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Not a Tiger but a Dagger: The Larva of *Comachara cadburyi* and Reassignment of the Genus to Acronictinae (Lepidoptera: Noctuidae)

DAVID L. WAGNER,¹ ERIC W. HOSSLER,^{1,2} AND FRED E. HOSSLER²

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ABSTRACT *Comachara cadburyi* Franclemont has been classified as a sarrothripine (Noctuidae), lithosiine (Arctiidae), and afridine (Nolidae). Larval morphology and behavior indicate a close phylogenetic relationship with *Polygrammate hebraicum* Hübner, an acronictine noctuid. The egg and larva of *Comachara* are described and illustrated with line drawings and scanning electron micrographs. Photographs of last instars of both *Comachara* and *Polygrammate* are provided. Larval feeding and pupation habits of *C. cadburyi* are briefly described and compared with those of *Polygrammate*. Larvae of both *Polygrammate* and *Comachara* exhibit a dramatic coloration change in the last instar, transitioning from a green phase to a mottled, steely gray form. As the color change progresses, the larva ceases feeding and enters a wandering phase, during which it seeks out wood in which to pupate. Interpretation of L group setal homologies on the ninth abdominal segment is briefly addressed. *Comachara* provides a poignant example of the importance of immatures in elucidating phylogeny—adult features of *Comachara* misled a number of the twentieth century's finest lepidopterists.

KEY WORDS *Nyssa*, *Acronicta*, larval evolution, wood-boring

Doug Ferguson piqued our interest in *Comachara* after we sent him images of caterpillars from *Nyssa* collected along the shore of Lake Michigan that logically had to be *Polygrammate hebraicum* Hübner, but which Doug determined as *Comachara cadburyi* Franclemont. Although his identification ultimately proved to be in error, his suggestion led us down a path of investigation to what we think is the correct taxonomic placement of *Comachara*.

In 1939, Franclemont described *C. cadburyi* as a new species and genus of Sarrothripinae (Noctuidae), but he noted that both its mouthparts and venation were anomalous relative to other North American members of the subfamily. Four years later, McDunnough (1943) transferred *Comachara* and *Afrida* Möschler, 1886 out of the Noctuidae, into the lithosiine Arctiidae. Forbes (1954) ignored McDunnough and left the genus in the Sarrothripinae but noted that it was “An odd genus, which McDunnough would even reject from the Noctuidae.” Largely on advice from McDunnough, Franclemont (1983) upheld *Comachara*'s status as a Lithosiinae (J. G. Franclemont, personal communication). Most subsequent authors have left the genus in the Lithosiinae (e.g., Covell 1984, Poole 1996) or failed to recognize the moth as a member of the Noctuidae (e.g., Rings et al. 1992). Kitching and Rawlins (1999) implied that *Comachara* belonged with

Afrida in the Afridinae (Nolidae), but they noted that their treatment was provisional.

Larval features of *Comachara* suggest that the moth is misplaced in the Lithosiinae, Sarrothripinae (sensu Franclemont and Todd 1983) and Afridinae, and instead belongs in the Acronictinae (dagger moths) with *Polygrammate* Hübner, 1818. Below we describe and illustrate *Comachara*'s early stages, provide photographic images of *Polygrammate* larvae, figure the male genitalia of *Comachara* and *Polygrammate*, and briefly discuss preliminary mitochondrial DNA findings. All data point to *Comachara*'s placement as the sister to *Polygrammate* in the Acronictinae.

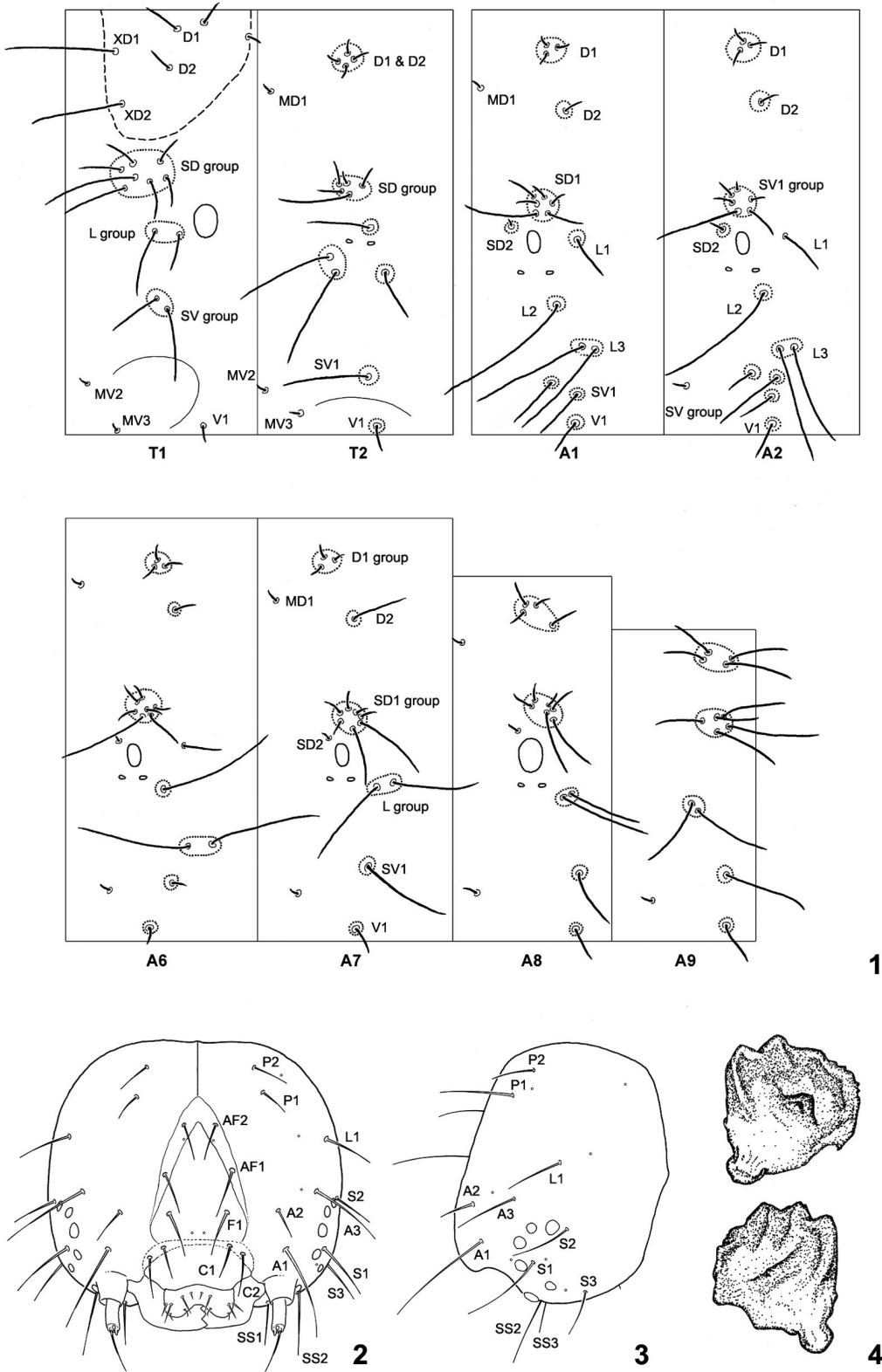
Materials and Methods

A female of *C. cadburyi* was collected on 15 June 2002 at Cypress Gardens, Berkeley County, South Carolina, and held in a plastic container for eggs. The female began laying eggs after 1 d in captivity. Larvae were reared to maturity on young leaves of black gum, *Nyssa sylvatica* Marsh (Cornaceae). A second cohort of 10 larvae from Millville, Cumberland County, New Jersey, were reared in 2005 to study the color change in the last instar. These larvae were monitored every 12 h from 30 June to 7 July, 2005.

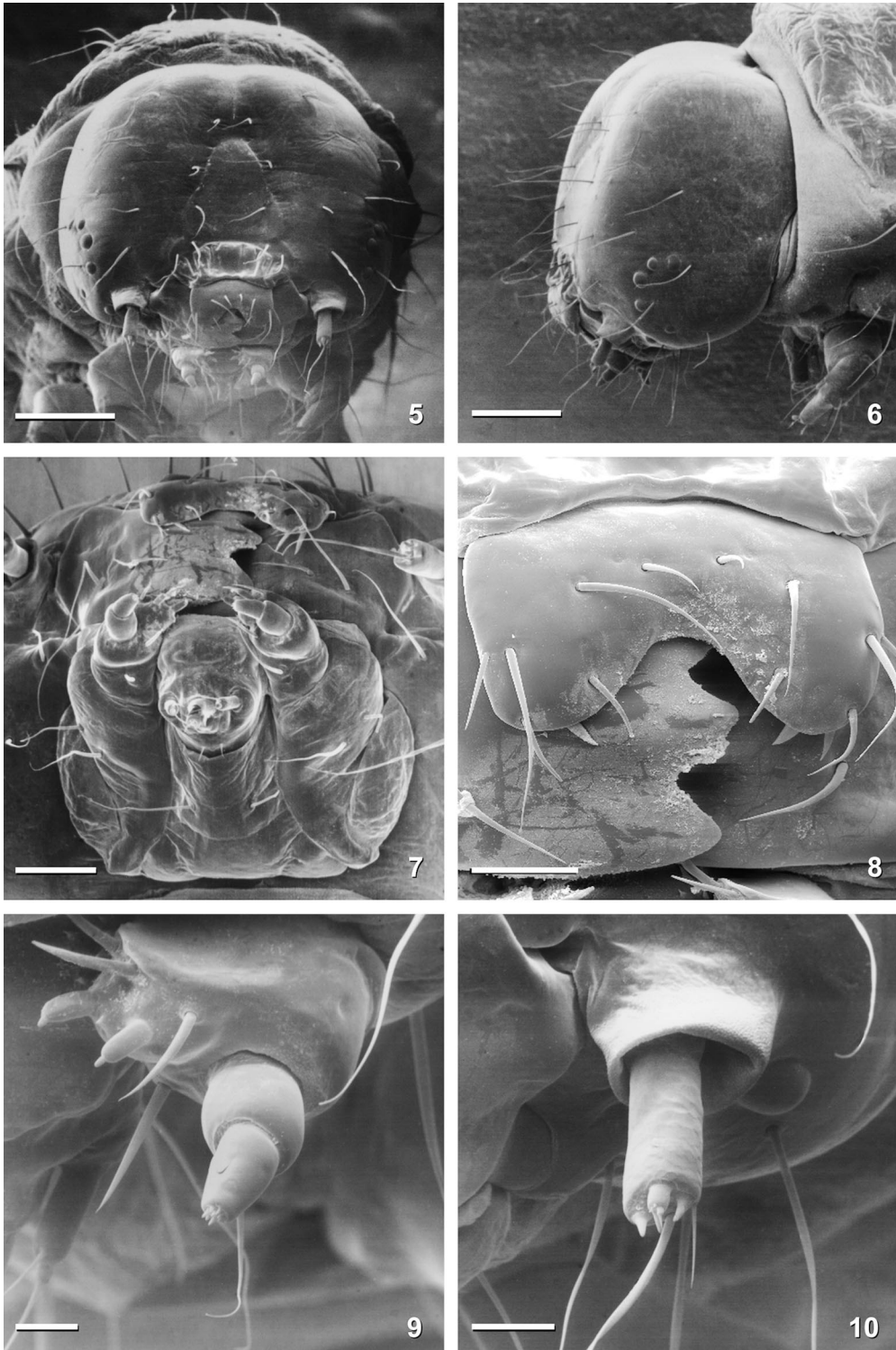
Male and female genitalia of six genera and 15 species of Acronictinae were examined: *Acronicta americana* (Harris), *Acronicta betulae* Riley, *Acronicta connecta* Grote, *Acronicta dactylinae* Grote, *Acronicta funeralis* Grote & Robinson, *Acronicta innotata* Guenée, *Acronicta longa* Guenée, *Acronicta morula* Grote & Robinson, *Acronicta radcliffei* (Harvey),

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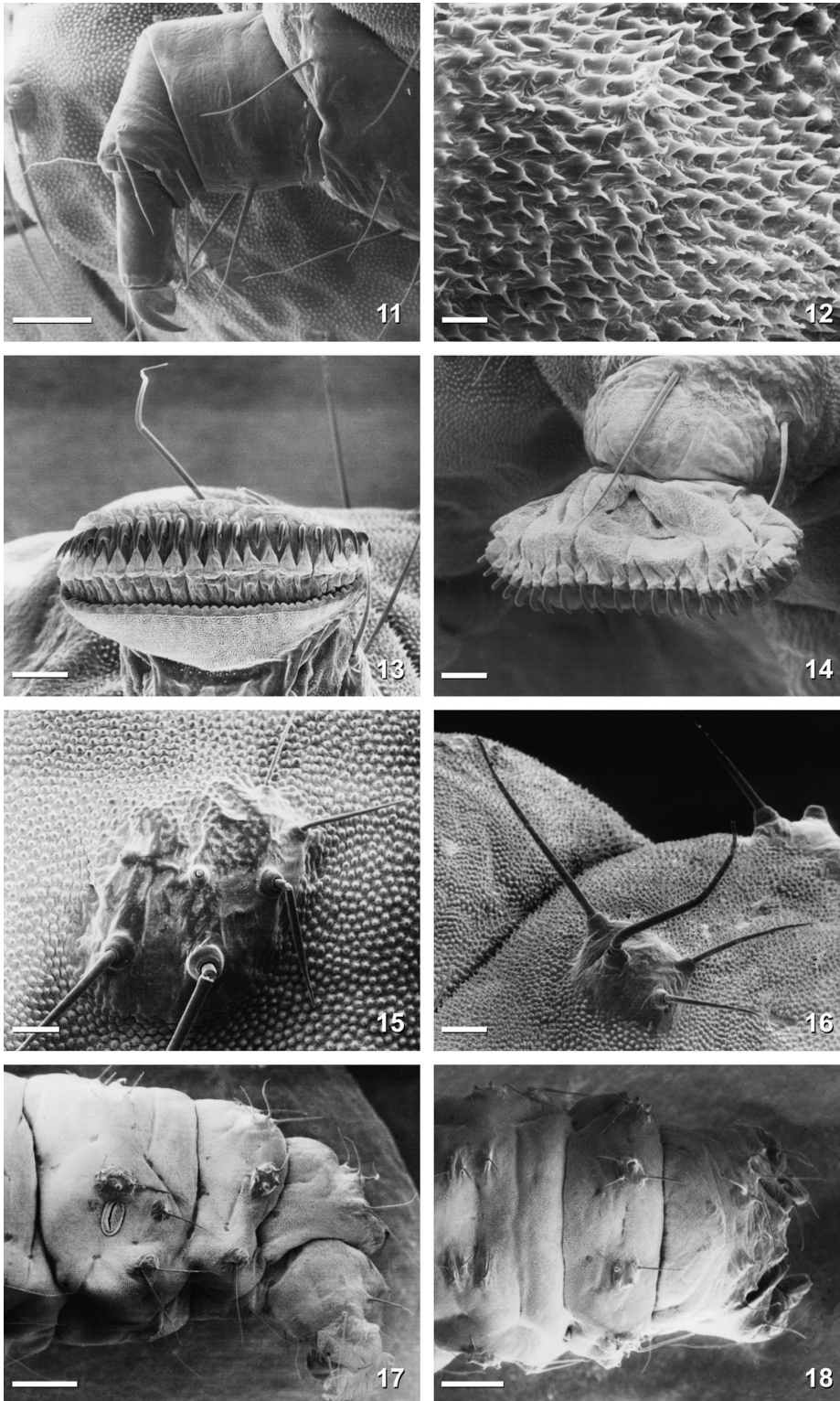
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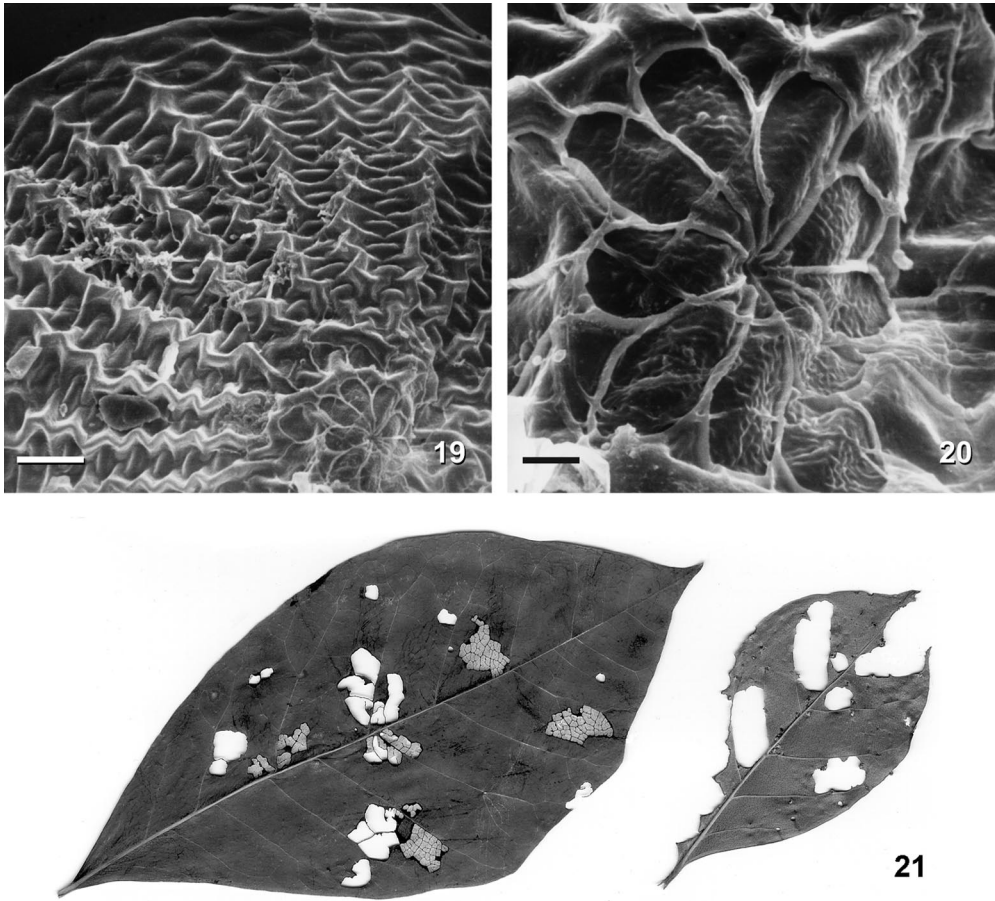
Figs. 1–4. Last instar of *C. cadburyi*. (1) Setal map. Note only one (of three) SV seta shown on A6. (2) Head, frontal, MD setae not shown. (3) Head, lateral. (4) Mandibles, mesal surfaces.



Figs. 5–10. Head of last instar of *C. cadburyi*. (5) Frontal (scale = 500 μm). (6) Lateral (scale = 500 μm). (7) Maxillo-labial complex (scale = 200 μm). (8) Labrum (scale = 125 μm). (9) Maxilla (scale = 50 μm). (10) Antenna (scale = 100 μm).



Figs. 11–18. Last instar of *C. cadburyi*. (11) Thoracic claw (scale = 200 μm). (12) Integumental spines on A1, laterad to ventral midline (scale = 20 μm). (13) Crochets on midabdominal proleg, ventral view (scale = 100 μm). (14) Crochets on midabdominal proleg, lateral view (scale = 100 μm). (15) SD1 chalaza on A6 (scale = 50 μm). (16) Fused D1 and D2 chalaza on A9 (scale = 100 μm). (17) A8–A10, lateral (scale = 500 μm). (18) A8–A10, dorsal (scale = 500 μm).



Figs. 19–21. *C. cadburyi*. (19) Egg, chorion sculpturing (scale = 50 μm). (20) Micropyle (scale = 10 μm). (21) Feeding damage of middle instar (left) and last instar (right).

Acrionicta vinnula Grote, *Agriopodes fallax* (Herrich-Schäffer), *Comachara cadburyi*, *Harrismemna trisignata* (Walker), *Polygrammate hebraicum*, and *Simyra henrici* (Grote).

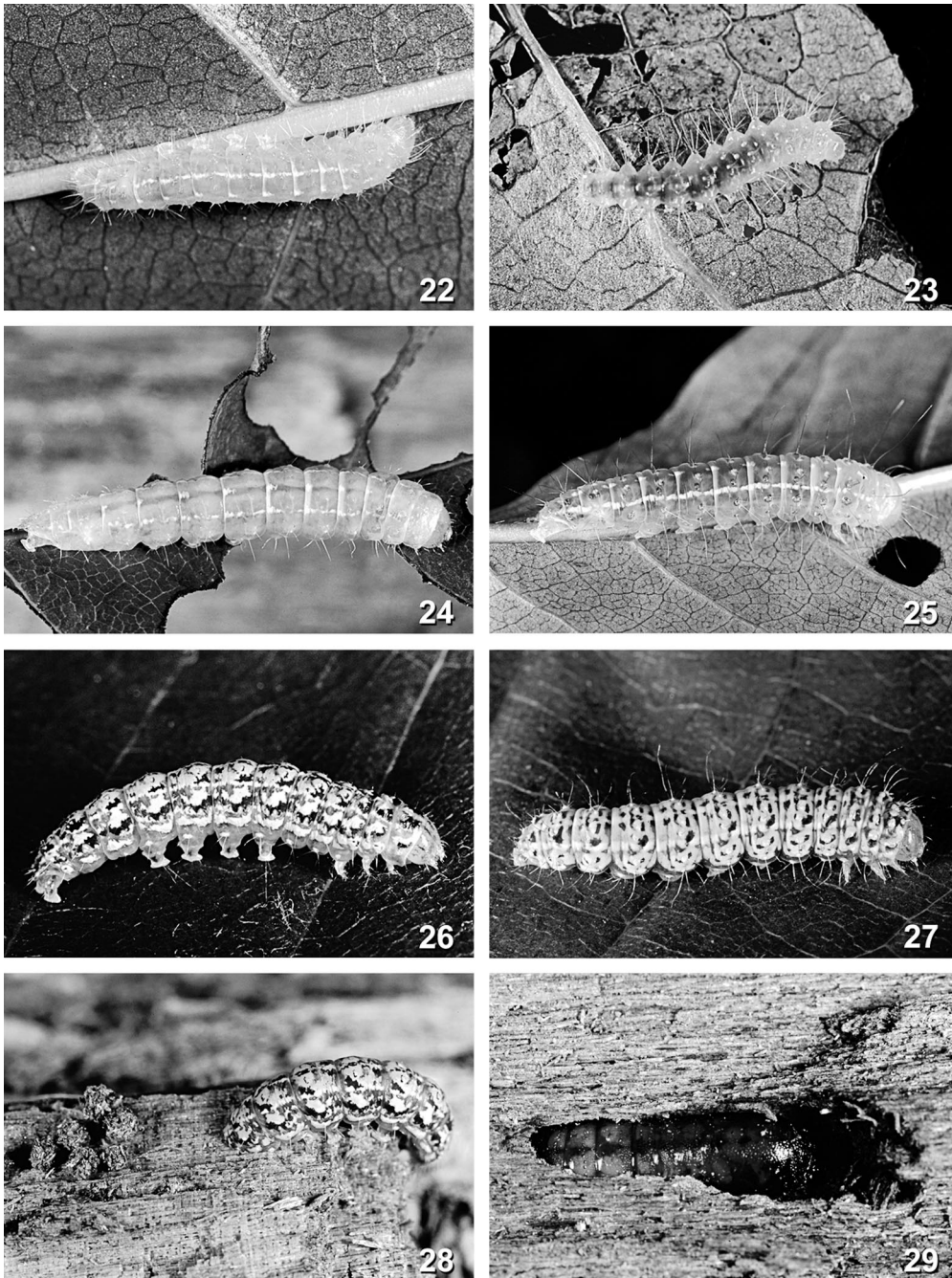
The following larval description is based on five preserved larvae and 83 larval photographs. Adult, larval, and pupal vouchers and slides (transparencies) are deposited at the University of Connecticut.

Results

Egg. Diameter: 0.75 mm ($n = 2$); shallowly hemispherical, with ≈ 32 zigzagging ridges (Fig. 19) and inconspicuous micropyle in a shallow depression (Fig. 20). Micropylar area with 8–9 obovate loops (“petals”) radiating from its center (Fig. 20).

Last Instar Description. Length: 21 mm ($n = 5$). Setae short, generally less than the segment length, pale except caudally where they may be rusty. Ground color lime green with pale green head, which may have yellow or orange tinting; body with broken creamy subdorsal stripe best developed on A1–A7; pinacula green and unpigmented; T2–A7 with creamy middorsal spot along caudal margin; spiracles yellowed in living individuals (Fig. 24).

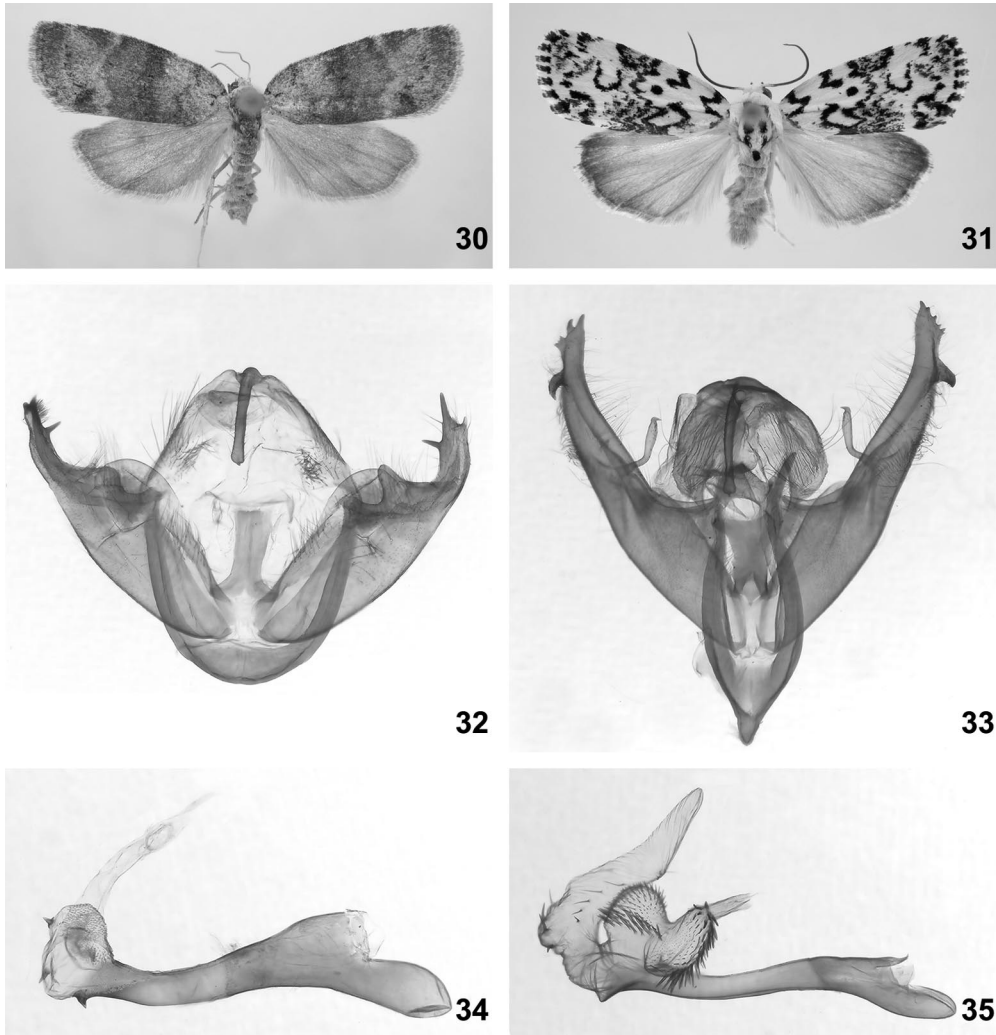
Mottled (wandering) form steely or blue-gray with irregular black patches; prothoracic shield with dark patch to either side of midline; middorsal stripe broken and ill-defined, consisting of alternating black and pale spots; black splotches running length of body above subdorsal stripe and spiracles; creamy subspiracular lines forming a broken stripe over abdominal segments; head with coronal bars over vertex and other weakly developed mottling (Fig. 26). **Head** (Figs. 2 and 3, 5–10): smooth with relatively short setae; secondary setae absent (Figs. 5 and 6). Clypeus only $\approx 3\times$ longer than broad (Fig. 5). Triangle extending more than halfway to epicranial notch (Figs. 2 and 5). A1 $2\times$ length of A2, longest on head; P setae short, displaced toward vertex; AF1 half again as long as AF2; SS3 much longer than SS1 or SS2. Spinneret short, cylindrical; strongly sclerotized at base and along sides, spout about as long as labial palpi (ignoring length of apical setae). Labrum proportionately long, nearly parallel-sided (Fig. 8). Maxilla as in Figs. 7 and 9. Right mandible with a prominent ridgelike mola, nearly as high as broad; left mandible grooved to receive opposing mola (Fig. 4); proximal seta $1.5\times$



Figs. 22–29. Larvae of *C. cadburyi* and *P. hebraicum*. (22) *C. cadburyi*, middle instar. (23) *P. hebraicum*, early instar, and “windowing” of leaf underside. (24) *C. cadburyi*, final instar, feeding phase coloration. Note caudally directed position of anal prolegs. (25) *P. hebraicum*, final instar, feeding phase coloration. (26) *C. cadburyi*, final instar, wandering phase coloration. (27) *P. hebraicum*, final instar, wandering phase coloration. (28) *C. cadburyi*, tunneling prepupal larva; head through A1 are within wood (to left). Note the six wood chip balls (left) fashioned by larva. (29), *C. cadburyi*, pupa in cell.

longer than distal seta. Antenna long (Figs. 5, 7, and 10). Thorax and abdomen (Figs. 1 and 11–18): Integument with either granules or spinules (Figs. 12 and 15, 16). Prothorax with poorly defined shield; two unnamed setae posterior to D1. Only two MV setae

were located on T1 and T2; all three setae present on T3. Spiracles on T1 and A8 roughly 2× those of A1–A7, elliptical, light brown. Two minute (microscopic) plates in shallow depressions above the L setae and/or below spiracles on T2–A8. Four D setae (three of



Figs. 30–35. Adults of *C. cadburyi* and *P. hebraeicum*. (30) *C. cadburyi*, male, wingspan 23 mm, Hampton, CT. (31) *P. hebraeicum*, male, wingspan 25 mm, Hampton, CT. (32) *C. cadburyi*, male genital capsule. (33) *P. hebraeicum* male genital capsule. (34) *C. cadburyi*, aedeagus. (35) *P. hebraeicum* aedeagus.

which assignable to D1 group) joined on a single pinaculum on T2 and T3. D1 pinaculum trisetose on A1–A8; setae enlarged and lengthened on A8. D2 solitary on separate pinaculum well below D1 group on A1–A7, proximate to D1 on A8 on common low wart. D1 and D2 setae enlarged and joined on single chalaza on A9 (Fig. 16). SD1 pinaculum multisetose: circa five setae on T2, six setae on T3, usually six to seven on A1–A8, and four to five on A9 (Figs. 1, 15, and 17). SD2 small, on separate pinaculum anterior to spiracle on A1–A8. L1 smallest of L group setae; L3 group bisetose on slightly raised wart, anterior to L2 on T2 and T3 (see Discussion), above SV1 on A1–A6. V1 setae short and closely situated on T1, roughly twice as long on T2–T3, roughly twice as long again on A1 and increasing in length to A9. Two SV seta on T1; 1 SV seta on T2–T3; usually two SV on A1; three on A2–A6; one on A7–A9. Prolegs homoideus (Figs. 13 and 14); those

on A3–A6 with 22–25 crochets in meseries; anal prolegs with 24 to 25 crochets.

Biology. The creamy eggs were laid on the lid and sides of a smooth plastic container that contained bark covered with lichen and blue-green algae. Eggs hatched after 6 d. The minute, creamy white first instars fed on *N. sylvatica*, mostly alongside the midrib on the under surface of the blade, removing small patches of tissue. Mature leaves were not accepted. Within a patch, the green (parenchymal) tissues were consumed all the way to the upper surface of the blade, thus forming a “window” (Figs. 21 and 23). The larva moved about the leaf making a series of windows (>8 per instar in one instance). Young larvae fed primarily from the underside of the blade, but occasionally removed patches from the upper side as well, again down to but not through the lower epidermis. The first stadium lasted 3 d ($n = 2$). Middle instars

skeletonized patches of leaf tissue from either side of the blade, especially from the lower surface. Late instars ate through the blade, removing irregular patches of tissue (Fig. 21, right). Leaf-edge feeding was relatively uncommon in the laboratory and may occur even less frequently in the field where access to foliage is not limited. Some larvae were observed to consume their shed cuticle after a molt.

The larval stage extended over 4 wk at 21°C. While feeding, the last instar was green, not unlike the color of *Nyssa* foliage (Figs. 22 and 24). The duration of the last instar (outside of the pupal excavation) ranged from 4.5 to 6 d (mean 5.1 d, $n = 6$). The green phase (Fig. 24) occupies much of the instar (mean 4.2 d, $n = 6$). Toward the end of the stadium, the larva took on a mottled coloration (Figs. 26 and 28). The duration of the mottled form was <24 h ($n = 8$) in all but one individual; this caterpillar was provided with an unsuitable pupation medium, a foam block. The change in coloration usually took place overnight. Once fully transitioned to the mottled phase, the larva showed no interest in feeding; rather, it wandered about its container, presumably in search of wood suitable for pupation.

Three *Comachara* caterpillars were observed throughout the tunneling phase: the larvae took 3 to 4 h to excavate their pupal chambers (Figs. 28 and 29). As larvae tunneled, they removed chips of wood and rolled them into little balls (six are visible in Fig. 28). After the pupal chamber was excavated, the larva backed into the tunnel and sealed the entrance with silk—pupal cells were extremely difficult to locate once closed ($n = 11$). Pupation occurred shortly after the tunnel was completed. Silk is not used to line the chamber. The pupal stage overwintered.

Discussion

Both adult and larval characters indicate that *Comachara* was misclassified as a lithosiine arctiid. For example, adults lack the microtymbals shared by other lithosiines (J. Adams, personal communication). The eggs of lithosiines are smooth, not richly ornamented as those of *Comachara* (Kitching and Rawlins 1999; Fig. 19). A number of larval features suggest that the moth is a poor fit for the Lithosiinae: the crochets are homoideus (some lithosiines are heteroideus) (Figs. 13 and 14), the planta is short, the spiracles are not round, and the setae are unbranched (Forbes 1954, Rawlins 1984, Habeck 1987, Jacobson and Weller 2001). Setae are incorporated into the cocoon in lithosiines; no cocoon is fashioned by *Comachara*. Additionally, lithosiines feed on lichens and blue-green algae (Rawlins 1984, Jacobson and Weller 2001, Robinson et al. 2002, Wagner 2005), whereas *Comachara* feeds solely on the leaves of *Nyssa* species. Although both lithosiines and *Comachara* have a mola, an unusual feature among noctuids, that of *Comachara* strikes us as exaggerated (Fig. 4) and of a different nature from those illustrated by Habeck (1987) of lithosiines.

Comachara was originally placed in the Sarrothripinae by Franclemont (1939), but the moth is a poor fit for the subfamily sensu Franclemont and Todd (1983). It lacks ocelli (which are present in most genera), the retinaculum is atypically short, the labial palpus is short, the forewing is smooth-scaled, and the genitalia are anomalous (Forbes 1954). The larva of *Comachara* differs from that of sarrothripines sensu Franclemont and Todd in the possession of secondary setae, raised chalazae, and comparatively short body setae.

Kitching and Rawlins (1999) pulled sarrothripines into the Nolidae and implied that *Comachara* be placed provisionally in the Afridinae: "New World lineages related to *Afrida* lack ocelli and were previously considered to be lithosiine arctiids (Franclemont and Todd 1983) [sic, Franclemont 1983]. They do not have the distinctive synapomorphies of Arctiidae and may be nolids of uncertain affinity, here tentatively retained in the Afridinae." Because of the heterogeneity of the Nolidae (as defined by Kitching and Rawlins), it is difficult to argue that *Comachara* is not a nolid. They suggest that the unique cocoon of nolids may be a defining apomorphy for the family—it is a dense, two-walled construction with a keel at one end through which the adult issues at eclosion (Forbes 1954, Kitching and Rawlins 1999). No cocoon is spun by *Comachara*: the larva simply tunnels into wood and fashions a cell largely free of silk in which transformation takes place (Fig. 29).

Larval characters suggesting that *Comachara* belongs in the Acronictinae (Noctuidae) include the presence of secondary setae, some of which are grouped on chalazae (Figs. 15 and 16), D1 and D2 being joined on a single pinaculum on T2 and T3, and the bisetose L3 group (Crumb 1956, Godfrey 1987, Merzheevskaya 1988, Kitching and Rawlins 1999). Curiously, both the latter features are shared with lithosiines (Kitching and Rawlins 1999). The prepupal tunneling behavior and pupation habits of *Comachara* are shared with many acronictines; no lithosiines, afridines, or sarrothripines are known to tunnel into wood to pupate and all spin cocoons.

The chaetotaxy of *Comachara* is sufficiently unusual that we were uncertain about setal homologies and nomenclature on a few segments. There are two extra setae caudad of D1 on the prothorax that we do not label; these seem to be the same setae that are joined onto the D1 pinaculum on T2-A9. Puzzling too are the L setae that share a common pinaculum on A7-A9. It is not clear whether these represent L1 and L2 or the paired L3 group setae; we label these simply as "L group" setae in Fig. 1. Although L1 is thought to always be present on A9 (e.g., Stehr 1987: 301), the length of the L setae on A9 and their paired condition suggests otherwise, i.e., that the lateral group setae on A9 are serially homologous to the L3 setae of more anterior abdominal segments (and that L1 is absent).

Larval features and behavior indicate a close (?sister) relationship with *P. hebraicum*, a most unexpected association given the remarkably different phenotypes of the two moths (Figs. 30 and 31). The

resemblance of the larvae of *Comachara* to those of *P. hebraicum* is undeniable (Figs. 24–27): the body shape, coloration, and posture of the two are closely similar. Both share a lime green color form that has middorsal spots along the caudal margin of T2–A7 and poorly developed subdorsal stripes; a mottled, wandering, wood-tunneling stage; a bootlike planta, which may have a faint pinkish cast; similar crochet numbers and arrangements; and short, posterior-directed anal prolegs. Setal lengths differ in the two: D1, D2, and SD1 setae are longer than the abdominal segment that bears them in *Polygrammate* but shorter in *Comachara*. The setae are often blackened or at least more strongly pigmented in *Polygrammate*, especially dorsad and caudad. Pinacula and chalazae are more produced in *Polygrammate*. In the last instar, the green phase larva of *Polygrammate* possesses addorsal spots on T2–A7 (Fig. 25) that are absent in *Comachara* (Fig. 24). Finally, the pinacula of the wandering form are often more yellow in living individuals of *Polygrammate*.

Both *Comachara* and *Polygrammate* are monophagous on *Nyssa*. Moreover, young and middle instars of both moths share an unusual feeding habit—they form “windows” by removing green tissue down to the opposite epidermal layer (Figs. 21 and 23). Both species tunnel into wood to form pupal chambers. Moreover, both species collect their frass (shavings) and roll these into balls that are individually withdrawn from the tunnel and tossed to the ground. Before pupation, larvae of *Polygrammate* may turn pink-red, a trait also seen among some members of the genus *Acrionicta* (and other groups of Lepidoptera). The color change was not seen in *Comachara*, but it might take place after the larva has tunneled into its pupal chamber. The forewing pattern of *Polygrammate* is reminiscent of *Agriopodes fallax* (Herrich-Schäffer) and some *Acrionicta*, e.g., *Acrionicta noctivaga* Grote and *Acrionicta fragilis* (Guenée). Taken as a whole, Acronictinae are a good fit for both *Comachara* and *Polygrammate*. Figures 24–27 convey the close association of the two insects; so close that one wonders whether the moths would be better classified in a single genus.

One of the most striking similarities of the two moths is the dramatic color (and behavioral) change that occurs in the last instar. The prepupal larva of *Comachara* and *Polygrammate* transitions from a green, foliage-feeding phase (Figs. 24 and 25) to a mottled, steely blue-gray, nonfeeding phase (Figs. 26 and 27). We think it likely that the unique mottled phase of *Comachara* and *Polygrammate* represents a (selected) phenotype, suitable for tunneling into bark or wood—a lime-green caterpillar would be conspicuous on wood during the 3–4 h period that is necessary to excavate a pupal chamber (as well as during the preceding wandering phase).

Genitalic features support an association of *Comachara* with *Polygrammate* and their placement in Acronictinae. Males of both species have modestly asymmetric valves, a juxta with a Y-shaped ventral portion, and an uncus that is strongly down-curved at one-third–one-half with a darkened tooth at its apex (Figs. 32–33). In both the aedeagus bears a lobe an-

terior to the insertion of the ejaculatory duct and the vesica is set with pegs that arise from rounded plates (Figs. 34–35). Females share a purse-shaped bulla seminalis, a long sclerotized antrum, and a bursa that is conspicuously sclerotized anteriorad.

Although there are no known genitalic features that are unique to Acronictinae (Kitching and Rawlins 1999), several structures seen in North American members of the subfamily suggest that both *Comachara* and *Polygrammate* would fit in the Acronictinae: a slender, elongate, distally toothed uncus is present in both genera as well as *Acrionicta* Ochseneheimer 1816, *Agriopodes* Hampson 1908, *Harrisimemna* Grote 1873, and *Simyra* Ochseneheimer 1816 (although this character state is widespread across other noctuid subfamilies). In many acronictines, the vesica is armed with a variety of spines and less commonly with peg-like studs. An ampullalike structure occurs in *Polygrammate* and many other members of the subfamily; a V-shaped vinculum extends well ventrad of the valves in *Acrionicta*, *Agriopodes*, *Harrisimemna*, *Polygrammate*, and *Simyra* (but not *Comachara*) (D.L.W. et al., unpublished data). In females the lateral scale patch between the tergite and sternite of the seventh abdominal segment shared by *Comachara*, *Polygrammate*, and some *Acrionicta* may be noteworthy (J. Bolling Sullivan, personal communication).

Individuals of *C. cadburyi* were sequenced as part of the All Taxa Biodiversity Inventory currently underway in Great Smoky Mountains National Park (GSMNP). To date >4,000 individuals representing >900 species from the Park have had a 648-base pair fragment of their mitochondrial cytochrome oxidase I (COI) gene sequenced (COI 5' region). The GSMNP data set includes 313 species of noctuids (24 Arctiidae, four Lymantriidae, 251 Noctuidae, four Nolidae, and 30 Notodontidae). The Kimura 2-parameter neighbor-joining tree for the fauna places *Comachara* as the sister of *Polygrammate* (D.L.W. et al., unpublished data).

Acronictines provide interesting examples of the decoupling of natural selection between the adult and larval stages. Larvae of *Acrionicta* are remarkably diverse phenotypically (Smith and Dyar 1898, Porter 1997, Wagner et al. 1998, Wagner 2005): some have few secondary setae, whereas others have an abundance; secondary setae may be confined to verrucae that correspond in placement to the primary setae or they may be scattered over the larval integument; setae may be long or short, straight or paddle-like; warts, lashes, pencils, and tufts may be present or absent. Coloration is marvelously varied. We know of no other moth genus with caterpillars as phenotypically diverse as *Acrionicta*. *Acrionicta* adults, by contrast, are so uniform in appearance (Covell 1984, Handfield 1999) that some would say that they border on monotonous. It is as if natural selection is pushing larval phenotypes about morphological and chromatic space, while largely ignoring phenotypic features of the nocturnal adults. *Comachara* and *Polygrammate* provide a contra example—their larvae are exceedingly similar, whereas their adult phenotypes are so

disparate that generations of lepidopterists failed to recognize their close relationship.

The importance of immatures to systematics and phylogenetic reconstruction are well known, *Comachara* provides but another compelling reminder. Adult characters are so anomalous that the moth has been placed in three separate noctuid families over the past 70 yr, none of which we think to be correct. Had Forbes, Franclemont, McDunnough, and others examined the immatures of *Comachara*, the moth's affinities to the acronictine Noctuidae would have been recognized before now.

Acknowledgments

Doug Ferguson, a strong advocate of life history work, encouraged our efforts: this article is dedicated to his memory. J. Bolling Sullivan graciously dissected and acquired photographic images of the male and female genitalia of six genera and 15 species of acronictines and provided suggestions on the contents of this article. J. Donald Lafontaine kindly supplied Figs. 32–35. The COI data and neighboring tree for the GSMNP moth fauna was sent to us by Paul Hebert. René Twarkins helped with drawings and assembled figures; Virge Kask prepared the larval photographic plate. A cohort of 10 late instars of *Comachara* was sent by Dale Schweitzer. Tim McCabe, Jack Franclemont, James Adams, and Nancy Jacobson provided unpublished observations and other assistance; McCabe also sent us a preserved larva. John Brown and two anonymous reviewers offered numerous helpful suggestions. Support for this study came from the U.S. Department of Agriculture, Forest Service, Forest Health Technology Enterprise Team, Cooperative Agreements 01-CA-11244225-215 and Discover Life in America to D.L.W.

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