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HIDDEN JEWEL: *CRYPTOCOSMA* LEDERER (LEPIDOPTERA: PYRALOIDEA: CRAMBIDAE), ITS TRANSFER TO THE GLAPHYRIINAE, AND THE SYNONYMY OF *GUYANYMPHULA* HEPPNER

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Abstract.—Based on morphological characters, *Guyanymphula cayennensis* Heppner, 2015, **new synonym,** the type species, is synonymized with *Cryptocosma perlalis* Lederer, 1863, the type species. As a result, *Guyanymphula* Heppner, 2015, **new synonym,** and *Cryptocosma* Lederer (1863) are subjective generic synonyms because they are not based on the same type specimen, and as the oldest name, *Cryptocosma* Lederer has nomenclatural priority. *Cryptocosma* is transferred from the Acentropinae to the Glaphyriinae with the new tribe, Guyanymphulini Heppner, created for this genus. Lectotypes are designated for the type species, *Cryptocosma perlalis* Lederer, and *Cryptocosma pigrissima* Dyar (1914), **revised status**, which is removed from synonymy with *C. perlalis*. We provide illustrations of type specimens and a new diagnosis for the genus. We discovered new country records for *C. perlalis* from Colombia, Costa Rica, Ecuador, Guatemala, Guyana, Peru, and for *C. pigrissima* from Venezuela. The morphology and distribution of reduced adult mouthparts in the Glaphyriinae and the cataclystiform pattern, or metallic spots, along the hindwing outer margin in crambid subfamilies is discussed.

Key Words: Acentropinae, distribution, mouthparts, cataclystiform wing pattern, Brazil, Costa Rica, Panama, Venezuela

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Recently, while working on the Acentropinae (Lepidoptera: Pyraloidea: Crambidae) of the Área de Conservación Guanacaste (ACG), we identified specimens collected in Costa Rica as *Cryptocosma perlalis* Lederer and recognized that this is the first record of *Cryptocosma* in Costa Rica. *Cryptocosma* was established by Lederer (1863) for the single species *C. perlalis* Lederer based on four male specimens from "Brazil?." Lederer used external characters, primarily of the head, to describe the genus. He especially noted the pectinate antennae, which he figured along with a habitus of *C. perlalis*. Nearly half a century, later, Dyar (1914) described a new genus, *Chalcoelopsis* Dyar in the Schoenobiinae for the single species, *C. pigrissima* Dyar, based on a single male and 47 female specimens from various localities in Panama. Dyar noted the absence of a proboscis or "aborted mouth parts" as a notable morphological structure for concluding *C. pigrissima* did not belong in *Cataclysta* Hübner (Acentropinae) and warranted placement in a new genus. Almost a century after Dyar, Munroe (1995) placed *Cryptocosma* in the Acentropinae and synonymized *Parapoynx obscuralis* (Möschler, 1881) from Surinam, *Cataclysta trilinealis* (Warren, 1889) from Brazil, and *C. pigrissima* with *C. perlalis*. Munroe (1995) did not provide characters to support these synonymies or note in his checklist that *C. pigrissima* was newly synonymized. Recently, Heppner (2015) described a monotypic genus, *Guyanymphula cayennensis* Heppner, from French Guiana in the Acentropinae noting the unusual bipectinate antennae.

The taxonomic status of the genera and type species mentioned above are assessed in this paper and we discuss the difficulty in evaluating derived characters of the head, such as reduced mouthparts, and the presence of a cataclystiform pattern or spots in the hindwing in various crambid subfamilies. Further, we test the preliminary hypothesis that *Cryptocosma* belongs in the Glaphyriinae, not the Acentropinae, contrary to Munroe (1995). Although the images of modern specimens of the adult habitus and genitalia were very good in Heppner (2015), we discuss observational, methodological, and nomenclatural issues with this paper, including the creation of a new tribe, Guyanymphulini, without providing characters to define the nominate tribe Nymphulini Duponchel, and not using the currently accepted family name, the Crambidae.

MATERIALS AND METHODS

We conducted a preliminary survey of the Glaphyriinae literature and searched for descriptions that included reduced mouthparts, specifically the labial palpi, proboscis, and maxillary palpi (Munroe 1964, Munroe 1972b, Solis and Adamski 1998), in order to compare *Cryptocosma* to other genera in the Glaphyriinae in a more in-depth manner. The mouthparts, as well as the presence or absence of ocelli and pectination of antennae, of specimens belonging to glaphyriine genera were studied using a Wild 3Z to determine the number of segments in the labial and maxillary palpi of both males and females, whether ocelli were present or absent, and if the proboscis was reduced, specifically measuring its length in comparison to the labial palpi. A male and a female head (♂ USNM slide #115921, ♀ USNM slide #115922) of *C. perlalis* from Brazil (Figs. 9–15) were dissected, soaked in 10% potassium hydroxide, washed in water, not stained, and then mounted in Euparal (Robinson 1976). Genitalia of specimens externally identified as *C. perlalis* from various South and Central American countries were dissected (See Material Examined below). Abdomens were soaked in 10% potassium hydroxide and washed in water, stained with Chlorazol black, and slide mounted in Euparal (Robinson 1976). Morphological structures were photographed using a Visionary Digital® imaging system and prepared for publication using Adobe Photoshop®. Photographs of type specimens were not modified. The handwritten label of Lederer was confirmed using Horn et al. (1990).

Primary type specimens were either borrowed or images taken by MAS and observed. The syntype series of *C. pigrissima* was studied and dissected. Types and other specimens studied are deposited in The Natural History Museum, London, United Kingdom (BMNH), Museum für Naturkunde der Humboldt-Universität, Berlin, Germany (ZMHB), Naturhistorisches Museum, Vienna, Austria (NHMV), McGuire Center for Lepidoptera and Biodiversity, Gainesville, Florida, United States (MGCL), National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM), and Museo Nacional de Costa Rica, San José, Costa Rica (MNCR-A).

RESULTS

Based on comparative morphological studies, we discovered that *Cryptocosma* does not belong in the Acentropinae, and we transfer it to the Glaphyriinae herein. Guyanymphulini is, therefore, available in the Glaphyriinae for future tribal designation; although tribes are not currently utilized in the Glaphyriinae. *Guyanymphula cayennensis* Heppner is synonymized with *C. perlalis*. As this is the type species of *Guyanymphula*, we also synonymize the genus with *Cryptocosma*. Additionally, we designate lectotypes for the type species *C. perlalis* Lederer, and *C. pigrissima* (Dyar), which is removed from synonymy with *C. perlalis.*

Crambidae

Glaphyriinae

Guyanymphulini

Cryptocosma Lederer (from Acentropinae)

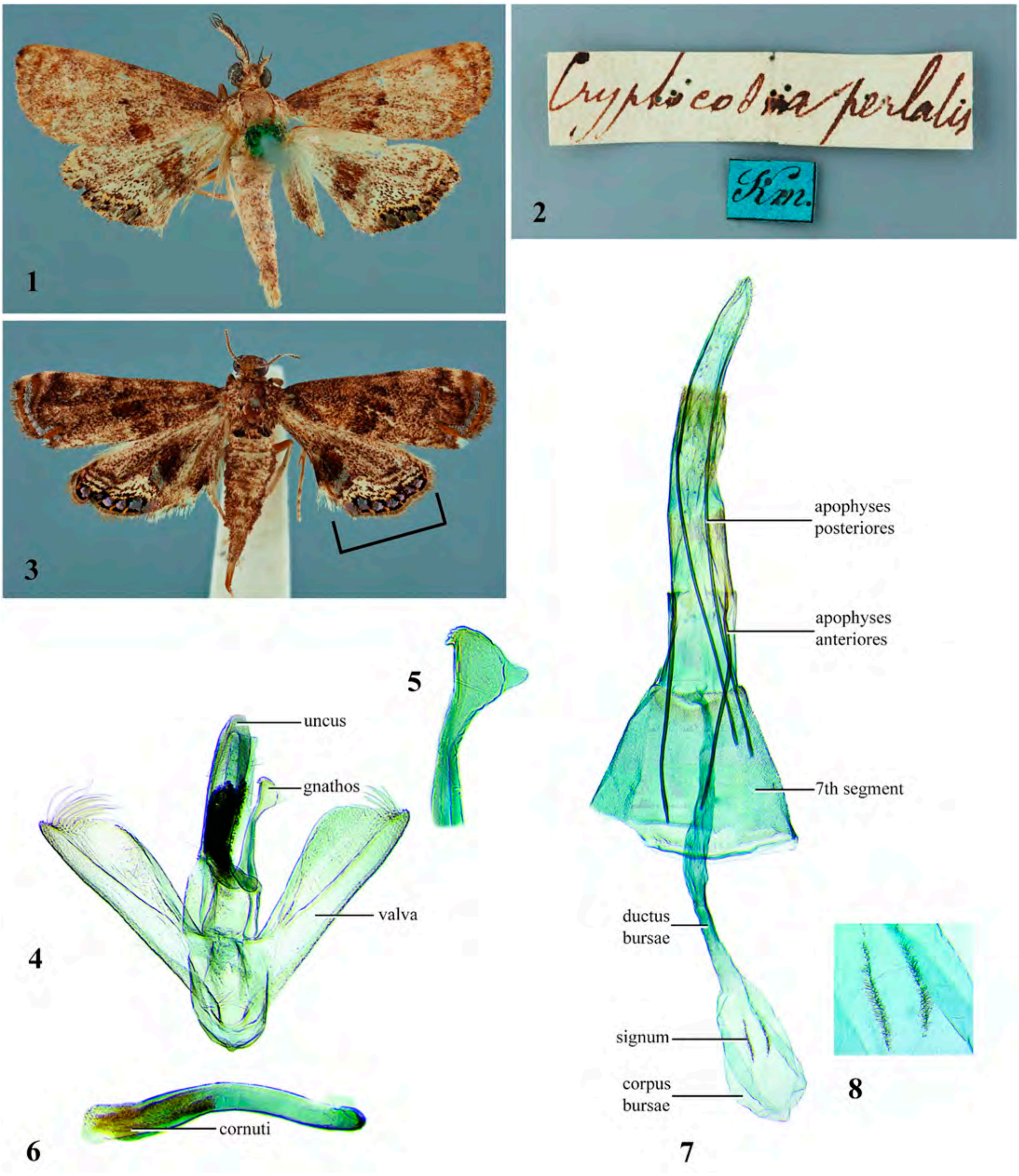
(Figs. 1–23)

Cryptocosma Lederer, 1863: 346 (original description). Type species: *Cryptocosma perlalis* Lederer, 1863: 347 by monotypy. Type locality: "Brazil?"

Chalcoelopsis Dyar, 1914: 314. Type species: *Chalcoelopsis pigrissima* Dyar, 1914: 314 by original designation (originally published as *Chalcoëlopsis*, an incorrect spelling under the ICZN Article 32(c)(i) (Fletcher and Nye 1984) (new synonym by Munroe 1995, but not stated)

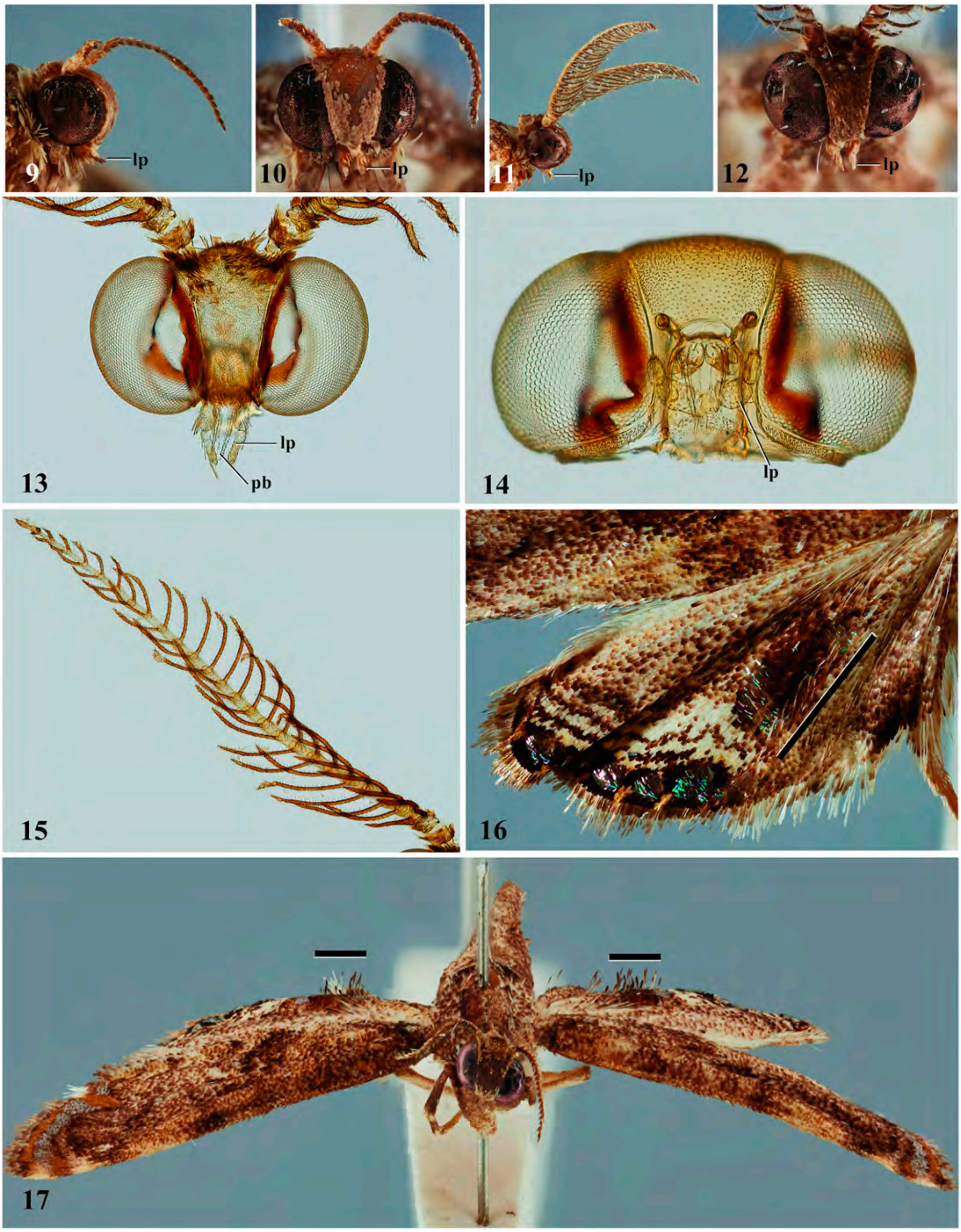
Guyanymphula Heppner, 2015: 48. Type species: *Guyanymphula cayennensis* Heppner, 2015: 49 by original designation, **new synonym**

Diagnosis.—*Head* (Figs. 9–15): Ocellus absent; chaetosemata a tuft of radiating scales extending posteriorly from the antennal base to the posterodorsal side of the eye, larger than in any other genera of Glaphyriinae, but absent in most genera; female antennae serrate and prismatic, male antennae bipectinate, a few lamellae expanded at tip, bipectinate antennae not known to occur in other glaphyriine genera; labial palpi (lp) reduced, with only 2 segments; proboscis (pb) reduced, only as long as labial palpi; maxillary palpus absent in the female, present as one segment in the male, more like stubs. *Abdomen:* With crambiform tympanal organs; praecinctorium simple, scoloparia absent, zona glabra tympani with a Y-shaped sclerotization, bulla tympani ovate, longer than wide, segment VIII with sclerotizations, tergite with a shallow Y-shaped sclerotizaton, sternite with an inverted U. *Male genitalia* (Figs. 4–6, 20–22): With the uncus subequal in width its entire length and rounded at apex not known to occur in other glaphyriine genera, and gnathos with a broad, triangular apex with thorn-like membranous projections apically (variable or non-existent in glaphyriine taxa), not evident in genitalia preparations if not mounted laterally (see Figs. 4–5, 20, 22), phallus with cornuti tiny, sclerotized



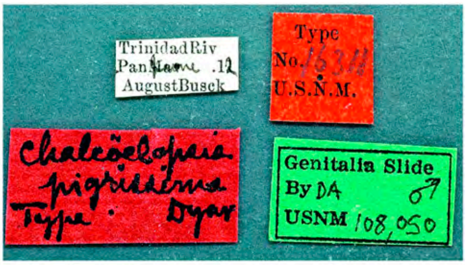
Figs. 1–8. *Cryptocosma perlalis* Lederer, Brazil?. 1, Lectotype male. 2, Lectotype labels. 3, Adult female, French Guiana, bracket indicates cataclystiform pattern or spots. 4, Male genitalia, Costa Rica, INBIOCRI000358846. 5, Gnathos magnified, lateral view. 6, Phallus. 7, Female genitalia, Costa Rica, INBIOCRI002402352. 8, Signa magnified.

spines (Fig. 6). *Female genitalia:* Telescopic (n = 9, Figs. 7, 23), unknown in other glaphyriine genera (apophyses posteriores ≥ 3.2 mm, apophyses anteriores ≥ 1.72), bursa copulatrix membranous (length ≥ 2.48 mm), apophyses anteriores extending to abdominal segment 7 or slightly beyond (in *C. perlalis*).



Figs. 9–17. *Cryptocosma perlalis* Lederer, Brazil and French Guiana. 9, Female head, lateral view, USNM slide #115922. 10, Female head, frontal view, USNM slide #115922. 11, Male head, lateral view, USNM slide #115921. 12, Male head, frontal view, USNM slide #115921. 13, Male head, dissected, frontal view. 14, Male head, dissected, ventral view. 15, Male bipectinate antenna. 16, Hindwing, just above bar indicates area of upraised, modified scales (French Guiana, same specimen from #3 above). 17, Frontal view, adult, just below bars indicates upraised, modified scales (French Guiana, same specimen from #3 above). (lp = labial palpi, pb = proboscis)


18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Type. Dyar

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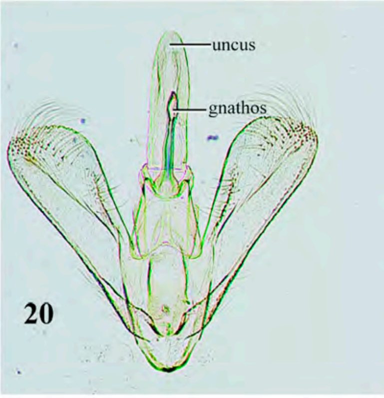

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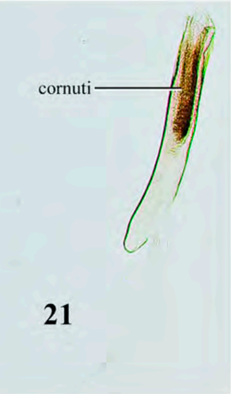

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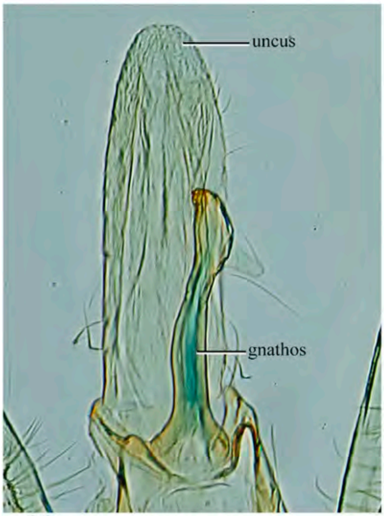

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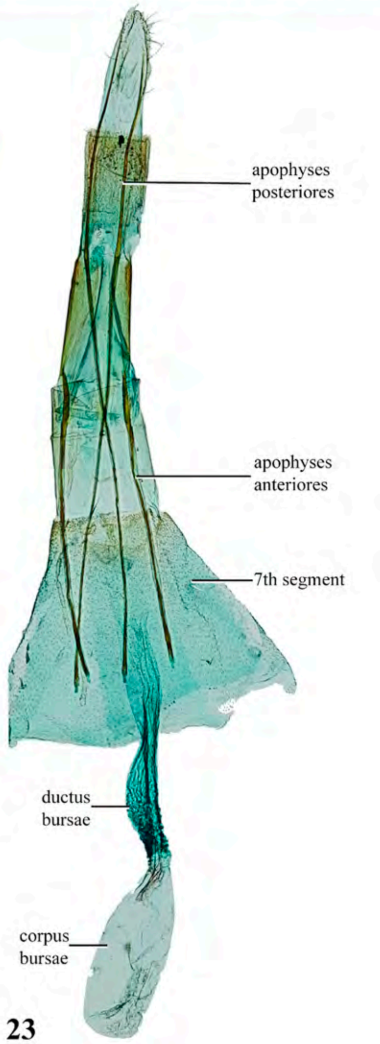

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Figs. 18–23. *Cryptocosma pigrissima* (Dyar), Panama. 18, Lectotype male. 19, Labels. 20, Male genitalia, USNM slide #108050, USNMENT01433851. 21, Phallus. 22, Uncus and gnathos magnified, slide angled. 23, Paralectotype female genitalia, USNM slide #115947, USNMENT01238758.

Comparison to other glaphyriine genera.—We conducted a preliminary survey of glaphyriine genera that narrowed the number of genera with reduced mouthparts and other shared characters to *Chalcoela* and *Pseudoligostigma* Strand, 1920, although *Cryptocosma* shares other characters with various other glaphyriine genera as discussed below. Originally, Zeller (1872) compared *Cryptocosma* to his newly described genera *Chalcoela* Zeller (1872) (p. 529) and *Dicymolomia* Zeller (1872) (p. 530). *Chalcoela* and *Dicymolomia* were subsequently placed in Glaphyriinae by Forbes (1923), and most recently both appeared as the only glaphyriines and as sister genera in the molecular phylogeny by Regier et al. (2012).

In the head, *Cryptocosma* lacks an ocellus, as in *Chalcoela*. In the wing-locking mechanism, the male and female frenulum of *Cryptocosma* is one spine, as in *Chalcoela*; but most glaphyriine genera have 2 spines in the female, such as *Pseudoligostigma*. *Cryptocosma* and *Pseudoligostigma* also share a retinaculum that is a row of scales at the base of the Cu vein pointing toward the costa and another row of scales on the costa pointing toward the outer margin in both sexes, and other glaphyriine genera have a frenulum hook as a retinaculum. The forewing of *Cryptocosma* has silver scales that form a subterminal line basal to the orange terminal line, the subterminal and terminal line are angled toward the wing base at the tornus; silver on the forewing is known in a few other glaphyriine genera, for example, *Cosmopterosis* Amsel, 1956 (Solis et al. 2009). In older specimens, including the 19th century type specimen of *C. perlalis*, the silver scales in the subterminal line are almost clear and hard to see, and the line and spot are more prominent in males than females. It should be noted that the reddish scales of fresh specimens shown in Heppner (2015) fade over time to brown or light brown. On the male hindwing, *Cryptocosma* and *Pseudoligostigma* share modified scales at the base of Cu and beyond, that are raised, and with both piliform and spatulate scales (Figs. 16, 17), but they also occur in other species of *Glaphyria* Hübner, 1823 (including the type species, *G. sesquistrialis* Hübner), and *Lipocosma* Lederer, 1863 (Solis and Adamski 1998). *Cryptocosma* has six silver-metallic, black-margined cataclystiform spots (plus one at the tornus not black-margined) along the hind margin (Fig. 16), as in many glaphyriine genera, and is most like the seven spots in *Pseudoligostigma*; visible ventrally in both genera. The *Cryptocosma* hindwing has an invagination between Rs_4 and M_1, but this invagination also occurs in several glaphyriine genera, and even other crambid subfamilies.

Placement in the Glaphyriinae.—The Glaphyriinae is currently composed of 74 genera and 490 species (Léger et al. 2021) and "a revision and phylogenetic analysis of the entire subfamily (sensu stricto) is greatly needed. . . " (Solis and Adamski 1998). Due to the extreme variation of glaphyriine species and genera, members of this subfamily are distinguished by a combination of characters. Externally, they can be distinguished by a simple or unilobed praecinctorium associated with the tympanal organs (Minet 1985, Munroe 1972b), and raised, and piliform and/or spatulate, scales present on the hindwing at the base of the Cu vein and beyond between CuA_2 and CuP in males (Forbes 1923, Munroe 1964, Munroe 1972b) (Figs. 16, 17). But the upraised scales are often difficult to see due to flattening of the scales during wing preparation. A survey of Costa

Rican glaphyriines showed that these scales may be absent in all species of some glaphyriine genera (Solis and Adamski 1998). Acentropinae also lack these modified, raised scales in the hindwing near the Cu vein (Lange 1956, Munroe 1972a, Solis 2019). *Cryptocosma* also lacks the swollen scoloparia found in the tympanal organs of adult acentropines (Minet 1985). The Acentropinae is also defined by characters of the immatures that are associated with wet habitats (Habeck and Solis 1994, Passoa 1988, Solis 2019, Speidel 1981, Speidel and Stüning 2005, Yoshiyasu 1985), but the immatures and biology of *Cryptocosma* are unknown.

Biology.—Unknown.

Remarks.—*Cryptocosma* is currently represented by two described species, *C. perlalis* and *C. pigrissima*. The general morphology of the female genitalia is diagnostic for *Cryptocosma,* and there is significant variation at the species level among *C. perlalis*, *C. pigrissima*, and putative new species in South America, but a revision of this genus is needed to include undescribed species in South America. We find the etymology particularly pleasing for this beautiful genus by Lederer; *Cryptocosma* is "verborgen" and "Schmuck" that means "hidden jewel." Telescopic female genitalia in the Pyraloidea is not common. In the Pyralidae, *Macalla* Walker (Epipaschiinae), and some genera in Old World Pyralinae and Galleriinae have been observed to have telescopic female genitalia, presumably for laying eggs under bark or crevices (Howard and Solis 1989).

Cryptocosma perlalis Lederer

(Figs. 1–17)

Cryptocosma perlalis Lederer, 1863: 346, BRAZIL?, male lectotype [NHMV], is designated here to fix and stabilize the current concept of the name, labeled: "Cryptocosma perlalis [handwritten white label]; Km. [handwritten blue label]." (Figs. 1, 2). Externally examined, not dissected.

Parapoynx obscuralis Möschler, 1882 (1881): 432, type locality: Surinam (synonymized by Munroe 1995) [ZMHB], image examined, not dissected.

Cataclysta trilinealis Warren, 1889: 295, type locality: Brazil (synonymized by Munroe 1995) [BMNH], types not found, not examined.

Guyanymphula cayennensis Heppner, 2015: 49, type locality: French Guiana, **new synonym**. [MGCL], not examined, based on images in Heppner 2015.

Other specimens examined.—BRAZIL: 5 ♂♂, 5 ♀♀, Matto Grosso do Sul, Corumba, 23–25.IV.1985, V. O. Becker Coll., 180 m (♀ USNM slide #115948) [USNM]. COLOMBIA: 1 ♂, 6 ♀♀, Amazonas, Leticia, 1–3.II.69 (USNM slides ♀ #115914 and ♂ #115913) [USNM]. COSTA RICA: 2 ♀♀, 1 ♂, Alajuela, Los Chiles, Caño Negro, 3–23.IV.1995, R. Villalobos, 20 m, 10.893812, -84.788847, (♀ slide INBIOCRI002402352, Figs. 7, 8) [MNCR-A]; 1 ♀, Heredia, Sarapiquí, Est. Magsasay, P. N. Braulio Carrillo, IV.1991, M. Zumbado, 200 m, 10.401255, -84.049314 [MNCR-A]; 1 ♀, Limón, Pococí, Río Sardinas, R.N.F.S. Barra del Colorado, 11–19.X.1993, F. Araya, 10 m, 10.64405, -83.742005 [MNCR-A]; 85 ♂♂, 43 ♀♀, Limón, Pococí, Cerro Tortuguero, 30.IV.1989 to 31.III.1996 by various collectors J. Solano, R. Delgado, R. Aguilar, and E. Rojas, 10.584815, -83.529205 (♂ slide INBIOCRI000358846, Figs. 4–6) [MNCR-A]. ECUADOR: 2 ♀♀, Guayas, Guayaquil, no date, D. S. Bullock. FRENCH GUIANA: 22 ♀♀, St. Jean Maroni, no date, Dognin Collection (♀ USNM slide #115918) [USNM]; 2 ♀, Piste Nancibo, 4.I.1985, J. F. Landry, km 6, in logged rainforest, 4.68333333,

-52.41666667 [USNM]. GUATEMALA: 1 ♀, Cayuga, III, Schaus and Barnes Collection [USNM]. GUYANA: 1 ♀, Georgetown, no date, Wm Schaus Coll. [USNM]; 1 ♀, White Water Cmp., Burra Burra R., Iwokrama Res., 26.II.02, Davis, Pogue, and Solis, 250–330 m, 4.6752778, -58.83305556 [USNM]. PERU: 1 ♀, Loreto, Rio Amazonas, Explorama Inn, 25 E. Iquitos, 9–12 and 17–21. IX. 1990, R. Leuschner, 200 m. [USNM]; 1 ♀, on Amazon R., nr. San Pablo at ship's light, 11 pm., 27.II.1992, R. A. Raguso [USNM]. SURINAM: 4 ♂♂, 2 ♀♀, Gelderland, Surinam River, no date, Wm Schaus Coll. (♂ USNM slide #115917) [see text: identified by Schaus as] "Cataclysta perlalis Led., trilinealis W." [USNM].

Remarks.—*Cryptocosma perlalis* and *C. pigrissima* have very similar morphology externally and in the male genitalia. The female genitalia (Figs. 7, 8) has a ductus bursae that is almost the same width throughout its entire length, the signa of the corpus bursae are two sclerotized, linear lines, and the apophyses anteriores extend just beyond abdominal segment 7. The specimens from Colombia, Costa Rica, Ecuador, Guatemala, Guyana, and Peru are new distribution records.

Cryptocosma pigrissima Dyar, **revised status**

(Figs. 18–23)

Chalcoelopsis pigrissima Dyar, 1914: 314, PANAMA: Trinidad River, male lectotype (USNM) is designated here to fix and stabilize the current concept of the name designated, labeled: "Trinidad Riv/ Pan June .12/ August Busck [printed white label]; Chalcöelopsis/ pigrissima/Type Dyar [handwritten red label]; Type/No.16311/ U.S.N.M. [printed red label]; Genitalia Slide/By DA ♂/ USNM 108050 [printed and handwritten green label]." (USNMENT01433851) (Figs. 18, 19). Synonymized by Munroe 1995.

Paralectotypes examined.—PANAMA: 45♀♀, Trinidad River and La Chorrera, May and June, 1912, August Busck (♀♀ USNM slides #s 115947, 116001, 116002, 116003, 116004, 116005, 116006) [USNM].

Other specimens examined.— GUATEMALA: 1 ♂, Cayuga, March, Schaus and Barnes coll. [USNM]. VENEZUELA: 2 ♂♂, 6 ♀♀, Guarico, Hato, Masagural, 45 km S. Calabozo, 23–24 April 1988, M. Epstein and R. Blahnik, 8.57 N, 67.58 W, Gallery Forest 10, 75 m (USNM slides #s 115915, 115916) [USNM].

Remarks.—*Cryptocosma perlalis* and *C. pigrissima* have very similar morphology externally and in the male genitalia. In the female genitalia (Fig. 23) the ductus bursae posterior to the corpus bursae is wide, almost lobe-like (i.e., not the same width along its length), the corpus bursae lacks signa, and the apophyses anteriores extend only to the anterior margin of abdominal segment 7. The specimens from Venezuela provide a new distribution record.

DISCUSSION

Throughout the history of Pyraloidea taxonomy, both reduced, adult mouthparts and, particularly, the cataclystiform pattern (Munroe 1991) in the hindwing (Figs. 1, 3, 16, 18) present in different subfamilies of Crambidae, have confounded the classification of genera. *Cryptocosma pigrissima* was originally placed in the Schoenobiinae by Dyar (1914), who stated:

> "Specimens from the Guianas have been labeled by Mr. Schaus "*Cataclysta perlalis* Led.; *trilinealis* Walk. but I have been unable to trace those names. The species cannot be a *Cataclysta* [i.e., a member of the Acentropinae] on

> account of the absence of the tongue."

Munroe (1991) mentioned *Cryptocosma* in his discussion on the distribution of cataclystiform patterns or "a row of black spots with contrasting white, blue, or metallic pupils..." in the hindwing of the Crambidae, specifically species in the Acentropinae, Glaphyriinae, and Spilomelinae, and mentions *Cryptocosma* as one of the "more bizarre Nymphulinae [=Acentropinae, Solis 1999]." But Munroe (1964) had previously transferred many species with a cataclystiform pattern from the Acentropinae to Glaphyriinae. Lederer (1863) noted a similarity in the *Cryptocosma* hindwing with *Cataclysta lemnata* Linnaeus (1758), a European species with cataclystiform spots and aquatic larvae in the Acentropinae. Warren (1889) described *Cataclysta trilinealis*, a synonym of *C. perlalis*, in Hydrocampidae, a synonym of the Acentropinae. Warren (1889) noted:

> "In the hind wings, before the marginal row of steel spots, are three curved parallel black lines, and the centre of the wings is sprinkled with lustrous scales."

Despite historical issues with the placement of taxa based on reduced mouthparts and the cataclystiform pattern, methodology and lack of rigorous observations by Heppner (2015) may have led to the taxon's misplacement. There was no "Materials and Methods" section, so it is not clear if an effort was made to study type specimens of Neotropical genera to see if it had been previously described. There was no mention if the head of the new species was dissected, placed on slides, and examined with a microscope. We presume not, because the head structures were described vaguely and incorrectly. For example, Heppner (2015) writes, "labial palpus greatly reduced, 3-segmented", but we found it only has two segments and "Maxillary palpus minute-3 segmented", but the maxillary palpus is absent in the female and present as one segment in the male. Heppner (2015) based the new tribe "particularly [on] the bipectinate antennae and the minute decumbent labial palpi." We hypothesize that the bipectinate antennae and the labial palpi, along with other characters presented here in the diagnosis of the genus, are autapomorphies for *Cryptocosma*. The pectinate antenna in the male is a secondary sexual character and the labial palpi are secondarily reduced. It is premature to use these characters as a basis for the new genus or tribe without studying the distribution of these and other characters throughout the subfamily.

Heppner (2015) created a new tribe, Guyanymphulini, for the monotypic genus *Guyanymphula*, and classified all remaining acentropine taxa in the nominate tribe Nymphulini Duponchel. He did not provide a diagnosis for Nymphulini and created a potentially polyphyletic taxon. Heppner (2015) also did not use the currently accepted family name, Crambidae, for these subfamilies despite overwhelming evidence (see Munroe and Solis 1999, Nuss et al. 2003–2020, Regier et al. 2012). Heppner (2015) used Pyralidae (*sensu lato*) because the separation of the two families, Pyralidae and Crambidae, is "based on subjective views involving a SINGLE [our emphasis] character between two groups." The separation and monophyly of these two families were recognized as early as the 1800's and are based on many morphological characters (e.g., in wings, tympanal organs, larvae) as well as molecular characters (Regier et al.

2012), not "a single character" as stated by Heppner (2015). A molecular phylogenetic study by Regier et al. (2012), confirmed the morphological support for the monophyly of these families. For a review of all characters diagnosing Crambidae and Pyralidae see, for example, Regier et al. (2012) or Munroe and Solis (1999).

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LITERATURE CITED

Amsel, H. G. 1956. Microlepidoptera Venezolana I. Boletin de Entomologia Venezolana, Maracay 10(1954)(1–2): 1–336.

Dyar, H. G. 1914. Report on the Lepidoptera of the Smithsonian Biological Survey of the Panama Canal Zone. Proceedings of the United States National Museum 47: 139–350.

Fletcher, D. S. and I. W. B. Nye. 1984. The Generic Names of Moth of the World. Volume 5. Trustees of the British Museum (Natural History), London. 185 pp.

Forbes, W. T. M. 1923. The Lepidoptera of New York and neighboring states. Part I. Cornell University Agricultural Experiment Station Memoirs 68: 1–729.

Habeck, D. and M. A. Solis. 1994. Transfer of *Petrophila drumalis* (Dyar) to *Argyractis* based on immature and adult characters with a larval description of *Argyractis subornata* (Hampson) (Lepidoptera: Crambidae: Nymphulinae). Proceedings of the Entomological Society of Washington 96(4): 726–734.

Heppner, J. B. 2015. *Guyanymphula*, new genus, and a new species of aquatic moth from French Guiana, in the new tribe Guyanymphulini (Lepidoptera: Pyralidae: Nymphulinae). Lepidoptera Novae 8: 47–52.

Horn, W., I. Kahle, G. Friese, and R. Gaedike. 1990. Collectiones entomologicae. Eine Kompendium über den Verbleib entomologischer Sammlungen der Welt bis 1960. Vol. I: A to K, Vol. II: L to Z. Akademie der Landwritschaftswissenschaften der Deutschen Demokratischen Republik, Berlin. 573 pp.

Howard, F. W. and M. A. Solis. 1989. Distribution, life history, and host plant relationships of the mahogany webworm, *Macalla thyrsisalis* (Lepidoptera: Pyralidae). Florida Entomologist 72(3): 469–479.

Hübner, J. 1819–1823 [imprint "1823"]. Zuträge zur Sammlung exotischer Schmettlinge [sic], bestehend in Bekundigung einzelner Fliegmuster neuer oder rarer nichteuropäischer Gattungen. Augsburg. [1]–[3]–4–6–[7]–8–32–[33]–[40], pls. [36]–[69].

Lange, W. H. 1956. A generic revision of the aquatic moths of North America. (Lepidoptera: Pyralidae, Nymphulinae). Wasmann Journal of Biology 14: 59–144.

Lederer, J. 1863. Beitrag zur Kenntnis der Pyralidinen. Wiener Entomologische Montschrift 7(10): 331–501.

Léger, T., R. Mally, C. Neinhuis, and M. Nuss. 2021. Refining the phylogeny of Crambidae with complete sampling of subfamilies (Lepidoptera, Pyraloidea). Zoologica Scipta 50: 84–99.

Minet, J. 1985. Étude morphologique et phylogénétique des organes tympaniques de Pyraloidea. 2-Pyralidae, Crambidae, première partie (Lepidoptera Glossata). Annales de la Société Entomologique de France (N. S.) 21: 69–86.

Möschler, H. B. 1882 (1881). Beiträge zur Schmetterlingsfauna von Surinam IV. Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien 31: 393–442.

Munroe, E. G. 1964. New general and species of Glaphyriinae (Lepidoptera: Pyralidae). The Canadian Entomologist 96: 1261–1307.

Munroe, E. G. 1972a. Pyraloidea, Subfamilies Scopariinae, Nymphulinae, pp. 14–112. *In* Dominick, R. B., C. R. Edwards, D. C. Ferguson, J. G. Franclemont, R. W. Hodges, and E. G. Munroe, eds. The Moths of America North of Mexico. Fasc. 13. 1A. E.W. Classey, London. 134 pp.

Munroe, E. G. 1972b. Pyraloidea, Subfamilies Odontiinae, Glaphyriinae, pp. 137–250. *In* Dominick, R. B., C. R. Edwards, D. C. Ferguson, J. G. Franclemont, R. W. Hodges, and E. G. Munroe, eds. The Moths of America North of Mexico. Fasc. 13. 1B. E.W. Classey, London. 250 pp.

Munroe, E. 1991. Transfer of *Aulacodes eupselias* Meyrick to Pyraustinae, with Notes on the Genus *Marasmia* Lederer and on Cataclystiform Wing Patterns in the Family Crambidae (Lepidoptera: Pyralidae). Bishop Museum Occasional Papers 31: 122–130.

Munroe, E. G. 1995. Nymphulinae, pp. 48–51. *In* Heppner, J. B., ed. Atlas of Neotropical Lepidoptera. Checklist: Part 2. Hyblaeoidea–Pyraloidea–Tortricoidea. Association of Tropical Lepidoptera, Gainesville. 243 pp.

Munroe, E. and M. A. Solis. 1999. Pyraloidea, pp. 233–256. *In* Kristensen, N., ed. Lepidoptera, Moths and Butterflies, Vol. 1, Arthropoda, Insect, Vol.4, Part 35. Handbook of Zoology. Walter de Gruyter and Co. Berlin. 491 pp.

Nuss, M., B. Landry, R. Mally, F. Vegliante, A. Tränkner, F. Bauer, J. E. Hayden, A. Segerer, R. Schouten, H. Li, T. Trofimova, M. A. Solis, J. de Prins, and W. Speidel. 2003–2020. Global Information System on Pyraloidea. www.pyraloidea.org (accessed August 16, 2019).

Passoa, S. 1988. Systematic positions of *Acentria ephemerella* (Denis and Schiffermüller), Nymphulinae, and Schoenobiinae based on morphology of immature stages (Pyralidae). Journal of the Lepidopterists' Society 42: 247–262.

Regier, J. C., C. Mitter, M. A. Solis, J. E. Hayden, B. Landry, M. Nuss, T. J. Simonsen, S. H. Yen, A. Zwick, and M. P. Cummings. 2012. A molecular phylogeny for the pyraloid moths (Lepidoptera: Pyraloidea) and its implications for higher-level classification. Systematic Entomology 37:635–656.

Robinson, G. S. 1976. The preparation of slides of Lepidoptera genitalia with special reference to the microlepidoptera. Entomologist's Gazette 27: 127–132.

Solis, M. A. 1999. Nymphulinae Duponchel [1845] (Insecta: Lepidoptera): proposed precedence over Acentropinae Stephens, 1836. Case 3048. Bulletin of the International Commission on Zoological Nomenclature 56 (1): 31–33.

Solis, M. A. 2019. Aquatic and semiaquatic Lepidoptera, pp. 765–789. *In* Merritt, R. W., K.W. Cummins, and M. B. Berg, eds. Aquatic Insects of North America, 5th Edition. Kendall/Hunt Publishing Company, Dubuque, Iowa. 1480 pp.

Solis, M. A. and D. Adamski. 1998. Review of the Costa Rican Glaphyriinae (Lepidoptera: Pyraloidea: Crambidae). Journal of the New York Entomological Society 106(1): 1–55.

Solis, M. A., M. Metz, and D. H. Janzen. 2009. Phylogenetic analysis of *Cosmopterosis* Amsel (Lepidoptera: Crambidae: Glaphyriinae) with discussions on male secondary sexual characters and larval feeding on *Capparis* L. (Capparaceae) in the Pyraloidea and Lepidoptera (Insecta). Annals of the Entomological Society of America 102(5): 766–784.

Speidel, W. 1981. Die Abgrenzung der Unterfamilie Acentropinae (Lepidoptera: Pyraloidea). Atalanta 12: 117–128.

Speidel, W. and D. Stüning. 2005. *Ambia naumanni* sp. n., a new species of Musotiminae from Yunnan (Lepidoptera: Crambidae). Bonner Zoologische Beiträge 53: 221–225.

Strand, E. 1920 (1919). Beiträge zur Kenntnis der Verbreitung und Formen exotischer Heterocera, insbesondere Pyrlididen, auf Grund von Material im Beutschen Entomologischen Museum. Archiv für Naturgeschichte 85(A) 12: 132–133.

Warren, W. 1889. On the Pyralidina collected in 1874 and 1875 by D. J. W. H. Trail in the Basin of the Amazons. Transactions of the Entomological Society of London 1889: 227–295.

Yoshiyasu, Y. 1985. A systematic study of the Nymphulinae and the Musotiminae of Japan (Lepidoptera: Pyralidae). Scientific Report of the Kyoto Prefecture University 37: 1–163.

Zeller, P. C. 1872. Beiträge zur Kenntnis der nordamerikanischen Nachtfalter besonders der Microlepidopteren. Erste Abtheilung. Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien 22: 447–566.