SYSTEMATICS OF THE WEST INDIAN MOTH GENUS
HEURETES GROTE AND ROBINSON
(LEPIDOPTERA: LIMACODIDAE)

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Abstract.—The genus Heuretes Grote and Robinson, 1868, is revised. Heuretes was previously monotypic, comprised of H. picticornis Grote and Robinson, 1868, and known only from the Island of Saint Thomas, U.S. Virgin Islands. Monoleuca albicollis Forbes, 1930, known from Puerto Rico, is recognized as a junior synonym of H. picticornis. New records expand the range of H. picticornis to include the island of Tortola, British Virgin Islands. Heuretes daidaleos, new species, and H. divisus, new species, are described from the Dominican Republic. Phylogenetic analysis and transitional character states support placement of the new species in Heuretes. Heuretes appears to be closely related to other Caribbean genera Alarodia Moeschler and Leucophobetron Dyar.

Key Words: Puerto Rico, Virgin Islands, Hispaniola, Greater Antilles, systematics, cladistics, Caribbean, Zygaenoidea

In the Lepidoptera it is not uncommon for conspecific males and females to be described in different genera as different species. Epstein recognized Monoleuca albicollis Forbes (Limacodidae) as the junior synonym of Heuretes picticornis Grote and Robinson while examining a female syntype of the H. picticornis. Concurrently, fieldwork by Miller in the British Virgin Islands yielded good series of male specimens of a moth that matched the holotype of Monoleuca albicollis, known only from males. Later, Becker collected both males and females at the same locality in Puerto Rico, verifying the synonymy. These events, plus the finding of two new species from the Dominican Republic prompted us to revise and investigate the systematic placement of Heuretes.

This work is based primarily on specimens in the U.S. National Museum of Natural History (USNM), but we have also used material in or checked the collections of the American Museum of Natural History (AMNH), Bernice P. Bishop Museum (BPBM), British Museum (Natural History) (BMNH), Carnegie Museum of Natural History (CMNH), Natural History Museum of Los Angeles County (LACM), Museum of Comparative Zoology, Zoologisches Museum der Humboldt Universitaet (ZMHB), Zoologische Sammlungen des Bayerischen Staates, and V. O. Becker private collection (VOB). Color descriptions follow Smithe (1975).

Heuretes Grote and Robinson

Type species.—*Heuretes picticornis* Grote and Robinson, by monotypy.

Diagnosis.—Small moths, salmon to gray forewing and thorax, usually light-colored hindwing and abdomen. Conspicuous oval or quadrate spots present (at least) on male forewing apex or middle of inner margin. Male anterior thorax with dorsal collar of buff or white scales. Foreleg dark, with coxa and femur scarlet orange or dark brown. Mid- and hindlegs light colored. Hind tibia with two pairs of spurs. Male antenna bipectinate to tip or near, with light-colored scales in contrast at apex.

Discussion.—Presumed synapomorphies of *Heuretes* within Limacodidae include the scale patterns on the body and wings. These patterns include a distinct collar behind the head in males, dark-scaled forelegs in contrast to light mid- and hindlegs, and light-colored scales at the apex of the antenna in contrast to dark segments on all other segments or only near the apex.

Although found in other limacodid genera, the forewing radial vein pattern in *Heuretes*, R3+R4 branched off R2, may be independently derived. Presumed sister genera *Alarodia* Moeschler, *Leucophobetron* Dyar and *Phobetron* Huebner, possess wing veination pattern in which R3+R4 branch off R5 or nearby—the primitive condition according to Brock (1971).

*Heuretes picticornis* Grote and Robinson

Figs. 1, 2, 5, 6, 9


Diagnosis.—Small moths with either salmon or dark-brown forewings. Front legs orange. Pale-form males have antemedian and postmedian bands on forewing visible, cream-colored hindwing; dark-form males with forewing bands not visible, either cream or dark-brown hindwing. Both male forms with conspicuous quadrate white patch medially along inner margin. Female without white patch. Male antenna broadly bipectinate, becoming unpectinate with branches abruptly shortening toward apex, scarlet-orange scales on shaft. Uncus unusually short, baglike, with lateral socii; gnathos S-shaped laterad. Valva bifid distally; acrodeagus straight basally, reaching end of valva, upturned distally.

Adult male (Fig. 1).—Forewing length 6–7 mm (one aberrant reared male, 8 mm).

**Head:** Frons mostly white. Vertex cream colored (54) (= color code in Smithe 1975). Antenna ca. half length of forewing; bipectinate, maximum width about 5 x length of a segment, slightly tapering to near apex, then abruptly short. First two short apical segments bipectinate, remaining nine segments short, unpectinate, and bristly. Scales on shaft scarlet orange; scales on apex and pectinations buff (124). Labial palpus porrect, extending past frons, covered with scarlet-orange scales. Haustellum coiled, longer than basal segment of labial palpus.

**Thorax:** Dorsum with white scale bundle behind head on basal one-fifth, remainder matching forewing. Foreleg with coxa and femur scarlet orange, tibia and tarsus burnt orange (116) with dark bands distally. Midleg and hindleg a lighter cream color, with brushlike scales dorsally on tibia and tarsus. Midtibia with one pair of spurs and hindtibia with two pairs. Forewing R3 and R4 nearly fused, arising from R2 (Fig. 5). Dorsal surface of forewing in two forms, either salmon or dark brown. Diffuse postmedian and antemedian bands of dark-brown scales visible only in pale morph (Fig. 1). These bands connect, with mostly dark-brown scales from wing base to tornus, below discal cell. Conspicuous white quadrate patch on middle of inner margin, smaller dark
spot where M2 and M3 arise from discal cell. Margins orange scarlet, preceded by dark brown scales on fringe and costal margin, scattered orange scales along veins. Ventral forewing with inner margin cream colored, base of costa scarlet, otherwise burnt orange. Dorsal hindwing cream colored, or dark brown, outer margin fringe with a few dark scales. Salmon-forewing morph with pale hindwing, dark-forewing morph with either pale or matching dark hindwing. Ventral hindwing warm buff (118) with hint of orange, more cream color along inner margin and fringe.

Abdomen: Cream colored. Genitalia as in Fig. 6. Valva bifid about three-fourth distance from base. Gnathos simple, with gently undulating margins. Uncus short, expanded ventrally above gnathos, caudal end of uncus divided. Socii forming lateral pockets with setae. Aedoeagus straight and about same length as valva; stout basally, but beyond gnathos, becoming narrow, upturned 90° distally.

Adult female (Fig. 2).—Forewing length 7.5–8.0 mm.

Head: Frons salmon colored (106). Vertex cream colored. Antenna short, ca. one-
third length of forewing, bristly, with short pectinations, curved at tip, cream colored to near apex, dark-brown scales and lighter scales distally, nearly buff. Palpus shaped as in male, covered with warm-buff and salmon scales.

Thorax: Dorsum with brown scales, without white scale bundle of male. Legs colored as in male. Forewings as in male dark morph, less scarlet underneath, with white scale patch absent. Discal spot faint. Only pale hindwings known.

Abdomen: Genitalia as in Fig. 9. Bursa copulatrix short, with ductus seminalis broadly connected from base to middle of corpus bursae. Signum absent. Lobes of papillae anales disk shaped, irregularly toothed on margins, and covered with setae.

Types.—Lectotype female, here designated (ZMHB), and paralectotype female (AMNH) (H. picticornis); Holotype male, AMNH (M. albicollis).

Type localities.—[U.S. Virgin Islands], [Island of] Saint Thomas (H. picticornis); Puerto Rico, Coamo Springs (M. albicollis). Hosts.—Buchenavia capitata (Vahl) Eichl. (Combretaceae) (USNM); Byrsonima coriacea (Sw.) DC (Malpighiaceae) (Martorell 1948: 549, as B. spicata (Cav.) Rich.; Wolcott 1951: 746, as B. spicata; Martorell 1976); Cedrela odorata Linn. (Meliaceae) (Wolcott 1951: 746, as C. mexicana Roem.; Martorell 1976); Montezuma speciosissima Sessé & Moc. (Malvaceae) (Wolcott 1951: 746; Martorell 1976); Swietenia mahagoni (Linn.) Jacq. (Meliaceae) (Martorell 1948: 549, 1976).

Immature stages.—This description of the previously undescribed larva is from an exuvium found inside a cocoon associated with an adult male ("Hopk. US 33101K," USNM). The exuvium was softened in 10% KOH and stored in glycerin (descriptions of tubercles are vague because precise interpretation was difficult).

Final instar: No prolegs or crochets, subdorsal row of tubercles well developed (T2–3, A2–9), extending to near middorsum, lateral tubercles short. Most subdorsal tubercles with long, filamentous hairs, maximum length ca. 1 mm, dark brown and light colored, with short lateral branches. Second or third subdorsal tubercle from anterior end with dense coat of short, filamentous hairs interspersed with long hairs, appearing darker than others. Unbranched urticating setae well developed on dorsal, basal portion of tubercles. Middorsal strip with small "skin spines."

Cocoon: Ovate, about 5 mm long, 4 mm wide, 4 mm high. Typical circular emer-

Figs. 6–8. 6, Heuretes picticornis, male genitalia: a) lateral view, right aspect (dotted outline indicates position of aedoeagus) (USNM 28109); b) aedoeagus (USNM 28025); c) ventral view of slide mounted specimen with aedoeagus removed (g = gnathos; s = socius) (USNM 28025) (scale = 0.5 mm). 7, Heuretes daidaleos, male genitalia: a) lateral view, left aspect (USNM 28110); b) aedoeagus (USNM 28358); c) ventral view of slide mounted specimen with aedoeagus removed, right valva (p = valval process) (USNM 28358) (scale = 0.5 mm). 8, Heuretes divisus, male genitalia: a) lateral view, right aspect (CMNH); b) aedoeagus (CMNH) (scale = 0.5 mm).
Fig. 9. *Heuretes picticornis*, female genitalia (ZMHB lectotype): a) lateral view; b) ventral view (c = corpus bursae, d = ductus seminalis; c) papillae anales (scale = 0.5 mm).

gence hatch at end. Whitish, mottled with brown, surface smooth and hard.

Flight period.—December to August.

Distribution.—Puerto Rico and the Virgin Islands, above 360 m.

Material examined.—65 males and 5 females. PUERTO RICO: Coamo Springs, 5-7 June 1915 (AMNH, holotype of *M. albicollis*); El Semil, near Villabla, 1700 feet [520 m], 10-V-1940, W. A. Hoffman (USNM); El Verde Field Station, Luquillo Experimental Forest, 435 m, 29-XII-1970 to 21-I-1971, C. P. Kimball (USNM); Hotel Barranquitas, Barranquitas, 650 m, 22-26-II-1971, Kimball (USNM); Maricao, 11-14-VIII-1987, V. O. Becker (VOB); Maricao Fish Hatchery, 23-XII-1962, P. & P. Sanger (USNM); Reserva Forestal Guajataca, 360 m, 18-28-III, 14-20-IV-1971, Kimball (USNM); Patillas, [Sierra de Cayey, ca. 20 km NE Campamento Real], 590 m, 5-25-VIII-1987, Becker (USNM, VOB); Villabla, ex *Buchenavia capitata*, Hopkins no. 33101K, 1-V-1940 (USNM); U.S. VIRGIN ISLANDS: [Island of] Saint Thomas, [no further data] (ZMHB, lectotype of *H. picticornis*; AMNH, paralectotype); BRITISH VIRGIN ISLANDS: [Island of] Tortola, Mount Sage National Park, 480 m, 7-8-VII-1985, S. E. & P. M. Miller, 22-24-VII-1986, S. E. Miller & M. G. Pogue, 13-15-VII-1987, S. E. Miller & V. O. Becker, ultraviolet light trap in “aridulate rain forest” (USNM, BMNH, CMNH, LACM, VOB, BPBM).

Discussion.—The scarlet orange front coxa and femur in both male and female led to uncovering the synonymy between
Heuretes picticomis and Monoleuca albicol- lis. Collection of males and females at the same localities in Puerto Rico by Becker (see above) confirmed this finding, since the two types are from separate, though neighboring, islands of Saint Thomas and Puerto Rico.

This species is restricted to the Puerto Rican Bank, where it occurs between 360 and 2,500 m. Martorell (1948: 549) [as M. albicollis] considered it "fairly common" on Puerto Rico. In the United States Virgin Islands the species has not been recorded since the original description of specimens from Saint Thomas. This could be due to lack of subsequent collecting and destruction of native forest. We record it for the first time from the British Virgin Islands, from the moist forest on the top of Tortola (termed "aridulate rain forest" by D'Arcy 1967: 392). The forest in Sage Mountain National Park on Tortola appears to be the only suitable habitat in the British Virgin Islands (see also Lazell and Jarecki 1985). The species was not found in ultraviolet light surveys on Virgin Gorda and Guana Islands.

This distribution pattern makes sense biogeographically, because the islands of the Puerto Rican Bank have been extensively connected within recent geologic time. The principal islands of the Virgin Islands (except Saint Croix) lost their connection with each other and with Puerto Rico only about 8000 to 10,000 years ago, due to eustatic rise in sea level (Heatwole et al. 1981).

**Heuretes daidaleos, New Species**

Figs. 3, 7

Diagnosis.—Small moth with speckled gray-brown forewing without fascia, hindwing pale buff. Small buff-colored oval spot on forewing apex. Male antenna bipectinate to apex and gently tapering; light scales throughout except dark brown subapically. Uncus oblong, tapered to well sclerotized, clawlike tip. Valvae entire, slightly asymmetrical, curvilinear process on costal base and tegumen. Aedoeagus only about half length of valvae, with short obliquely curved process at distal end. Adult female and immature stages unknown.

Adult male (Fig. 3).—Forewing length 5.5–6.0 mm.

**Head:** Frons buff colored (124), infuscated with gray-brown scales. Vertex cream colored (54). Antenna length as in male *H. picticornis*, but pectinations relatively short and bipectinate to tip. Pectinations at maximum ca. 3 × length of a segment, gently tapering apically. Shaft and pectinations with pale-buff scales except distal fourth with dark-brown scales, buff on last two. Labial palpus and haustellum similar to *H. picticornis* except palpus buff scaled.

**Thorax:** Dorsum directly behind head with narrow band of burnt orange scales
(116), followed by wider collar of buff scales in basal seventh, remainder matching forewing. Foreleg as in *H. picticornis*, bands of dark scales alternating with buff rather than scarlet orange. Midleg, hindleg and thorax mostly buff ventrally. Tibial spurs as in *H. picticornis*. Forewing R veins as in *H. picticornis*, but wing shape differs. Outer angle more rounded, extending posteriorly, with inner margin short. Dorsum with dark gray-brown scales speckled over glaucus (79–80) to pale-buff scales; only one color morph known. Apex with small, conspicuous, pale-buff oval spot (0.7 mm long). Fringe dark gray brown; costal margin yellow orange. Venter with dark scales in discal cell and along outer margin; buff on inner margin and apex. Hindwing with basal and fringe scales buff, hint of gray toward outer margin.

Abdomen: Buff colored. Genitalia as in Fig. 7. Valvae entire, digitate and acuminate distally, slightly asymmetrical, left valva larger. Narrow, curvilinear process articulated with base of costa and vinculum. Uncus oblong, simple, tapering to downcurved and well-sclerotized tip. Gnathos relatively short, not reaching end of uncus. Aedeagus short, ca. half length of valvae; globular at base, with short, curved hook pointing obliquely upward from left to right at distal end.

Type.—Holotype male, USNM.
Type locality.—Dominican Republic, Dajabon Province, Rio Massacre, Balneario Don Miguel, 7 km SW Dajabon, 40 m elevation.
Flight period.—May and July.
Distribution.—Known only from the Dominican Republic.
Material examined.—Five males from the type locality (holotype and 4 paratypes) collected 26-V-1973 by D. & M. Davis (USNM, BMNH).

Etymology.—*Daidaleos* (Gr.) means dappled or spotted, descriptive of the forewing in this species. The unlatinized nomen is treated as indeclinable in accordance with Article 31b in the International Code of Zoological Nomenclature (1985).

Discussion.—*Heuretes daidaleos* shares several male genitalic character states with *Alarodia* and *Leucophobetron* Dyar, including valval asymmetry and a costal process, absent in its congener *H. picticornis*. However, phylogenetic evidence and transitional character states in another new species below support placement of *H. daidaleos* in *Heuretes*. The costal process on the valva is believed to be plesiomorphic with respect to *Heuretes*, found in *Phobetron*.

Although the simple, oblong shape of the uncus of *H. daidaleos* appears to be closer to the limacodid groundplan than that found in *H. picticornis* or *Alarodia*, it may represent the loss of the dorsal process found in the latter group.

*Heuretes divisus*, New Species
Figs. 4, 8

Diagnosis.—Male genitalic characters diagnostic (see below). Known from one male specimen.

Adult male (Fig. 4).—Forewing length 5.5 mm.

Head: Frons and vertex dark brown. Antenna length as in other *Heuretes*, bipectinate to near the tip, pectinations long as in *H. picticornis*, gently tapering apically. Shaft and pectinations with dark-brown scales throughout, buff on last two. Labial palpus similar to other *Heuretes*, the former dark scaled.

Thorax: Dorsum with buff scales behind head (remainder undetermined). Foreleg with dark-brown scales. Midleg, hindleg, and ventral thorax mostly buff. Tibial spurs as in other *Heuretes*. Forewing R3 and R4 fused, arising from R2. Dorsum appears to have gray and buff scales, with salmon scales on anterior discal cell (badly rubbed).

Abdomen: Buff colored. Genitalia as in Fig. 8. Valva deeply divided less than half its length from base into two thin digitate arms (hence the name *divisus*), the one ventrad slightly shorter. Process articulated with
base of costa and vinculum greatly reduced compared to *H. daidaleos*. Tegumen narrow with long setal brush near costa. Uncus simple, similar to *H. daidaleos* though broader. Gnathos undulated as in *H. picticornis*, but with knoblike structure ventroproximal to apex. Aedoeagus similar to *H. picticornis*, though relatively shorter and broader.

Distribution.—Known only from the Dominican Republic.

Material examined.—One male (holotype) from Pedernales Province, La Abeja, 38 km NNW Cabo Rojo, 18°09'N, 71°38'W, 1250 m, 15-VII-1987, J. E. Rawlins & R. L. Davidson (CMNH).

Discussion.—Male genitalic character states in *Heuretes divisus* are plausible transitions between character states of *H. daidaleos* and those in rather atypical *H. picticornis*. The curvilinear process at the base of its costa, much reduced compared to *H. daidaleos* and absent in *H. picticornis*, appears to be functionally replaced by the coastal arm of the deeply cleft valva. The valva in *H. picticornis*, in turn, may be derived from fusion of arms, as in *H. divisus*, to near the distal end. Other character states in *H. divisus* appear intermediate between *H. daidaleos* and *H. picticornis*, including shapes of uncus and gnathos, and relative size of aedoeagus. Shape of the aedoeagus more closely resembles that of *H. picticornis*.

Relationships of *Heuretes*

Forbes (1930) suggested that *Monoleuca albicollis* [*H. picticornis*] "might be better placed in *Protalima,*" but included it in *Monoleuca* Grote and Robinson based on wing pattern. Similarity in male antennal pectinations between the type species, *Monoleuca semifascia* Walker, and *M. albicollis*, may have also influenced Forbes' generic placement. Forbes (1930) considered *M. albicollis* [*H. picticornis*] to be a "primitive" *Monoleuca* based on the "nearly united" forewing R3 and R4 (R3 and R4 are fused in North American *Monoleuca*).

Other than Forbes' treatment (1930, as *Monoleuca*), the placement of *Heuretes* has remained uncertain. Grote and Robinson (1868: 190) considered *Heuretes* near *Tortricidia* Packard. Dyar (1905: 382) stated the "generic position [of *Heuretes*] is uncertain."

*Heuretes* is not congeneric with *Monoleuca* as the latter is presently defined, nor is *Heuretes* phylogenetically related to the *Parasa* complex of Epstein (1988) where *Monoleuca* belongs. Characters of *Monoleuca* (sensu stricto) that distinguish it from *Heuretes* are: 1) spiny type larva similar to those found in *Euclea* (Epstein 1988), 2) fused forewing R3+R4 arising from R5, rather than R2 as in *Heuretes*, 3) haustellum absent, 4) labial palpus stout, upturned, 5) signum present, and 6) one pair of hind tibial spurs.

*Heuretes* shares presumed apomorphic larval character states with *Alarodia* (only *A. slossoniae* known), *Phobetron*, and *Isochaetes* Dyar (Dyar 1899: 244); the "tropic hairy eucleids" of Dyar (1899). This group is defined by tubercles that are strongly developed subdorsally and weakly developed laterally, and branched, filamentous hair-like setae. Larval *Phobetron* differ from *Heuretes* and *Alarodia* by having tubercles: 1) with short and stout hairs only, 2) without unbranched urticating setae, and 3) that are deciduous, later incorporated into the cocoon. Immature characters shared between *Heuretes* and *Alarodia* include: 1) larval tubercles with long filamentous hairs, 2) short, unbranched urticating setae, and 3) white cocoons. Socii found on the uncus in *Alarodia slossoniae* (Packard) and *H. picticornis*, absent in all other taxa in both genera, are independently derived according to the phylogenetic analysis below.

*Leucophobetron argentiflava* (Geyer) from Cuba, the type species of *Leucophobetron*, is probably congeneric with *Alarodia* (Epstein in prep.). *Leucophobetron* includes one other species from Colombia, *Leucophobetron punctata* (Druce). Though we have not
examined it, *L. punctata* is of uncertain family status (Dyar unpublished, Nat. Agri. Libr.; Becker and Epstein in press). There are a number of taxa of this general description in several moth families in South American. Whereas, no other white species of Limacodidae are reported in the neotropics outside of the Caribbean basin.

A detailed phylogeny of the genera related to *Heuretes* and resolution of generic limits of *Alarodia* and *Leucophobetron* are beyond the scope of this paper. However, we present the results of a preliminary phylogenetic analysis that we undertook to determine the correct generic placement of *H. daidaleos* (*H. divisus* was not included because it was discovered after completion). The analysis was performed using McClade, with *Phobetron* as the outgroup. *Alarodia, Leucophobetron* (based on the type species only), and two species of *Heuretes* were the other terminal taxa. Eight characters with a total of 21 states were used in the analysis, and multistate characters were ordered with morphoclines.

*Heuretes daidaleos* was found to be the sister species of *H. picticornis* in two equally parsimonious cladograms (including Fig. 10, consistency index of .93). Figure 10 and a cladogram with *Alarodia* as sister group to *Leucophobetron* + *Heuretes* are supported biogeographically, since the Puerto Rican Bank (*H. daidaleos*) is closer to Hispaniola (*H. daidaleos*) than it is to Cuba (*Leucophobetron* and *Alarodia*), or Jamaica (*Alarodia*).

*Alarodia* (Dyar 1897, 1935) and now *Heuretes* are the only genera in Limacodidae (ca. 300 neotropical species), with more than one described species in the Greater Antilles (Becker and Epstein in press). Two undescribed species, one of uncertain placement (not in *Alarodia* or *Heuretes*) from Cuba and the Bahamas (USNM, AMNH, CMNH), the other in the *Perola* complex from the Dominican Republic (CMNH), indicate that the limacodid fauna may increase with future examination. Limacodid genera *Perola* Walker and *Semyra* Walker have one described species each in the Lesser Antilles. There is one undescribed species in the *Natada* complex in this region.

Poor dispersal ability of Limacodidae (Wood 1984), and related families Dalceridae (Miller in press) and Megalopygidae, may explain their low species richness in the West Indies. Dalceridae (85 spp.) and Megalopygidae (>200 spp.), mostly neotropical families, have only one West Indian species each.

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