Two New Species of Geometrid Moths
(Lepidoptera: Geometridae: Ennominae)
from Cocos Island, Costa Rica

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ABSTRACT. Seventy-five species of Lepidoptera are recorded from Cocos Island, Costa Rica, including seven species in the Geometridae. Two of these species in the subfamily Ennominae, Oxydia hoguei new species and Phrygionis steeleorum new species, are described and figured. Oxydia hoguei appears to represent the sister species of the Caribbean O. lalanneorum Herbulot, 1985, on the basis of long-bipectinate antennae in the male and an associated long epiphysis and by the configuration and spination of the furca in the male genitalia. The two species can be separated by color pattern, shape of the furca, and presence of spines on the gnathos. Phrygionis steeleorum can be distinguished from its congeners by the absence of metallic silver scaling on the medial band of the forewing and in the marginal "eye-spot" of the hindwing. The two new species are endemic to Cocos Island. The traditional biogeographic hypothesis of species colonization of Cocos Island and the Galápagos Archipelago by vagrants from the Central and South American mainland is questioned.

(Additional key words: eastern Pacific, vicariance biogeography, Caribbean, Oxydia hoguei, Phrygionis steeleorum.)

INTRODUCTION
Cocos Island is a small (46.6 km² [18 mi²]) tropical eastern Pacific island situated midway between Costa Rica and the Galápagos Archipelago (5°32'57"N, 86°6'17"W), approximately 500 km (310 mi) from the Central American mainland. The island is wholly volcanic in origin; the highest point, Cerro Iglesias, reaches 849 m in elevation. The vegetation of Cocos Island is dense and luxuriant with a flora that includes over 200 species (Fosberg and Klawe, 1966). In a recent study of the entomofauna, Hogue and Miller (1981) reported approximately 75 species of Lepidoptera, including seven species of Geometridae. The purpose of this paper is to describe two of these species as new. Both appear to be endemic to this isolated island.

MATERIALS AND METHODS
Although Lepidoptera from Cocos Island were borrowed from all major United States institutions, only the collection of the Natural History Museum of Los Angeles County (LACM) contained specimens of the two new species of Geometridae described here. Holotypes are deposited at the LACM; paratypes are distributed among the following institutions: American Museum of Natural History, New York, New York; United States National Museum of Natural History, Washington, D.C.; The Natural History Museum, London, England (formerly British Museum [Natural History]); and Costa Rican Institute for Biodiversity, San José, Costa Rica.

Dissection techniques followed those presented by Powell (1964). Nomenclature for genitalia structures follows Klots (1970) and Rindge (1973). Figures of the genitalia were drawn with the aid of a microprojector. Measurements were made using a standard grid mounted in a dissecting microscope.

SYSTEMATICS

GEOMETRIDAE: ENNOMINAE

Oxydia hoguei new species

Figures 1-4, 6-9

DIAGNOSIS. Superficially, O. hoguei can be distinguished from its congeners by the conspicuous and contrasting yellowish ground color of the anterior half of the dorsal surface of the hindwing, bearing a large solid-blackish and well-marked subapical quadrate spot, and the course of the forewing postmedian line, which is posteriorly concave then abruptly convex at vein M₁ and recurved proximally to the costa (this line is straight and terminates near the apex or is angled more acutely on most, if not...
all, other *Oxydia*). On the basis of the long-bipectinate male antenna and long epiphysis (about as long as the tibia), *O. hoguei* appears to be most closely related to *O. lalanneorum* Herbulot, because all other species of *Oxydia* have short-bipectinate (*O. brevipecten* Herbulot) or simple antennae and short epiphyses (i.e., about one-half the tibia length). The male genitalia of *O. hoguei* are most similar to those of *O. lalanneorum* in the shape of the furca and the size and distribution of...
the minute brushlike spines that adorn it; in *O. hoguei* the furca is sigmoid and the marginal spines of the gnathos are stout and subequal, whereas in *O. lalanneorum* the furca is evenly curved and concave to the left and the marginal spines on the gnathos are slender and irregular. Females of the two species are easily distinguished by color pattern (the female genitalia of *O. lalanneorum* have not been described).

DESCRIPTION. Adult a large brightly patterned brown and yellow geometrid, with conspicuous bipectinate male antennae. The wing pattern is extremely variable; no two specimens are identical in maculation.
Male. Head: Compound eyes well developed, spherical. Antenna bicpicinate from distal end of each flagellar segment, the longest rami 4 times the length of segment, each ramus terminating in loosely arranged groups of about six setae; scape, pedicel, few basal segments of flagellum gray (concolorous with vertex), remainder of flagellum light brown. Labial palpus erect, second segment projecting beyond front, third segment short, oblique. Labial palpi, frons, and postvertex dark brown; vertex gray. Thorax: Legs simple, only the tarsi bearing spines. Epiphysis nearly as long as tibia. Hind tibia swollen, with long hairpencil arising basally, concealed in a longitudinal mesal slit. Thorax dark brown dorsally, paler ventrally; legs light brown, irrorated with dark brown. Abdomen: Sternite III with median transverse row of long bristlelike setae. Abdomen concolorous with thorax dorsally and ventrally, genital scaling paler. Hairpencils and eversible glands absent. Forewing: Length 25–28 mm (x = 26; n = 12); apex minutely falcate. Dorsal pattern elements fairly uniform but their expression and coloration extremely variable. Ground color mottled medium brown to blackish brown, costal region paler; costal, basal, and subterminal areas with obscure fine to coarse striations. Transverse lines usually conspicuous: antemelial line white, usually margined both proximally and distally with blackish brown, traversing wing in an irregular but nearly straight path from costa at 0.25 the distance from base to apex of wing, outwardly oblique to cell, then more or less perpendicularly through cell to inner margin at 0.4 the distance from wing base to apex of anal vein, somewhat sinuous: slightly concave through cell, and again through submedian fold, then abruptly convex from anal vein to inner margin. Postmedial line white, usually margined proximally with blackish brown, traversing wing from the base of vein R, (adjacent to costa at ca 0.66) then concave and obliquely distad to vein M, where it abruptly curves through 90° and is nearly straight to vein Cu, then gently concave to anal vein and convex to inner margin; postmedial line occasionally produced distally as a whitish patch in cell R4-M1, fusing with subterminal line to set off an irregular subapical costal patch of ground (or darker) color. Subterminal line dentate distally on veins, blackish brown, variable, sometimes macular or widened, most pronounced anterad of vein R, where it is blacker and edged distally with white, bearing an extra distally directed tooth in cell R4-R3; posteral of vein R, roughly parallel to postmedial line to vein Cu, then directed abruptly distad to tornus. A single black discal spot at origin of vein M1, often obscured by large irregular quadrate dark brown patch distad of spot. Fringe concolorous with wing. Hindwing: Outer margin minutely scalloped, angulate at vein M3. Dorsally, cell and inner margin mottled medium brown to solid brownish black, terminating abruptly at the postmedial line, ground color distad of postmedial line varies from dark brown to light brown or yellowish mottled and striate with brown; costal one-third of wing pale yellow, bearing a large black submarginal quadrate spot from (or near) costa to the M1 fold; postmedial line pale yellow to yellowish white, sometimes obscure, a posterior extension of the costal yellow and evident only from M1 nearly straight to inner margin at 0.75. Single black discal dot at base of M3 fold obscured by dark basal ground color. Fringe concolorous with wing. Ventral wing pattern similar, more mottled and less contrasting, ground color pale yellowish, black discal dots more prominent on both wings. Genitalia: As in Figures 6–8 (n = 3; drawn from C.L. Hogue prep. no. 78-87). Uncus long, slender, gradually curved, apex acute and simple. Gnathos strongly sclerotized with truncate anterior portion bearing a transverse row of 7–11 elongate marginal spines. Valva with costa sclerotized, unarméd, saccus weakly sclerotized, remainder of valva semimembranosus; mesal surface ventral of costa densely setose (other setae as figured). Juxta complex, asymmetrical: lateral margins convex, revolute (more pronounced on left side); an elongate digitate sinusus furcal lobe arising basally on left, projecting posteriorly to beyond base of costa of valva, bearing a strip of dense minute brushlike spines on the meso-dorsal surface for most of its length. Aedeagus stout, straight, apex acute ventrally; exserted vesica with a small central oval plate like cornutus bearing slender deciduous setae and two groups of uneven stout setose cornutus a compact basal group of 7–10, contiguous to apex of aedeagus, and a cluster of smaller ones near the center of the vesica.

Female. Head: As in male except antennae simple. Thorax: As in male, but hindtibia not swollen and hairpencil lacking. Abdomen: Unmodified. Wings: Falcate forewing apex more pronounced than in male; length 28–30 mm (x = 29; n = 3). Pattern as in male, dorsal ground color variable, but two of the three specimens with forewing ground color more uniform than in males, median area only slightly darker; discal dots conspicuous, postdiscal and subapical shades absent; ventral ground color variable, forewing pale apical patch prominent, hindwing with broad subterminal dark shade followed by a paler contrasting terminal band. Genitalia: As in Figure 9 (n = 2; drawn from J.W. Brown slide no. 314). Papillae anales (= ovipositor lobes) simple. Sterigma lightly sclerotized; ostium a sclerotized collar with an irregular quadrate sclerite posterior. Bursa copulatrix not differentiated into distinct ductus and corpus bursae; entire structure with numerous longitudinal creases; posterior one-half slightly more narrow, strongly sclerotized; ductus seminalis from attenuate stout lobe at posterior right side of ductus bursae. Signum a large hollow hemisphere, with numerous pointed projections laterally and internally, a few of them bifurcate.


REMARKS. Although Oxydia hoguei differs considerably from other species in the genus in general appearance and in the possession of bipectinate male antennae (a character state found in only two other recently described Caribbean species of Oxydia, O. lalanneorutn Herbulot, 1985, and O. brevipicten Herbulot, 1985), other features of adult morphology and genitalia (larged hindtibia, female genitalia on the ventral surface of abdominal segment III, male with hairpencil concealed in slit of enlarged hindtibia, female genitalia with hemispherical stellate signum, outer margin of hindwing angulate midway, and hindwing with subapical submarginal dark macula (evanescent to distinct). Putative synapomorphies for the genus include the distinctive furca and row of strong sclerotized spines on the gnathos. Other features of Oxydia Guéene, 1857, all of which may be found in one or more other genera of Ennominae—often present or absent within the same genus—include the following: male with row of bristles on the ventral surface of abdominal segment III, male with hairpencil concealed in slit of enlarged hindtibia, female genitalia with hemispherical stellate signum, outer margin of hindwing angulate midway, and hindwing with subapical submarginal dark macula (evanescent to distinct).

According to Rindge (1983) and Herbulot (1985), the character state of bipectinate male antennae represents the plesiomorphic condition. On this basis, O. hogue and O. lalanneorutn appear to represent the most primitive members of the genus. The unique configuration of the furca and associated brushlike spines represent a putative synapomorphy supporting the sister status of these two species.

Oxydia lignata (Warren, 1905) from the Galápagos Archipelago (Rindge, 1973) is a diminutive species with similarities to O. hogue and O. vesulia (Cramer, 1779) but distinct from both in several characteristics probably correlated with its small size (i.e., male forewing length = 14–16 mm): furcal lobe short, broad, and brushlike; unlobed vesica without distal ovate plate; and nearly unicolorous wing pattern.

ETYMOLOGY. We take great pleasure in naming this species after Charles L. Hogue, who was the first to collect specimens of this striking species in the course of his exhaustive survey of the entomofauna of Cocos Island.

[NOTE: We follow Herbulot (1977:40; 1983:34) and Ferguson (1983:97) in placing Oxydia in the Ennominae, characterized by the absence of a tubular M3 vein in the hindwing. We assume that Fletcher's (1979:149) assignment of Oxydia to the Oenochrominae was in error.]

Phrygionis steeleorum new species

Figures 5, 10, 11

DIAGNOSIS. Phrygionis steeleorum can be distinguished from all other species in the genus by the absence of metallic silver edging on the pale mediad band of the forewing and the absence of metallic scaling in the marginal "eye-spot" of the hindwing.

DESCRIPTION. Phrygionis steeleorum is a medium-sized gray-brown geometrid, with pale yellow antemedial and medial bands and a small marginal "eye-spot" on the hindwing between veins M3 and M4.

Male. Head: Scaling on frons smooth, short, fawn brown; scaling on vertex short, suberect, concolorous with frons. Antenna shortly bipectinate, inner rami approximately 0.5 the length of outer rami; basal 12 (more or less) segments of flagellum white-scaled ventrally, width of white line attenuating distally. Compound eyes well developed. Ocelli vestigial, minute, or apparently absent. Labial palpus short, extending slightly above ventral edge of frons.

Thorax: Fawn brown; legs unmodified. Abdomen: Fawn brown; paired subdorsal patches of elongate scales (hairpencil) from posterior edge of segment VI. Forewing: Length 15.2–17.2 mm (x = 16.2; n = 2). Ground color gray-brown; medial band narrow, diffuse, irregular, transverse, yellow, nearly perpendicular to costa at about half way from base, arched weakly to inner margin at ca 0.8 of distance from base, bordered proximally by irregular thin brown line; antemedial line yellow, irregular, excurred through cell and incurved over fold, bordered internally and externally with brown; antemedial line widest below costa and above inner margin, sometimes incomplete; minute yellow basal dash on costa, and two black basal dots, proximally edged with yellow, perpendicularly arranged between bases of CuP and second A. Fringe concolorous with wing. Hindwing: Outer margin angled at M3, without tail. Ground proximally concolorous with forewing, then brown from inner edge of postmedial line to termen. Postmedial line narrow, yellow, evenly excurred, followed by a metallic silver line, interrupted across the veins to form a series of linear spots. Marginal "eye-spot" between M2 and M3, extending slightly into cell M1-M2; a narrow (widen proximally and distally) yellow ring; proximal 0.5–0.66 of area inside of ring orange, distally black, and a similar smaller adjacent "eye-spot" (ca. 0.3 times as large in cell M2–CuP).

Genitalia: As is Figure 10 (n = 2; drawn from J.W. Brown slide no. 312). Uncus long, slender, with sclerotized attenuate tip. Sodiac long, narrow, curved,

Contributions in Science, Number 423

Brown, Donahue, and Miller: New Geometrids • 15
densely scaled. Gnathos narrow, arched, u-shaped. Valva long, narrow; a pair of longitudinal creases; ventral base with dense patch of fine non-deciduous setae. Transtilla a triangular plate bearing a distal pair of slender digitate processes. Aedeagus simple, straight; cornuti absent.

**Female.** *Head, Thorax, and Abdomen:* As in male except antenna simple and abdominal segment VI without hairpencil. **Forewing:** Length 15.6–17.5 mm ($\bar{x} = 16.5$; $n = 10$). As described for male. **Hindwing:** As described for male. **Genitalia:** As in Figure 11 ($n = 2$; drawn from J.W. Brown slide no. 313). Papillae anales (= ovipositor lobes) simple. Sterigma lightly sclerotized, membranous around ostium. Bursa copulatrix differentiated into moderately long narrow ductus and rounded corpus; junction of ductus and ostium indicated by sclerotized collar, open dorsally. Ductus bursae with numerous faint longitudinal creases; corpus bursae simple, unmodified, signa absent.


**REMARKS.** Prout (1933) listed 18 species in his treatment of *Phrygionis* Hübner, 1825, distributed from Florida to northern Argentina, with several species endemic to Caribbean islands (e.g., Jamaica, Cuba, Puerto Rico, Dominica, Martinique). Putative synapomorphies for the genus include male antenna minutely bipectinate in middle (i.e., unmodified at base and tip), legs long and slender, male with paired hairpencil from enlarged base of sixth tergite [lacking in *P. flavilimes* (Warren, 1907) and *P. sumptusaria* (Möschler, 1886)], hindwing angled or tailed at distal end of vein $M_3$, and frenulum absent. Figures 10 and 11 represent the first published genitalic illustrations of the genus. For comparisons of the adult moth with *P. argentata* (Drury, 1773), illustrations of the latter can be found.
in Holland (1903:pl. 44, fig. 35), Kimball (1965:pl. 23, fig. 20), and Covell (1984:286, pl. 56, fig. 3).

In the absence of comparative material from throughout the range of Phrygionitis, it is premature to speculate on the phylogenetic position of P. steeleorum within the genus.

ETYMOLOGY. We take pleasure in naming this species in honor of Richard, Elizabeth, and Patricia Steele, sponsors of the 1978 LACM expedition to Cocos Island.

DISCUSSION

In addition to the two new ennomines described here, five other species of Geometridae have been collected on Cocos Island, one in each of the following genera: Synchroa Guenée, 1857 (Geometrinae), Psiloides Guenée, 1857 (Larentiinae), Eu-pithecia Curtis, 1825 (Larentiinae), Idaea Treitschke, 1825 (Sternhinae), and Tricentrogyna Prout, 1932 (Sternhinae). Although these five species have not been studied adequately to render specific determinations (and even the generic assignments are equivocal for the Sternhinae), it is likely that one or more represent undescribed species. It is possible that all seven geometrids recorded from Cocos Island are endemic to the island. A similar situation is evident on the Galápagos Archipelago, where 12 geometrids have been recorded: nine (75%) are endemic; the other three are common widespread Neotropical species (Rindge, 1973), none of which has been recorded from Cocos Island. Cocos Island and the Galápagos Archipelago share only one genus, Oxydia, of which each supports a single endemic species.

In his discussion of the geometrid fauna of the Galápagos Islands, Rindge (1973) suggests that its depauperate nature may be attributable to the relatively limited vagility of many species of geometrids. He suggests that most of the resident species probably were blown out to the islands from the adjacent South and Central American mainland. Although it may seem likely that the fauna of the Central American mainland represents the species pools for the fauna of Cocos Island, phylogenetic affinities of some Cocos and Galápagos Islands insects with Caribbean congener suggests a more complicated biogeographic scenario than simple colonization by vagrants from the mainland. These islands may have been part of the Eastern Pacific-Caribbean vicariant track created by the Early Cenozoic breakup of the postulated proto-Antilles archipelago (Rosen, 1976:440). However, understanding of the tectonics of the region continues to evolve (Donnelly, 1988), and the place of Cocos Island within the regional tectonic events is unclear. Cocos Island is the summit of a seamount on the submerged Cocos Ridge, a proposed trace of the Galápagos volcanic hot spot. Cocos Island is about 2 million years old, although it lies on a portion of the ridge that is Middle Miocene in age (Castillo et al., 1988).

Thus the fauna of Cocos Island may represent a composite of vicariant relicts and recent invaders from the mainland. Such a hypothesis can be tested by careful phylogenetic analyses of taxa that occur on Cocos Island and the Galápagos Archipelago, the Central and South American mainland, and islands of the Caribbean. For example, Mathis and Wirth (1978) found Paracanace hoguei Mathis and Wirth, 1978 (Diptera: Canacidae), which is endemic to Cocos Island, to be the sister group to the species pair P. aicea Mathis and Wirth, 1978, and P. leban Mathis and Wirth, 1978, which are restricted to the West Indies. A similar biogeographic pattern is illustrated by Oxydia; the sister species of the endemic O. hoguei from Cocos Island appears to be O. lalanneorum from Guadeloupe Island in the West Indies. Further corroboration of this pattern awaits detailed revisions of taxa that have species endemic to Cocos Island, Central America, and the Caribbean regions.

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