19n) in *P. faracana*. The difference, 0.6 mm, is statistically significant ($t = 3.7$, $P\alpha < 0.001$). Although this difference represents only 7% of the longer forewing, it denotes a 25% lighter body weight because of the exponential relation between these variables (Miller 1977).

The species name refers to the family of hues marking the forewing.

Biology. The larval host is unknown. Adult capture dates range from 19 February to 20 May (21n).

Pseudexentera hodsoni Miller, new species

(Figs. 6, 27, 44)

Exentera spoliata (not Clemens 1865:513) (part); Heinrich (1923:175).

Diagnosis and description. Forewing pattern (Fig. 6) varying little between or within sexes (36n). Forewing veins R_4 and R_5 usually (97%) approximate or connate at origin, sometimes (3%) separate (34n). In males, valva constricted at $\frac{3}{4}$ distance between base and apex, valval length/cucullus length ratio 2.7 to 3.4, anal spine near lower edge of cucullus, radius of curvature of lower edge of cucullus exceeds cucullus height, lower edge of cucullus may have up to two inconspicuous projections ranging in shape from bumps to spinelets, and aedeagus has thin snoutlike apex (Fig. 27) (13n). In females, ostium bursae begins $\frac{1}{3}$ to $\frac{1}{2}$ its width behind front edge of sternum, forward end of sterigma tapers gradually if at all, corpus bursae spicule bases fused on one side near ductus bursae into a lightly sclerotized patch, signa unequal or subequal in size (Fig. 44) (13n). Forewing length of males 7.0 to 8.5 mm (19n) (holotype 8.0 mm), of females 7.5 to 9.0 mm (17n). *Head*. As described for *P. sepia*. *Thorax*. As described for *P. sepia* except forewing upper-side dark markings near dusky brown (19), and hindwing upper

side grayish brown. *Abdomen*. As described for *P. sepi*. *Male Genitalia*. Vesica containing 22 to 34 deciduous cornuti (4n).

Type data. Holotype male: Oak Station, Allegheny Co., PENNSYLVANIA, 10 April 1910, F. Marloff, genit. prep. CH 20, 13 Feb. 1920, *Exentera spoliata* Clem. det. C. H. (USNM). Thirty-five paratypes (AMNH, Craig, CU, Heitzman, INHS, Knudson, Mather, USNM, UCB): FLORIDA: Pensacola, 7 Feb. 1962, S. Hills, ♂ genit. prep. JAP 1424; ILLINOIS: Putnam Co., 7 April 1963, M. O. Glenn, ♂; same data except 13 April 1941, ♂ genit. prep. WEM 168851; LOUISIANA: Baton Rouge, 14 Feb. 1970, G. Strickland, ♀; MISSISSIPPI: Miss. State Univ., 1 March 1976, C. T. Bryson, ♂ genit. prep. SMG 916822; same data except 19 March, ♀ genit. prep. SMG 1029821 (Fig. 44); Hinds Co., 31 Jan. 1967, B. Mather, ♂ genit. prep. JAP 2441; same data except 13 Feb. 1959, ♂; same data; same data except ♂ genit. prep. SMG 916823; same data except 10 March 1963, ♂ genit. prep. JAP 1578; same data except 16 March 1963, ♀ genit. prep. JAP 1719; Rankin Co., 3 April 1960, B. Mather, ♀ genit. prep. JCL 1107836; Bovina, Warren Co., 7 March 1975, B. Mather, ♀ genit. prep. SMG 915824; same data except ♀ genit. prep. SMG 916821; same data except 14 March 1972, ♀ genit. prep. JCL 1128831; Vicksburg, Warren Co., 4 March 1980, B. Mather, ♀; same data except ♂; same data except 13 March 1981; same data except 30 March 1979, ♀ genit. prep. WEM 207841; Gulfport, 31 March 1978, R. Kergosien, ♀ genit. prep. SMG 916834; MISSOURI: "C. Mo.," reared from red oak, C. V. Riley, ♂ genit. prep. LKM 824765, *Proteopteryx spoliata* Clem. det. Walsingham 1887; Jackson Co., 13 April 1972, J. R. Heitzman, ♂ genit. prep. WEM 207844; same data except 18 April 1979, ♂ genit. prep. WEM 241852; Benton Co., 17 April 1970, J. R. Heitzman, ♂; St. Genevieve Co., 10 April 1981, J. R. Heitzman, ♀ genit. prep. WEM 304851; Columbia, 10 April 1971, W. S. Craig, ♀ genit. prep. JCL 1118833 (Fig. 6); same data except 12 April 1972, ♀ genit. prep. JCL 1118834; same data except 16 April 1971, ♀; same data except 18 April, ♂ genit. prep. WEM 207843; same data except 24 April, ♀; Kirkwood, reared from "L. oak," 1908, Murtfeldt, ♀ genit. prep. WEM 197844; PENNSYLVANIA: Allegheny Co., 30 April 1911, F. Marloff, ♀ genit. prep. JCL 11178310; TEXAS: Anderson Co., 15 March 1983, E. C. Knudson, ♂ genit. prep. ECK 584; Harris Co., 5 Feb. 1984, E. C. Knudson, ♂ genit. prep. ECK 817 (Fig. 27); same data except 19 Feb. 1985, ♂.

Comments. Heinrich (1923) included this species in what is here considered *Pseudexentera faracana*. The new species superficially resembles thin-banded *P. faracana* but differs structurally. The male valval constriction is at $\frac{1}{4}$ the distance between valval base and apex, compared to $\frac{1}{3}$ in *P. faracana*; and the lower edge of the male cucullus is slightly rounded, its curvature forming a circle whose radius exceeds cucullus height, while the lower edge of the cucullus in *P. faracana* is greatly rounded, its curvature forming a circle whose radius does not exceed cucullus height (Figs. 25, 27).

The species is named for Alexander C. Hodson, distinguished entomologist, teacher, and administrator.

Biology. The larval host is *Quercus* (2n), the species being given on labels as "L. oak" and "red oak." According to Riley's label information, the larva "slightly folds . . . leaves in May, pupates in (a) tough cocoon on (the) ground, and emerges early the following spring." Adult capture dates range from 31 January to 30 April (34n).

Pseudexentera knudsoni Miller, new species

(Figs. 7, 28, 45)

Diagnosis and description. Forewing pattern (Fig. 7) varying little within or between sexes (8n). Forewing veins R_4 and R_5 connate, approximate, or stalked at origin (8n). In males, valva constricted at $\frac{1}{3}$ distance between base and apex, valval length/cucullus length ratio 2.4 to 2.7, anal spine near lower edge of cucullus, lower edge of cucullus may have up to two inconspicuous projections ranging in shape from bumps to spinelets, aedeagus has falcate apex (Fig. 28) (5n). In females, ostium bursae begins $\frac{1}{2}$ its width

behind front edge of sternum, forward end of sterigma tapers gradually if at all, corpus bursae spicule bases fused on one side near ductus bursae into a lightly sclerotized patch, and signa unequal in size (Fig. 45) (2n). Forewing length of males 6.5 to 7.5 mm (6n) (holotype 7.0 mm), of females 7.0 to 7.5 mm (2n). *Head*. As described for *P. sepi*. *Thorax*. Mixed white, brown, and sometimes orange dorsally, shiny white ventrally; front and middle legs mixed white and brown, hind legs paler, tarsi of all legs banded; forewing upper-side dark markings near olive-brown (28) and glaucous (79); hindwing upper side pale brown, underside paler. *Abdomen*. As described for *P. sepi*. *Male Genitalia*: Vesica containing 19 to 29 deciduous cornuti (5n).

Type data. Holotype male (Fig. 7): Riviera Beach, Kleberg Co., TEXAS, 24 Feb. 1984, E. C. Knudson, genit. prep. WEM 168855 (USNM). Seven paratypes (Knudson, USNM, UMSP): TEXAS: San Antonio, 2 April 1978, ♂; same data except 6 May, ♂ genit. prep. WEM 154852; Canyon Lake, Comal Co., 8 May 1982, ♂ genit. prep. ECK 325 (Fig. 28); Conroe, Montgomery Co., 9 March 1982, ♂ genit. prep. ECK 570; Benbrook, Tarrant Co., ♂ genit. prep. WEM 168856; Austin, 13 April 1979, ♀ genit. prep. WEM 15852; Sam Houston Nat. For., San Jacinto Co., 29 March 1978, ♀ genit. prep. WEM 35852 (Fig. 45); all E. C. Knudson.

Comments. This species most resembles thin-banded *P. faracana*. Its aedeagus has a falcate apex, whereas that of *P. faracana* has a thin snoutlike apex (Figs. 25, 28). Also, it is a smaller-bodied insect, based on forewing length. Forewing length of males, the more abundant sex in the study sample, averages 6.9 mm (6n) compared to 8.4 mm (18n) in *P. faracana*. The 1.5 mm difference is statistically significant ($t = 7.2$, $P\alpha < 0.001$). Although this difference represents only 18% of the larger *P. faracana* forewing length, it denotes a 50% body weight difference because of the exponential relation between these variables (Miller 1977).

The species is named for Edward C. Knudson, its discoverer.

Biology. The larval host is unknown. Adult capture dates range from 24 February to 8 May (8n).

Pseudexentera haracana (Kearfott) (Figs. 8, 29, 46)

Proteopteryx haracana Kearfott (1907:46) (lectotype female: Hunter's Range, Pike Co., Pa., 1 May 1906, selected by C. Heinrich, designated by Klots 1942, forewing length 6.5 mm, in AMNH).

Exentera haracana; Heinrich (1923:176).

Pseudexentera haracana; Powell (1983:36).

Diagnosis. Forewing pattern (Fig. 8) varying little between or within sexes (67n). Forewing veins R_4 and R_5 usually (82%) connate or approximate at origin, sometimes (18%) stalked or separate (33n). In males, valva constricted at $\frac{3}{4}$ distance between base and apex, valval length/cucullus length ratio 2.3 to 2.7, anal spine near lower edge of cucullus, lower edge of cucullus has up to four inconspicuous projections ranging in shape from bumps to spinelets, and aedeagus has thick snoutlike apex (Fig. 29) (14n). In females, ostium bursae begins $\frac{1}{10}$ to $\frac{1}{8}$ its width behind front edge of sternum, forward end of sterigma tapers gradually if at all, corpus bursae spicule bases fused on one side near ductus bursae into a lightly sclerotized patch, signa unequal in size (Fig. 46) (16n). Forewing length of males 6.0 to 8.5 mm (32n), of females 6.0 to 8.0 mm (35n).

Comments. I examined adults from Connecticut, Florida, Michigan, Minnesota, Mississippi, Missouri, New Jersey, New York, Nova Scotia, Pennsylvania, Texas, and Wisconsin (AMNH, ANSP, Craig, Heitzman, Knudson, LACM, Mather, MSUE, NSM, UCB, UMSP, UWM). The study sample included paralectotypes (2n) and the lectotype. Adults superficially resemble *Gretchena delicatana* Heinrich; the two species are often mixed in collections.

Biology. The larval host is unknown. Adult capture dates range from 26 February to 15 June (67n).

Pseudexentera oreios Miller, new species

(Figs. 9, 30, 47)

Diagnosis and description. Forewing pattern (Fig. 9) varying little between or within sexes (7n). Forewing veins R_4 and R_5 approximate at origin (7n). In males, valva constricted at $\frac{3}{4}$ distance between base and apex, valval length/cucullus length ratio 2.8 to 2.9, anal spine near lower edge of cucullus, lower edge of cucullus may have one or more inconspicuous projections ranging in shape from bumps to spinelets, aedeagus has thin snoutlike apex (Fig. 30) (4n). In females, ostium bursae begins $\frac{1}{10}$ to $\frac{1}{8}$ its width behind front edge of sternum, forward end of sterigma tapers gradually, corpus bursae spicule bases fused on one side near ductus bursae into a lightly sclerotized patch, signa subequal in size (Fig. 47) (3n). Forewing length of males 7.5 to 8.0 mm (4n) (holotype 8.0 mm), of females 7.0 to 8.0 mm (3n). **Head.** As described for *P. sepia* except for white front and orange crown. **Thorax.** Similar to crown hues dorsally, shiny white ventrally; legs as described for *P. sepia*; forewing upper-side dark markings near tawny (38) and raw umber (223), the white and silver ocellus conspicuous, underside brown; hindwing upper- and undersides brown. **Abdomen.** Brownish white dorsally, paler ventrally. **Male Genitalia.** Vesica with 25 to 32 deciduous cornuti (3n).

Type data. Holotype male (Fig. 9): Rustler Park, Chiricahua Mts., ARIZONA, 3 July 1972, 8500' (2600 m), J. Powell, genit. prep. WEM 304853 (UCB). Six paratypes (UCB, UMSP): ARIZONA: Madera Canyon, Santa Rita Mts., Santa Cruz Co., 1-3 Aug. 1970, P. Rude, ♂ genit. prep. WEM 65853; same data except ♂ genit. prep. WEM 307851 (Fig. 30); same data except ♂ genit. prep. JAP 3614; same data except ♀ genit. prep. WEM 307853; Parker Canyon Lk., Cochise Co., 19 July 1972, J. Powell, ♀ genit. prep. WEM 35853 (Fig. 47); same data except ♀ genit. prep. WEM 307854.

Comments. This species most resembles *P. haracana* but differs structurally. The male valval constriction is at $\frac{3}{4}$ the distance between valval base and apex, compared to $\frac{2}{3}$ in *P. haracana*; and the snoutlike aedeagal apex is thin compared to that in *P. haracana*.

The species name denotes mountain dwelling.

Biology. The larval host is unknown. Adult capture dates range from 3 July to 3 August (7n).

Pseudexentera spoliata (Clemens)

(Figs. 10, 11, 31, 48)

Hedya spoliata Clemens (1865:513) (lectotype female: Virginia, no date, designated and illustrated by Miller 1973a, forewing length 8.0 mm, only right wings remaining, in ANSP).

Exentera improbana (not Walker 1863:337); Heinrich (1923:174).

Pseudexentera improbana (not Walker 1863:337); Heinrich (1940:242) (part), McDunnough (1940:244), Freeman (1942:213).

Pseudexentera cressoniana (not Clemens 1865:514); McDunnough (1959:2).

Pseudexentera spoliata; Miller (1973a:223).

Diagnosis. Forewing pattern varying within sexes, overlapping between sexes, females averaging higher in contrast (Figs. 10, 11) (409n). Forewing veins R_4 and R_5 usually (83%) connate or stalked at origin, sometimes (17%) approximate (52n). In males, valva constricted approximately at middle, valval length/cucullus length ratio 1.8 to 2.1, anal spine near lower edge of cucullus, lower edge of cucullus lacks projections, aedeagus has falcate apex (Fig. 31) (44n). In females, ostium bursae begins $\frac{1}{8}$ to $\frac{1}{4}$ its width behind front edge of sternum, forward end of sterigma tapers gradually if at all, corpus bursae spicule bases usually (98%) nowhere fused into a sclerotized patch, signa subequal in size (Fig. 48) (62n). Forewing length of males 7.0 to 9.5 mm (194n), of females 6.5 to 9.0 mm (217n).

Comments. The nomenclatural history of this species intertwines with that of *P. cress-*

soniana. *Pseudexentera spoliata* was long known as *P. improbana*, and most recently as *P. cressoniana* (McDunnough 1959). Because the syntype status of an earlier lectotype (Darlington 1947) seemed doubtful, a more plausible lectotype was designated (Miller 1973a). This action was not destabilizing because the specimens involved are conspecific. Although the lectotype lacks an abdomen, its well preserved forewing pattern (Miller 1973a: fig. 45) is diagnostic. This species accounts for the last of six known misidentifications of Clemens olethreutine types (Miller 1973a, 1973b, 1974, 1979, 1985, and earlier in this paper).

I examined adults from Colorado, Connecticut, District of Columbia, Illinois, Indiana, Iowa, Louisiana, Massachusetts, Michigan, Mississippi, Missouri, New Brunswick, New Hampshire, New Jersey, New York, Nova Scotia, Ohio, Ontario, Pennsylvania, Quebec, Texas, Virginia, and Wisconsin (AMNH, ANSP, CNC, Craig, CU, FMNH, Heitzman, INHS, Knudson, LACM, Mather, MSUE, NSM, UCB, UMMZ, UMSP, UWM). The study sample included the lectotype, adults whose wings were illustrated by Freeman (1942) (3n), and adults reared from *Quercus rubra* L. (24n) and *Q. sp.* (17n). The larva was described by MacKay (1959:122)

Biology. The larva feeds on *Quercus rubra* and perhaps other oaks, rolling the leaves. There is one generation per year (Heinrich 1923, Freeman 1942). Adult capture dates range from 11 February to 30 May (363n).

Pseudexentera mali Freeman

(Figs. 12, 13, 32, 49)

Pseudexentera mali Freeman (1942:213) (holotype male: Bell's Corners, Ont., reared from *Malus sylvestris* (L.) Mill., 7 Feb. 1942, J. McDunnough, wings illustrated by Freeman 1942, No. 5384 in CNC), Chapman & Lienk (1971:52).

Diagnosis. Forewing pattern varying within sexes, overlapping between sexes, females averaging higher in contrast (Figs. 12, 13) (73n). Forewing veins R_4 and R_5 usually (83%) stalked or connate at origin, sometimes (17%) approximate (41n). In males, valva constricted approximately at middle, valval length/cucullus length ratio 1.7 to 1.9, anal spine near lower edge of cucullus, lower edge of cucullus lacks projections, aedeagus has falcate apex (Fig. 32) (11n). In females, ostium bursae begins $\frac{3}{4}$ to $1\frac{1}{2}$ its width behind front edge of sternum, forward end of sterigma tapers gradually if at all, corpus bursae spicule bases nowhere fused into a sclerotized patch, signa unequal or subequal in size (Fig. 49) (16n). Forewing length of males 6.5 to 8.0 mm (33n), of females 6.0 to 7.5 mm (39n).

Comments. I examined specimens from Michigan, Missouri, New York, Nova Scotia, Ontario, Quebec, and Wisconsin (Craig, CNC, CU, Heitzman, MSUE, NSM, UCB, USNM, UWM). The study sample included paratypes (3n), holotype, and adults reared from *Malus sylvestris* (14n).

Biology. The larva feeds on *Malus* spp., mining buds and folding leaves. There is one generation per year, and the pupa winters on the ground (Chapman & Lienk 1971). Adult capture dates range from 13 March to 6 June (58n). The species is considered a pest of apple.

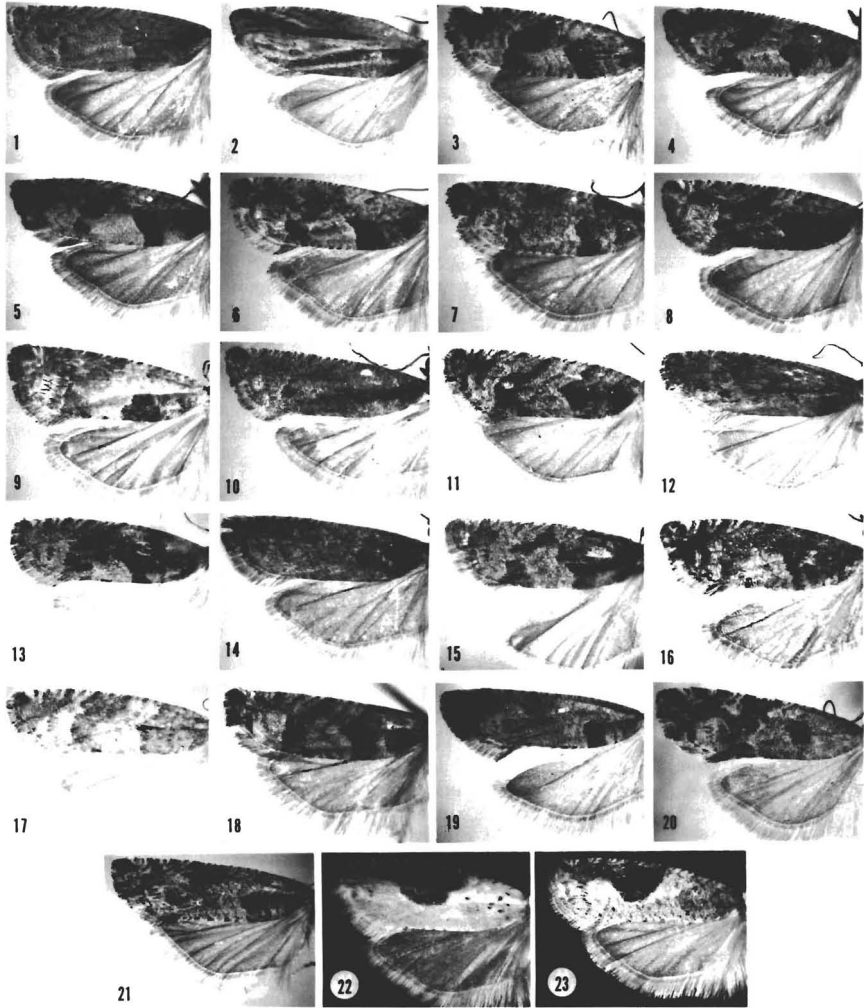
Pseudexentera oregonana (Walsingham)

(Figs. 14, 15, 33, 50)

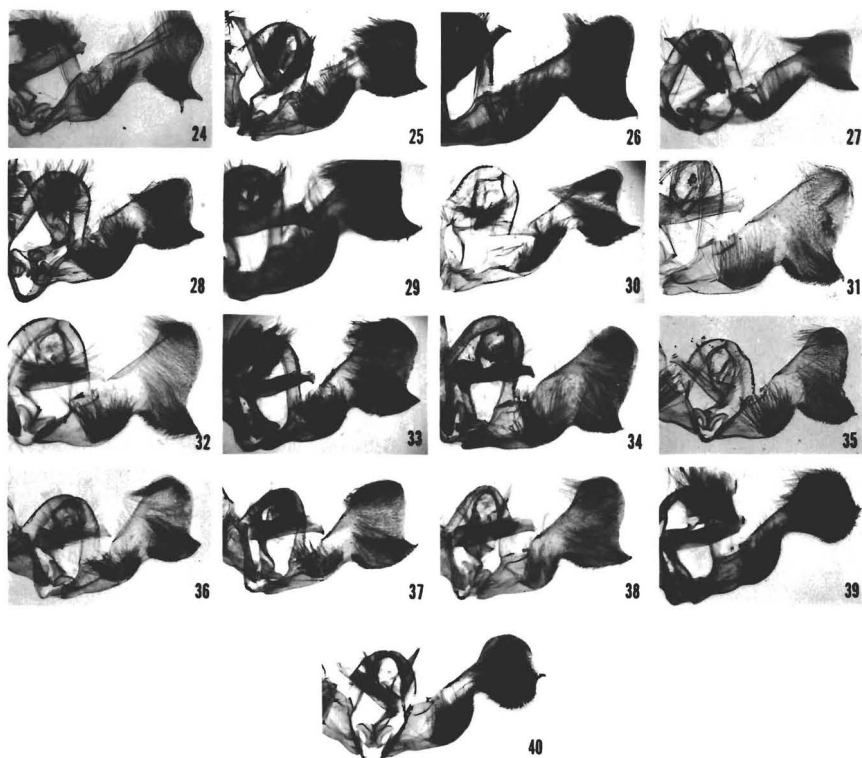
Semasia oregonana Walsingham (1879:62) (lectotype male: "Camp Watson, Grant Co., Ore., March-April 1872 . . . Type . . .," genit. prep. No. 5724, selected by N. S. Obraztsov, designated here, forewing length 9.0 mm, in BMNH).

Exentera improbana oregonana; Heinrich (1923:175).

Pseudexentera oregonana; McDunnough (1940:244), Freeman (1942:213), MacKay (1959:122, 1962:640, 1965:668).



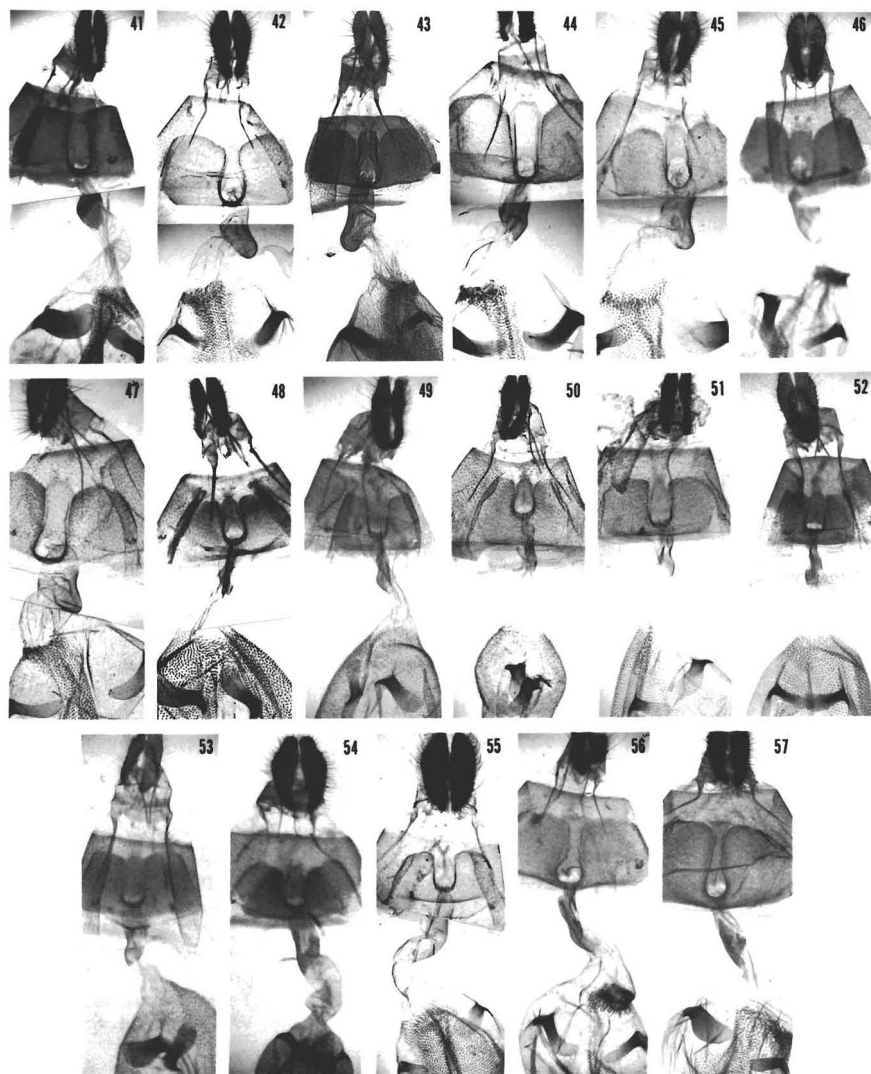
FIGS. 1-23. *Pseudexentera* wings, some images reversed. (1) *cressoniana* ♂, Columbia, Mo.; (2) *faracana* ♂, Putnam Co., Ill., striped; (3) *faracana* ♀, New Brighton, Pa., thick banded; (4) *faracana* ♀, Falls Church, Va., thin banded; (5) *sepia* ♀, Kansas City, Mo.; (6) *hodsoni* ♀, Columbia, Mo.; (7) *knudsoni* holotype ♂; (8) *haracana* ♀, New Lisbon, N. J.; (9) *oreios* holotype ♂; (10) *spoliata* ♂, Independence, Mo., diffuse pattern; (11) *spoliata* ♀, Aylmer, Que., distinct pattern; (12) *mali* ♂ paratype, Bell's Corners, Ont., diffuse pattern; (13) *mali* ♀ paratype, Bell's Corners, Ont., diffuse pattern; (14) *oregonana* ♂, S. Ottawa, Ont., diffuse pattern; (15) *oregonana* ♀, Aweme, Man., distinct pattern; (16) *kalmiana* ♂ paratype, Halifax, N.S.; (17) *maracana* ♂, Shiawassee Co., Mich.; (18) *vaccinii* holotype ♀; (19) *habrosana* ♂, San Luis Obispo Co., Calif., diffuse pattern; (20) *habrosana* ♀, O'Brien, Calif., distinct pattern; (21) *senatrix* ♀ paratype, Cochise Co., Ariz.; (22) *costomaculana* ♀, Dryden, N.Y.; (23) *virginiana* ♂, Ithaca, N.Y.



FIGS. 24–40. *Pseudexentera* male genitalia, some images reversed. (24) *cressoniana*, Livingston Co., Mich., prep. MAM 314792; (25) *faracana*, Mt. Airy, Pa., prep. WEM 137844; (26) *sepia*, Kansas City, Mo., prep. SMG 905822; (27) *hodsoni*, Bellaire, Tex., prep. ECK 817; (28) *knudsoni*, Comal Co., Tex., prep. ECK 325; (29) *haracana*, Lakehurst, N.J., prep. WEM 197843; (30) *oreios*, Sta. Cruz Co., Ariz., prep. WEM 307851; (31) *spoliana*, Blain, Pa., prep. VA 265; (32) *mali*, Oneida Co., Wis., prep. VA 106; (33) *oregonana*, Meach Lk., Que., prep. WEM 97851; (34) *kalmiana*, Mer Bleue, Ont., prep. WEM 135853; (35) *maracana*, Livingston Co., Mich., prep. JAB 80; (36) *vaccinii*, Ingham Co., Mich., prep. JAB 79; (37) *habrosana*, Alameda Co., Calif., prep. WEM 257852; (38) *senatrix* paratype, Cochise Co., Ariz., prep. WEM 237844; (39) *costomaculana*, Ithaca, N.Y., prep. WEM 251852; (40) *virginiana*, Ithaca, N.Y., prep. WEM 251854.

Diagnosis. Forewing pattern varying within sexes, overlapping between sexes, females averaging higher in contrast (Figs. 14, 15) (157n). Forewing veins R_4 and R_5 usually (92%) stalked or connate at origin, sometimes (8%) approximate (37n). In males, valva constricted approximately at middle, valval length/cucullus length ratio 1.9 to 2.2, anal spine near lower edge of cucullus, lower edge of cucullus lacks projections, aedeagus has falcate apex (Fig. 33) (14n). In females, ostium bursae begins $\frac{1}{2}$ to $1\frac{1}{2}$ its width behind front edge of sternum, forward end of sterigma tapers gradually if at all, corpus bursae spicule bases nowhere fused into a sclerotized patch, signa unequal or subequal in size (Fig. 50) (18n). Forewing length of males 7.5 to 10.0 mm (85n), of females 7.5 to 9.5 mm (53n).

Comments. I examined adults from Alberta, British Columbia, Maine, Manitoba, Michigan, Nova Scotia, Ontario, Oregon, Quebec, Saskatchewan, and Wisconsin (BMNH,



FIGS. 41-57. *Pseudexentera* female genitalia. (41) *cressoniana*, Barry Co., Mo., prep. SMG 1109824; (42) *faracana*, Putnam Co., Ill., prep. DH 617812; (43) *sepia*, Putnam Co., Ill., prep. DH 630812; (44) *hodsoni*, Oktibbeha Co., Miss., prep. SMG 1029821; (45) *knudsoni*, San Jacinto Co., Tex., prep. WEM 35852; (46) *haracana*, Vicksburg, Miss., prep. SMG 923821; (47) *oreios*, Cochise Co., Ariz., prep. WEM 35853; (48) *spoliata*, Columbia, Mo., prep. SMG 1206821; (49) *malii*, Ithaca, N.Y., prep. WEM 304852; (50) *oregonana*, Ottawa E., Ont., prep. WEM 95854; (51) *kalmiana*, Constance Bay, Ont., prep. WEM 218851; (52) *maracana*, Putnam Co., Ill., prep. DH 701814; (53) *vaccinii*, Washtenaw Co., Mich., prep. VA 252; (54) *habrosana*, O'Brien, Calif., prep. WEM 105853; (55) *senatrix*, Yavapai Co., Ariz., prep. WEM 119851; (56) *costomaculana*, New Brighton, Pa., prep. WEM 301853; (57) *virginiana*, Pittsburgh, Pa., prep. WEM 116852.

CNC, LACM, MSUE, NSM, UCB, UMMZ). The study sample included the lectotype, a paralectotype, adults whose wings were illustrated by Freeman (1942) (3n), and adults reared from *Populus tremuloides* Michx. (23n) and *Salix* sp. (15n).

Biology. The larva eats new foliage and rolls leaves of *Populus tremuloides* and *Salix* sp. There is one generation per year, with the pupa wintering on the ground (Freeman 1942, MacKay 1962, McDunnough 1940, Prentice 1966, Wong & Melvin 1967). Adult capture dates range from 15 March to 14 June (96n).

Pseudexentera kalmiana McDunnough

(Figs. 16, 34, 51)

Pseudexentera kalmiana McDunnough (1959:4) (holotype male: White Point Beach, Queens Co., Nova Scotia, reared from *Kalmia* sp. [*angustifolia* L. according to Ferguson 1975] 15 April 1954, J. McDunnough, genit. prep. WEM 148851, forewing length 6.0 mm, No. 6807 in CNC).

Diagnosis. Forewing pattern (Fig. 16) varying little between or within sexes (58n). Forewing veins R_4 and R_5 usually (80%) connate or approximate at origin, sometimes (20%) stalked or separate (34n). In males, valva constricted at middle, valval length/cucullus length ratio 1.8 to 1.9, anal spine near lower edge of cucullus, lower edge of cucullus lacks projections, aedeagus has falcate apex (Fig. 34) (14n). In females, ostium bursae begins $\frac{1}{3}$ to $\frac{1}{2}$ its width behind front edge of sternum, forward end of sterigma tapers gradually if at all, corpus bursae spicule bases nowhere fused into a sclerotized patch, signa subequal in size (Fig. 51) (16n). Forewing length of males 5.0 to 6.5 mm (36n), of females 5.5 to 6.5 mm (22n).

Comments. I examined adults from Michigan, Newfoundland, New York, Nova Scotia, and Ontario (CNC, CU, MSUE, NMS). The study sample included paratypes (4n) and holotype.

Biology. The larva feeds on *Kalmia angustifolia* L. (Ferguson 1975). Adult capture dates range from 11 April to 14 June (57n).

Pseudexentera maracana (Kearfott)

(Figs. 17, 35, 52)

Proteopteryx maracana Kearfott (1907:46) (lectotype male: Cincinnati, Ohio, 3 April 1906, A. F. Baun, selected by C. Heinrich, designated by Klots 1942, in AMNH).

Exentera maracana; Heinrich (1923:177).

Pseudexentera maracana; Powell (1983:36).

Diagnosis. Forewing pattern (Fig. 17) varying little between or within sexes, females possibly averaging higher in contrast (24n). Forewing veins R_4 and R_5 usually (95%) stalked or connate at origin, sometimes (5%) approximate (22n). In males, valva constricted approximately at middle, valval length/cucullus length ratio 1.6 to 1.8, anal spine near lower edge of cucullus, lower edge of cucullus lacks projections, aedeagus has falcate apex (Fig. 35) (9n). In females, ostium bursae begins $\frac{1}{2}$ to $1\frac{1}{2}$ its width behind front edge of sternum, forward end of sterigma tapers gradually if at all, corpus bursae spicule bases nowhere fused into a sclerotized patch, signa unequal or subequal in size (Fig. 52) (11n). Forewing length of males 7.0 to 7.5 mm (12n), of females 6.0 to 7.0 mm (12n).

Comments. I examined specimens from Illinois, Michigan, Minnesota, Mississippi, Missouri, New York, Ohio, Pennsylvania, Quebec, and Texas (AMNH, CNC, Craig, CU, Heitzman, INHS, Knudson, LACM, Mather, MSUE, UCB, UMMZ). The study sample included the lectotype, a paralectotype, and adults reared from *Crataegus* sp. (4n).

Biology. The larva feeds on *Crataegus*. Adult capture dates range from 30 January to 15 May (20n).

Pseudexentera vaccinii Miller, new species

(Figs. 18, 36, 53)

Diagnosis and description. Forewing pattern (Fig. 18) varying little between or within sexes, females possibly averaging higher in contrast (36n). Forewing veins R_4 and R_5 usually (60%) connate at origin, sometimes (40%) approximate or stalked (30n). In males, valva constricted approximately at middle, valval length/cucullus length ratio 1.8 to 2.0, anal spine near lower edge of cucullus, lower edge of cucullus lacks projections, aedeagus has falcate apex (Fig. 36) (19n). In females, ostium bursae begins $\frac{1}{4}$ to $1\frac{1}{2}$ its width behind front edge of sternum, forward end of sterigma tapers gradually if at all, corpus bursae spicule bases nowhere fused into a sclerotized patch, signa subequal in size (Fig. 53) (16n). Forewing length of males 6.5 to 8.0 mm (21n), of females 6.0 to 7.5 mm (17n) (holotype 7.0 mm). *Head.* Labial palpus brownish white, paler on inner side, second segment subequal in length to eye diameter, apical segment $\frac{1}{3}$ length of second; front and crown brownish white. *Thorax.* Hues similar to front and crown dorsally, shiny white ventrally; front and middle legs mixed white and brown, hind legs paler, tarsi of all legs banded; forewing upper-side dark markings near tawny (38) and fuscous (21), underside pale brown; hindwing upper side pale brown, underside paler. *Abdomen.* Brownish white dorsally, paler ventrally. *Male Genitalia.* Vesica with 17 to 23 deciduous cornuti (11n).

Type data. Holotype female (Fig. 18): S. March, ONTARIO, 22 April 1944, J. McDunnough, reared from *Vaccinium* sp., genit. prep. Exen 11a (CNC). Thirty-seven paratypes (ANSP, CNC, LACM, MSUE, NSM, UMMZ, UMSP): MASSACHUSETTS: Barnstable, 22 June 1951, C. P. Kimball, ♀ genit. prep. *Pseud.* B; same data except 8 July 1950, ♂ genit. prep. *Pseud.* B; MICHIGAN: Ingham Co., 8 April 1967, J. P. Donahue, ♂ genit. prep. JAB 76; same data except ♂ genit. prep. 71; same data except 12 April 1968, ♂; same data except ♀ genit. prep. WEM 87853; same data except ♀ genit. prep. JAB 69; same data except ♂ genit. prep. VA 277; same data except ♂ genit. prep. VA 278; same data except ♂ genit. prep. VA 279; same data except 15 April 1967, ♂ genit. prep. JAB 79 (Fig. 36); same data except 26 April 1970, ♀ genit. prep. HS 3177311; same data except 2 May 1968, ♀ genit. prep. WEM 87851; same data except 18 May 1966, ♀ genit. prep. PJ 61; Chippewa Co., 25 May 1966, J. P. Donahue, ♀ genit. prep. PJ 54; same data except ♂ genit. prep. PJ 56; Otsego Co., 3 May 1970, J. P. Donahue, ♂ genit. prep. HS 317787; Crawford Co., 28 April 1951, R. R. Dreisbach, ♂ genit. prep. RBM 198; Wash-tenaw Co., 14 April 1936, W. W. Newcomb, ♀ genit. prep. VA 252 (Fig. 53); Midland Co., 21–31 May 1961, R. R. Dreisbach, ♀ genit. prep. PJ 234; MINNESOTA: Cass Co., 14 May 1936, R. H. Daggy, ♀ genit. prep. ACC 427781; NEW JERSEY: New Lisbon, 24 April 1933, E. P. Darlington, ♀ genit. prep. KL 191; same data except 6 May, ♀ genit. prep. WEM 1022735; same data except ♂ genit. prep. WEM 218853; same data except 14 May, ♂ genit. prep. WEM 1022734; same data except 16 May, ♂ genit. prep. KL 196; same data except 14 May 1932, ♂ genit. prep. KL 195; ONTARIO: Same data as holotype except ♀ genit. prep. WEM 85853; Bell's Corners, 20 April 1941, T. N. Freeman, ♀; same data except ♀ genit. prep. LKM 824769; same data except 25 April, ♂ genit. prep. WEM 87855; Constance Bay, 28 April 1941, J. McDunnough, ♂ genit. prep. WEM 218852; same data except T. N. Freeman, ♂; same data except ♂ genit. prep. Exen 11; same data except 26 April 1935, W. J. Brown, ♂ genit. prep. WEM 87854; same data except G. S. Walley, ♂ genit. prep. WEM 177841; PENNSYLVANIA: Allegheny Co., 10 April 1910, F. Marloff, ♀ genit. prep. WEM 97853.

Comments. This species most resembles *Pseudexentera maracana*. It differs in its thinner middle forewing crossband (Figs. 17, 18), its statistically different R_4 and R_5 origins, its statistically different ostium bursae position and in larval host. The frequency distribution of approximate, connate, and stalked R_4 and R_5 in *P. vaccinii* is 7, 18, and 5, respectively, compared to 1, 10, and 11 in *P. maracana* ($G_{adj} = 10.4$, $P\alpha < 0.01$). In *P. vaccinii* the ostium bursae begins on average 0.58 its width behind the front edge of the sternum compared with 0.95 in *P. maracana*. The difference, 0.37, is significant ($t = 3.50$, $P\alpha < 0.01$). The unnamed *Pseudexentera* larva on *Vaccinium* described by MacKay (1959:121) is probably this species.

Biology. The larva feeds on *Vaccinium* (2n). Adult capture dates range from 8 April to 8 July (36n).

Pseudexentera habrosana (Heinrich)

(Figs. 19, 20, 37, 54)

Exentera habrosana Heinrich (1923:178) (holotype male: San Diego, Calif., 17 March 1912, W. S. Wright, genitalia illustrated by Heinrich 1923, No. 24833 in USNM).
Pseudexentera habrosana; Powell (1961:203).

Diagnosis. Forewing pattern varying within sexes, overlapping between sexes, females possibly averaging higher in contrast (Figs. 19, 20) (59n). Forewing veins R_4 and R_5 usually (97%) approximate or connate at origin, sometimes (3%) stalked (56n). In males, valva constricted approximately at middle, valval length/cucullus length ratio 1.8 to 2.1, anal spine located near lower edge of cucullus, lower edge of cucullus may have up to two inconspicuous projections ranging in shape from bumps to spinelets, aedeagus has falcate apex (Fig. 37) (20n). In females, ostium bursae begins $\frac{2}{3}$ to $1\frac{1}{2}$ its width behind front edge of sternum, forward end of sterigma tapers gradually if at all, corpus bursae spicule bases nowhere fused into a sclerotized patch, signa subequal or unequal in size, forward end of sterigma tapers gradually if at all, corpus bursae spicule bases nowhere wing length of males 7.5 to 9.5 mm (35n), of females 7.0 to 8.5 mm (24n).

Comments. I examined adults from the California counties of Alameda, Contra Costa, Lake, Los Angeles, Marin, Mendocino, Orange, Placer, Riverside, San Diego, San Francisco, San Luis Obispo, Santa Barbara, Santa Clara, Shasta, Sonoma, Stanislaus, Tuolumne, and Ventura (LACM, Leuschner, UCB, USNM). The study sample included adults listed by Powell (1961) (6n), adults reared later by Powell from *Quercus agrifolia* Née or *Q. wislizeni* A. DC. (12n), and a paratype. The larva was described by Powell (1961).

Biology. The larva feeds on *Q. agrifolia* and *Q. wislizeni* foliage. Adult capture dates range from 21 January to 17 April (47n).

Pseudexentera senatrix (Heinrich)

(Figs. 21, 38, 55)

Exentera senatrix Heinrich (1924:390) (holotype male: Paradise, Cochise Co., Ariz., 8-15 March, in USNM).

Pseudexentera senatrix; Powell (1983:36).

Diagnosis. Forewing pattern (Fig. 21) varying little within or between sexes, females possibly averaging higher in contrast (25n). Forewing veins R_4 and R_5 usually (90%) connate or stalked at origin, sometimes (10%) approximate (20n). In males, valva constricted approximately at middle, valval length/cucullus length ratio 2.0 to 2.1, anal spine near lower edge of cucullus, lower edge of cucullus may have up to four inconspicuous projections ranging in shape from bumps to spinelets, aedeagus has falcate apex (Fig. 38) (6n). In females, ostium bursae begins $\frac{1}{2}$ to $1\frac{1}{2}$ behind front edge of sternum, forward end of sterigma tapers gradually if at all, corpus bursae spicule bases nowhere fused into a sclerotized patch, signa unequal or subequal in size, forward and rear halves of papillae anales subsymmetrical in outline (Fig. 55) (7n). Forewing length of males 8.0 to 8.5 mm (16n), of females 8.0 to 8.5 mm (9n).

Comments. I examined adults from Arizona and San Bernardino Co. (Barnwell, New York Mts.), California (Leuschner, LACM, UCB, USNM). The study sample included paratypes (3n).

This species has not been adequately differentiated from any congener. It most resembles *P. habrosana*. It differs statistically in R_4 and R_5 origin, in size as well as symmetry of papillae anales, and in other ways. The frequency distribution of approximate, connate, and stalked R_4 and R_5 in *P. senatrix* is 2, 10, and 8, respectively, compared to 33, 21, and 2 in *P. habrosana* ($G_{adj} = 22.0$, $P\alpha < 0.005$). Length \times width maxima of one papilla analis ranges from 0.14 to 0.16 mm² in *P. senatrix* (7n) compared to 0.08 to 0.12

mm² in *P. habrosana* (12n). The respective means are 0.15 and 0.10, and the difference, 0.05, is significant with or without dividing individual values by forewing length to adjust for body size ($t \geq 8.4$, $P\alpha < 0.001$). Also, forewing pattern varies less in *P. senatrix* than in *P. habrosana*. The former has coarse-grained ashy gray forewings, with brown scaling in the terminal area obscure and visible only under magnification. The latter has fine-grained forewing coloration with brown scaling conspicuous in the dark areas and often elsewhere as well. The two species are allopatric, *P. senatrix* occurring in Arizona and southeastern California, and *P. habrosana* in many areas of California, but not in the southeastern part. The known larval hosts of *P. habrosana* do not occur in the range of *P. senatrix*, which indicates the latter has a different host or hosts.

Biology. The larval host is unknown. Adult capture dates range from 18 March to 6 May (25n).

Pseudexentera costomaculana (Clemens)

(Figs. 22, 39, 56)

Anchylopera costomaculana Clemens (1860:349) (lectotype female: North America, no date, No. 139, designated by Darlington 1947, forewing length 7.0 mm, wings illustrated by Miller 1973a, in ANSP).

Batodes bipustulana Walker (1863:316) (lectotype female: "N. Amer. . . . , Type" no date, genit. prep. No. 11635, selected by N. S. Obraztsov, designated here, forewing length 7.5 mm, in BMNH).

Exentera costomaculana; Heinrich (1923:178).

Pseudexentera costomaculana; McDunnough (1954:2), MacKay (1962:640).

Diagnosis. Forewing pattern (Fig. 22) varying little between or within sexes, pale areas near yellow ocher (123C) (60n). Forewing veins R_4 and R_5 approximate or separate at origin (27n). In males, valva constricted at $\frac{1}{2}$ distance between base and apex, valval length/cucullus length ratio 2.8 to 2.9, anal spine near middle of cucullus, aedeagus has unmodified apex (Fig. 39) (8n). In females, ostium bursae begins $\frac{1}{4}$ to $\frac{3}{4}$ its width behind front edge of sternum, forward end of sterigma tapers sharply, corpus bursae spicule bases fused on one side near ductus bursae into a lightly sclerotized patch, signa unequal in size (Fig. 56) (8n). Forewing length of males 6.5 to 8.5 mm (19n), of females 7.0 to 8.0 mm (13n).

Comments. I examined adults from Connecticut, Maryland, Michigan, Mississippi, New Hampshire, New York, North Carolina, Nova Scotia, Pennsylvania, and West Virginia (LACM, MSUE, NSM, UCB, UMMZ, USNM). The study sample included adults reared from *Hamamelis* sp. (prob. *virginiana* L.) (3n), and lectotypes of *P. costomaculana* and *P. bipustulana*. The larva was described by MacKay (1962).

Biology. The larva mines buds and folds leaves of *Hamamelis virginiana* L., and the pupa winters (McDunnough 1954, MacKay 1962, Ferguson 1975). Adult capture dates range from 9 April to 18 July (55n).

Pseudexentera virginiana (Clemens)

(Figs. 23, 40, 57)

Anchylopera virginiana Clemens (1865:512) (type unknown).

Exentera virginiana; Heinrich (1923:179).

Pseudexentera virginiana; Miller (1973a:224).

Diagnosis. Forewing pattern (Fig. 23) varying little between or within sexes, pale areas near drab (27) (46n). Forewing veins R_4 and R_5 approximate or separate at origin (22n). In males, valva constricted at $\frac{1}{2}$ distance between base and apex, valval length/cucullus length ratio 2.5 to 2.6, anal spine near middle of cucullus, aedeagus has unmodified apex (Fig. 40) (6n). In females, ostium bursae begins $\frac{1}{4}$ to $\frac{3}{4}$ its width behind front edge of sternum, forward end of sterigma tapers sharply, corpus bursae spicule bases fused on

one side near ductus bursae into a lightly sclerotized patch, signa unequal in size (Fig. 57) (8n). Forewing length of males 7.5 to 9.0 mm (9n), of females 7.5 to 9.5 mm (13n).

Comments. I examined adults from Connecticut, Maryland, Michigan, Mississippi, New York, Pennsylvania, and South Carolina (LACM, Mather, MSUE, UCB, UMMZ, USNM).

Biology. The larval host is unknown. Adult capture dates range from 7 March to 11 May (46n).

CONCLUSION

Only three adults, less than 0.3% of the number studied, were not satisfactorily resolved to any of the above species (UCB, CNC, MSUE). All three are different and may represent extreme variants of named species or single examples of unnamed species.

Of the 13 species previously recognized (Powell 1983), the names of eight appear valid, and the names of five are revised here. With the five new species described here, the number of *Pseudexentera* species now totals 17. Thirteen occur only east of the Great Plains, three occur only westward, and one is transcontinental. The following table of equivalents summarizes *Pseudexentera* species names here relative to those in Hienrich's (1923) revision:

Here	Heinrich
<i>cressoniana</i> (Clem.)	<i>improbana</i> (part)
<i>faracana</i> (Kft.)	<i>faracana</i> and <i>spoliana</i> (part)
<i>sepia</i> n. sp.	<i>spoliana</i> (part)
<i>hodsoni</i> n. sp.	<i>spoliana</i> (part)
<i>knudsoni</i> n. sp.	—
<i>haracana</i> (Kft.)	<i>haracana</i>
<i>oreios</i> n. sp.	—
<i>spoliana</i> (Clem.)	<i>improbana</i> (part)
<i>mali</i> Freeman	—
<i>oregonana</i> (Wlsm.)	<i>improbana oregonana</i>
<i>kalmiana</i> McD.	—
<i>maracana</i> (Kft.)	<i>maracana</i>
<i>vaccinii</i> n. sp.	—
<i>habrosana</i> (Heinr.)	<i>habrosana</i>
<i>senatrix</i> (Heinr.)	—
<i>costomaculana</i> (Clem.)	<i>costomaculana</i>
<i>virginiana</i> (Clem.)	<i>virginiana</i>

So far as known, larval host associations by plant family and number of *Pseudexentera* species are: Fagaceae (4), Rosaceae (2), Ericaceae (2), Juglandaceae (1), Salicaceae (1), and Hamamelidaceae (1). Larval hosts are unknown for six species. Fragmentary larval host information may be the single greatest deficiency hindering progress and strengthening of *Pseudexentera* taxonomy.

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