Cracking Complex Taxonomy of Costa Rican Moths: Anacrusis Zeller (Lepidoptera: Tortricidae: Tortricinae)

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CRACKING COMPLEX TAXONOMY OF COSTA RICAN MOTHS: *ANACRUSIS* ZELLER (LEPIDOPTERA: TORTRICIDAE: TORTRICINAE)

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ABSTRACT. Remarkably similar forewing patterns, striking sexual dimorphism, and rampant sympatry combine to present a taxonomically and morphologically bewildering complex of five species of *Anacrusis* tortricid moths in Central America: *Anacrusis turrialbae* Razowski, *Anacrusis piriferana* (Zeller), *Anacrusis terrimccarthyae*, **n. sp.**, *Anacrusis nephrodes* (Walsingham), and *Anacrusis ellensatterleeae*, **n. sp.** Morphology and DNA barcodes (i.e., the mitochondrial gene COI) corroborate the integrity of the five species, all of which have been reared from caterpillars in Area de Conservación Guanacaste (ACG) in northwestern Costa Rica. These species are polyphagous, with larval foodplants spanning many families of flowering plants. In ACG they occupy different forest types that are correlated with elevation.

Additional key words: systematics, cryptic species, Neotropics, food plant generalists, DNA barcoding

Members of the genus *Anacrusis* Zeller, 1877 are among the largest New World moths, with forewings frequently exceeding 18 mm in length. Extremely similar forewing patterns, pronounced sexual dimorphism, and sympatric occurrence render them among the more challenging Lepidoptera from a taxonomic perspective. The genus includes about 15 described species (the number depending upon subjective synonymy), five of which are now known from Central America. DNA barcodes of a large sample (i.e., over 500 individuals) of *Anacrusis* from Area de Conservación Guanacaste (ACG) in northwestern Costa Rica revealed five distinct groups of haplotypes that are correlated with morphology—three formerly described and two undescribed species, each occupying one of three parapatric elevationally distinct habitats. The purpose of this study is to reconcile the DNA evidence with facies, morphology, and existing nomenclature, and to briefly touch on patterns of host use exhibited by members of the species complex.

MATERIALS AND METHODS

Rearing. An ongoing inventory of the caterpillars of ACG in northwestern Costa Rica began in 1977–1978 by Daniel Janzen and Winnie Hallwachs (Janzen & Hallwachs 2013). Currently, the bulk of collecting and rearing is done by local parataxonomists (Janzen & Hallwachs 2011). Caterpillars discovered in the field are taken to "rearing barns" where they are placed singly in plastic bags or bottles with cuttings of the host species upon which they were discovered. As adults emerge, they are frozen, pinned, and labeled. Field-collected caterpillars are labeled with a unique voucher number in the form of YY-SRNP-X…… (e.g., 09-SRNP-15328), where the prefix is the last two digits of the year (e.g., 2009), "SRNP" refers to the project "call letters" assigned in 1977 (when the initial project site was referred to as Santa Rosa National Park), and the suffix is a unique number assigned within the year. Because the voucher number actually applies to the event of finding the caterpillar and is so coded in the project data base, the resultant adult specimen (if successfully reared) receives the same voucher code.

Food plant names are from the on-line database of Janzen & Hallwachs (2013). In the species accounts, food plant data are presented in alphabetical order by family, genus, and species.

Barcoding. DNA sequencing (i.e., obtaining a COI barcode) followed standard methods employed at the Biodiversity Institute of Ontario, University of Guelph (Craft et al. 2010, Wilson 2012), using the tissue in the leg of an oven-dried adult moth. A total of 753 vouchers was sampled for DNA, resulting in 422 high quality 658 bp DNA barcodes in BOLD (http://www.boldsystems.org) as well as many more somewhat shorter barcodes that are functional for identification. Owing to minimal divergence within species, Fig. 1 includes only 394 of the most common sequences in order to minimize space. Sequence divergences greater than 2% often correspond to interspecific differences, while lower values are typical of intraspecific variation (e.g., Hausmann et al. 2011). However, because the significance of the level of divergence varies among taxa, we do not assign an arbitrary level to species status, we merely report values in the discussion. All adult vouchers are permanently deposited at the National Museum of Natural History, Washington, DC. Images for the BOLD records were taken of pinned moths, done at the moment of removing a leg.

Species Circumscription. Species initially were sorted by barcode clusters and sex. Then, representative examples (at least three males and three females) of each cluster were dissected to search for differences in genitalia among the species. In the two largest clusters, particular attention was given to deep splits (i.e., subclusters with genetic divergence of greater than about 2%) and outliers. Representatives of the five groups for which barcode data and morphology provided compelling evidence of species-level distinctness were compared with type specimens of described species of *Anacrusis*, mostly at The Natural History Museum, London, and relevant literature (e.g., Razowski 2004, Razowski & Becker 2004, 2011).

Dissection and Morphological Terminology. Dissection methods follow those presented in Brown and Powell (1991). Terminology for genitalia structures and forewing pattern elements follows Powell and Brown (2012). The hind margin of the forewing is referred to as the dorsum, based on its position when the moth is in typical resting posture. The phallus of all dissected male genitalia was examined using a compound microscope to determine the presence/ absence and shape of cornuti and/or scars representing attachment points for deciduous cornuti. The highly modified scaling on the venter of the posterior end of the female is referred to as "corethrogyne" scaling.

Illustrations. Images of adults and genitalia were captured using a Canon EOS 40D digital SLR (Canon U.S.A., Lake Success, NY) mounted on a Visionary Digital BK Lab System (Visionary Digital, Palmyra, VA). For observations of hindwing ultrastructure, the wings were detached from the metathorax of pinned adult specimens and placed on carbon-adhesive tabs (a product of Electron Microscopy Sciences) that were premounted onto a 25-mm aluminum stub. Specimens were coated with 30–35 nm of gold-palladium using a Cressington Scientific 108A sputter coater and observed using a Zeiss EVO scanning electron microscope, model number MA15 at an accelerating voltage of 12 kV.

Depositories and abbreviations. Institutions abbreviated in the text include the following: BMNH, The Natural History Museum, London, UK; EME, Essig Museum of Entomology, University of California, Berkeley, CA, U.S.A.; INBio, Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica; and USNM, United States National Museum of Natural History, Washington, DC, U.S.A. The following abbreviations are used: em = emerged; P.N. = Parque Nacional; r.f. = reared from; and TL = type locality.

SYSTEMATICS

The tribe Atteriini is among the smallest in the family Tortricidae on the basis of the number of described species, but its included members are the among the largest based on forewing length. The group is restricted to the New World tropics, comprising eight described genera (Powell et al. 1995). As currently defined, the genus *Anacrusis* includes 18 described species (excluding the species described herein), the number varying with taxonomic opinion (i.e., subjective synonymy), distributed from Mexico to Brazil. All known species exhibit dramatic sexual dimorphism in forewing pattern, frequently accompanied by only subtle differences in structures of the male and female genitalia. We discuss five species herein, but it is possible that two or more additional species of *Anacrusis* occur in Central America. Although most of the Costa Rican material discussed below is identified based on DNA barcodes, other examined specimens from Central America are associated with the barcode clusters by male and female genitalia and male secondary structures. Males and females of the Costa Rican species were associated by DNA barcodes.

Anacrusis turrialbae Razowski & Becker
(Figs. 2, 7, 12, 17)

Anacrusis turrialbae Razowski & Becker 2011: 164. TL: Costa Rica (Turrialba).

The cluster (including outliers) in Fig. 1 includes 72 specimens that agree in forewing pattern (Figs. 2, 7) and male and female genitalia (Figs. 12, 17) with specimens illustrated by Razowski & Becker (2011) as *Anacrusis turrialbae*. The five females termed "*Anacrusis turrialbae*DHJ02" likewise agree in forewing pattern.

Diagnosis. Male. The male of *Anacrusis turrialbae* is easily distinguished from other Central American *Anacrusis* by forewing pattern alone (Fig. 2): brown ground color with a large maroon triangular patch near the middle and a small oblong orange blotch in the subterminal area, the latter narrowly outlined by white along its inner and upper edges. The species is most similar to *Anacrusis aulaeodes* (Meyrick) (TL: Colombia, Mount Tolima), from which it can be distinguished by

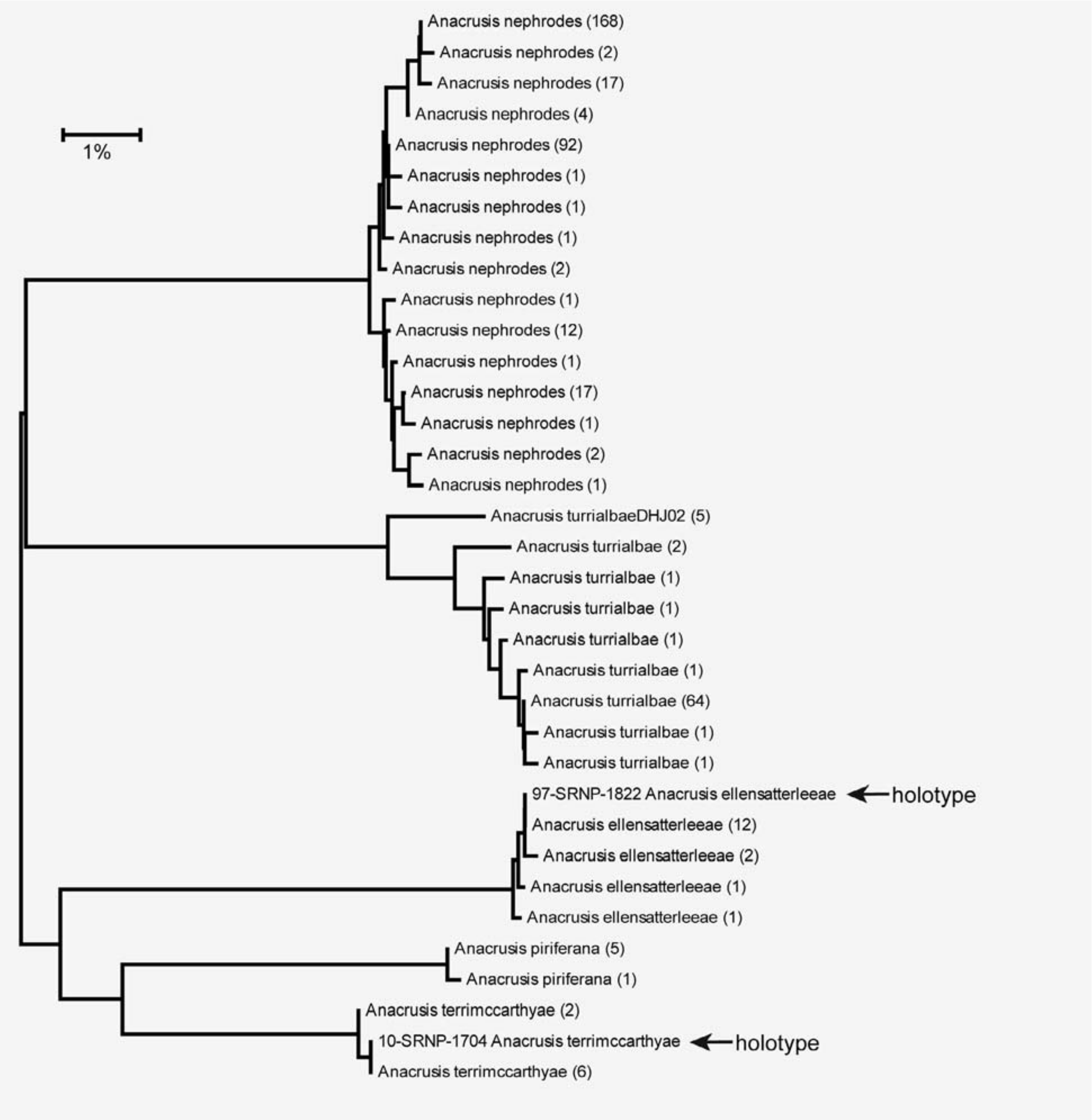


FIG. 1. Neighbor-joining tree based only on ACG *Anacrusis* COI sequences for complete (658 bp) DNA barcodes [not all specimens included].

the shape of the narrow white line in the apical region of the forewing (curved and forming the upper and inner edge of the orange oval blotch in *Anacrusis turrialbae* (Fig. 2), straight and oblique from the apex in *Anacrusis aulaeodes*) and the termination of the sacculus in the male genitalia (angulate-triangular in *Anacrusis turrialbae* (Fig. 12), rounded in *Anacrusis aulaeodes*). The hindwing cubital pecten of *Anacrusis turrialbae* is short with blunt-tipped scales (Fig. 22, 23) similar to that of *Anacrusis aulaeodes*, *Anacrusis piriferana*, and *Anacrusis terrimccarthyae*, and distinct from that of *Anacrusis nephrodes* and *Anacrusis ellensatterleeae* (Fig. 24, 25). The male genitalia (Fig. 12) are most easily distinguished by the conspicuously angled distal 0.3 of the uncus with a single undivided "hood" and by the triangular process at the distal end of the sacculus.

Female. The female of *Anacrusis turrialbae* (Fig. 7) is extremely similar to that of *Anacrusis piriferana* and

Anacrusis terrimccarthyae (that of the South American *Anacrusis aulaeodes* is not yet associated with the male) with a small, dark, circular brown patch in the subapical region narrowly outlined with white and a small white blotch at its outer edge. It can be distinguished from that of *Anacrusis piriferana* and *Anacrusis terrimccarthyae* by the absence of the small dark brown dot or dots in the middle of the subterminal area which are present in the latter two. The middle corethrogyne scales on the venter of A8 are pearly cream; the lateral scales have just a hint of honey-coloring. In the sterigma (Fig. 17), the lateroanterior lobes are evenly rounded, and the lateral arms are relatively short and rounded distally. The signum is a hollow, evenly curved thorn.

Barcode Data. The one moderately deep divergence in the barcode data (Fig. 1) is not corroborated by wing pattern, genitalia, or ecology evidence. The five divergent specimens are females, each hyperdiversely different in one place (nt 315-406) but identical to the others in the remainder of the barcode (Sean Prosser, personal communication). We conclude that they do not represent another cryptic species.

Geographic Distribution. In addition to the long series of reared and barcoded specimens from ACG, we examined 18 males and six females from other parts of Costa Rica (USNM, EME), two males from Panama, one male from Colombia, one female from French Guiana, and one female from Peru (USNM) that all appear to represent this species based on phenotype and genitalia (although none of these was barcoded). Four males and a female from Ecuador (USNM, EME) are indistinguishable from *Anacrusis turrialbae* in facies and genitalia, but the single barcoded male has considerably divergent COI (about 7%) and, hence, these specimens likely represent an undescribed, cryptic species, and this may be true of the specimens from Peru, as well. We examined four males of the closely related *Anacrusis aulaeodes*, one from Colombia and three from Ecuador (BMNH), and all agree in facies and genitalia with the holotype.

In ACG, *Anacrusis turrialbae* is a lowland to intermediate elevation rain forest species, encountered primarily below 500 m elevation, with a few scattered records as high as 620 m.

Host plants. *Anacrusis turrialbae* is extremely polyphagous, with larvae collected and reared from the following plants in ACG (numbers of rearings for each species of plant are available in Janzen and Hallwachs 2013): *Stenanona costaricensis* (Annonaceae), *Rhodospatha pellucida* (Araceae), *Lepidaploa tortuosa* (Asteraceae), *Vernonia patens* (Asteraceae), *Mansoa hymenaea* (Bignoniaceae), *Cordia polycephala* (Boraginaceae), *Clethra mexicana* (Clethraceae), *Rourea schippii* (Connaraceae), *Asplundia utilis* (Cyclanthaceae), *Cyclanthus bipartitus* (Cyclanthaceae), *Davilla nitida* (Dilleniaceae), *Adelia triloba* (Euphorbiaceae), *Acalypha diversifolia* (Euphorbiaceae), *Satyria panurensis* (Ericaceae), *Inga punctata* (Fabaceae), *Lonchocarpus guatemalensis* (Fabaceae), *Drymonia macrophylla* (Gesneriaceae), *Hernandia stenura* (Hernandiaceae), *Aegiphila cephalophora* (Lamiaceae), *Nectandra hihua* (Lauraceae), *Persea americana* (Lauraceae), *Lomariopsis vestita* (Lomariopsidaceae), *Stigmaphyllon lindenianum* (Malpighiaceae), *Hampea appendiculata* (Malvaceae), *Trichospermum grewiifolium* (Malvaceae), *Clidemia hirta* (Melastomataceae), *Cedrela odorata* (Meliaceae), *Guarea bullata* (Meliaceae), *Siparuna thecophora* (Monimiaceae), *Sorocea trophoides* (Moraceae), *Brosimum alicastrum* (Moraceae), *Otoba novogranatensis* (Myristicaceae), *Psidium guajava* (Myrtaceae), *Heisteria concinna* (Olacaceae), *Sobralia* sp. (Orchidaceae), *Sobralia mucronata* (Orchidaceae), *Piper auritum* (Piperaceae), *Piper peltatum* (Piperaceae), *Piper umbellatum* (Piperaceae), *Coccoloba tuerckheimii* (Polygonaceae), *Ardisia auriculata* (Primulaceae), *Ardisia compressa* (Primulaceae), *Ardisia standleyana* (Primulaceae), *Myrsine coriacea* (Primulaceae), *Clematis haenkeana* (Ranunculaceae), *Coccocypselum herbaceum* (Rubiaceae), *Coussarea caroliana* (Rubiaceae), *Hamelia patens* (Rubiaceae), *Lindenia rivalis* (Rubiaceae), *Palicourea guianensis* (Rubiaceae), *Pentagonia donnell-smithii* (Rubiaceae), *Posoqueria latifolia* (Rubiaceae), *Rudgea cornifolia* (Rubiaceae), *Serjania mexicana* (Sapindaceae), *Chrysophyllum brenesii* (Sapotaceae), *Cestrum megalophyllum* (Solanaceae), *Cestrum racemosum* (Solanaceae), *Solanum hazenii* (Solanaceae), and *Luehea seemannii* (Tiliaceae).

Discussion. *Anacrusis turrialbae* has been misidentifed as *Anacrusis aulaeodes* in North American collections for decades. This probably reflects the fact that one of the specimens from Meyrick's (1926) original type series of *Anacrusis aulaeodes*, currently in the USNM and previously undissected, is actually a specimen of *Anacrusis turrialbae* from the type locality of *Anacrusis aulaeodes* (Colombia, Tolima Canyon) – a remarkable and very useful case of sympatry. Clarke (1958) illustrated the lectotype male of *Anacrusis aulaeodes* (BMNH), along with its genitalia, but the similarity of Costa Rican specimens (i.e., *Anacrusis turrialbae*) to the black-and-white photograph of the rubbed lectotype and the lack of a dissection (of the USNM specimen) disguised the identity of this closely related species until Razowski & Becker (2011) recognized it as new.

FIGS. 2–6. *Anacrusis* males. **2.** *Anacrusis turrialbae* Razowski. **3.** *Anacrusis terrimccarthyae* Brown. **4.** *Anacrusis piriferana* (Zeller). **5.** *Anacrusis nephrodes* (Walsingham). **6.** *Anacrusis ellensatterleeae* Brown.

FIGS. 7–11. *Anacrusis* females. **7.** *Anacrusis turrialbae* Razowski. **8.** *Anacrusis terrimccarthyae* Brown. **9.** *Anacrusis piriferana* (Zeller). **10.** *Anacrusis nephrodes* (Walsingham). **11.** *Anacrusis ellensatterleeae* Brown.

Anacrusis terrimccarthyae Brown, **new species**
(Figs. 3, 8, 13, 18)

A small divergent barcode cluster of ecologically distinct specimens (Fig. 1) revealed distinct genitalia in both sexes. Based on male genitalia, we associate with this barcode cluster five additional specimens (EME). Finding no described material that matched these specimens, we treat them as a new species.

Diagnosis. Male. The male of *Anacrusis terrimccarthyae* (Fig. 3) is superficially nearly indistinguishable from all species treated here except *Anacrusis turrialbae*. The short, blunt-tipped scales of the hindwing cubital pecten are similar to those of *Anacrusis piriferana* and *Anacrusis turrialbae*, and conspicuously different from the long, slender, lanceolate-tipped scales of *Anacrusis nephrodes* and *Anacrusis ellensatterleeae*. The male genitalia (Fig. 13) are distinguished from those of *Anacrusis piriferana* by the smaller, less divergent lobes of the distal portion of the uncus, the nearly straight anterior edge of the transtilla, and the rounded, longer, less sclerotized sacculus that extends to about 0.75 the distance from base to apex of the valva.

Female. The female of *Anacrusis terrimccarthyae* (Fig. 8) is superficially similar to that of *Anacrusis piriferana*, with a small circular brown patch in the subapical region narrowly outlined with white, a small white blotch at its outer edge, and the presence of one or two small dark brown dots in the middle of the subterminal area. The corethrogyne scales on the venter of A8 are pearly cream-white throughout. In the sterigma (Fig. 18), the lateroanterior lobes are somewhat angulate, and the lateral arms are extremely long and digitate. The signum is slightly broader, slightly straighter, and more platelike than that of *Anacrusis turrialbae*.

Description. Male. *Head*: Vertex and upper frons rough scaled, maroon; lower frons smooth scaled, cream; labial palpus pale maroon on outer surface, paler on inner surface, length (all segments combined) about 1.25 times diameter of compound eye, second segment very weakly upcurved, third segment nearly concealed by scaling of second; ocellus conspicuous. Antenna with scape and pedicel maroon; scaling of flagellum maroon on basal 6–8 segments, becoming progressively paler toward distal end of antenna, with two rows of scales per flagellomere; sensory setae dense, with length about 0.5–0.6 times width of flagellomere. *Thorax*: Anterior portion of prothorax and base of tegula maroon, remainder fawn brown. Proleg with dense fascicle of long scales originating near trochanter, extending along femur (as illustrated in Brown 1990: fig. 5). Forewing length 10.2–11.5 mm (mean = 11.5; n = 5); forewing ground pale reddish brown, with faint, irregular, brown striations and irregular areas of paler overscaling; a large, triangular, maroon patch based on middle portion of costa (from about 0.30–0.75 distance from base to apex), extending toward and attenuating at or just before mid-dorsum; a large, darker maroon-brown sub-circular blotch occupying most of subterminal region, bulging inward near distal end of discal cell; a variable, ill-defined, pale bluish white spot between bulge on subterminal blotch and triangular patch. Fringe concolorous with forewing ground. Hindwing uniformly brown, except for paler region near anal margin; cubital pecten a dense patch of short, blunt-tipped scales (Fig. 22, 23); fringe pale reddish brown. *Abdomen*: Shiny pale gray dorsally, with some cream scales on venter; scales at distal end of abdomen and externally on genitalia slightly to conspicuously darker. Genitalia (Fig. 13) with tegumen short, broad; vinculum rather long; uncus with base broad, middle narrow, distal process hood-like and expanded; socius with basal 0.5 broad, distal 0.5 digitate, scaling long and dense; gnathos arms narrow, with large, flat, crescent-shaped process at mesal junction of arms; valva broad, upturned, mostly parallel-sided, costa conspicuously sclerotized in basal 0.5, narrowly sclerotized in distal 0.5; sacculus narrow, confined to ventral edge of basal 0.5 of valva, then upturned, slightly diverging from edge of valva, ending in a poorly defined, rounded tip; base of valva weakly sclerotized with digitate, slightly attenuate region of similar sclerotization extending from basal region toward apex; transtilla a somewhat uniform band with small spines on posterior margin, most dense in middle; juxta a broad, mostly semicircular plate with pointed process at middle (attachment of phallus). Phallus bent at about 90° near middle, basal 0.5 broad, rounded, distal 0.5 uniformly narrow; vesica with fascicle of about 17–18 slender, aciculate, subbasally attached, deciduous cornuti and a single broad, spindle-shaped non-deciduous cornutus.

Female. *Head and Thorax*: As described for male except proleg without modified scaling and hindwing lacking dense scale patch at base of Cu. Forewing length 12.0–15.0 mm (mean = 13.5; n = 7); forewing ground pale reddish brown, with faint, irregular, pale brown striations; a brownish maroon, oblique fascia from costa about 0.35 distance from base to apex, expanding to triangular termination near lower edge of discal cell; a concolorous circular blotch just below costa about 0.7 distance from base to apex, narrowly outlined by white, with small triangular expansion of white scales toward outer margin of wing; area between oblique fascia and circular patch with faint trace of pale bluish scales; a small black dot between CuA and M_3 midway between discal cell and termen; termen with conspicuous concavity in apical 0.4. Fringe concolorous with forewing ground in tornal region, darker brown along concavity. Hindwing mostly brown, paler along outer margin. *Abdomen*: Gray brown dorsally, corethrogyne scaling of venter pearly cream-white throughout. Genitalia (Fig. 18) with papillae anales broad, unmodified; apophyses posteriores slightly longer than anteriores; lateral arms of sterigma extremely long, digitate, fairly uniform in width; ductus bursae about 1.5 times as long as corpus bursae, colliculum comparatively long; corpus bursae rounded, finely punctuate; signum fin-shaped from a small, irregularly rounded base.

Barcode Data. The barcode data (Fig. 1) show a tight cluster of nine individuals with a divergence of less than 0.3 percent.

Geographic Distribution. In addition to the ACG reared series, we examined five specimens from Alajuela (700–850 m), Costa Rica, that are conspecific with the reared specimens based on genital morphology. In ACG this species lives in a narrow elevational band (710 to 1220 m) that is the boundary between cloud forest (above) and intermediate elevation rain forest (below) on Volcan Cacao which, as an isolated peak, has cloud forest at lower elevation than is the case on Costa Rican mountain massifs. In this position it is immediately below *Anacrusis ellensatterleeae* and immediately above the other three ACG species of *Anacrusis*.

Food plants. Larvae of *Anacrusis terrimccarthyae* were collected and reared from the following ACG food plants: *Desmopsis schippii* (Annonaceae), *Trema micrantha* (Cannabaceae), *Persea americana* (introduced) (Lauraceae), *Eugenia basilaris* (Myrtaceae), *Ardisia compressa* (Primulaceae), *Myrsine coriacea* (Primulaceae), *Billia hippocastanum* (Sapindaceae), *Paullinia faginea* (Sapindaceae), *Pouteria exfoliata* (Sapotaceae), and *Solanum schlechtendalianum* (Solanaceae).

Larva. The head is pale coffee brown; the thorax has a black prothoracic collar; and the body is pale yellow with fine white hairs (Janzen & Hallwachs 2013).

Discussion. Variation within both sexes of this species renders them superficially indistinguishable from adults of *Anacrusis piriferana*. The sexes were associated solely on the basis of the barcode data; subsequent dissections revealed that the genitalia are distinct from related congeners as described above.

Holotype ♂, Costa Rica, Alajuela, Sector Rincon Rain Forest, Sendero Albergue Crater, 980 m, 10.84886N, -85.3281W, 25 Mar 2010 (1♂), r.f. *Ardisia compressa*, O. Espinoza, em: 8 Apr 2010 (10-SRNP-1704) (USNM).

Paratypes (10♂, 7♀). COSTA RICA: Alajuela: San Ramon, Reserva Biologia Alberto M. Brenes, 850 m, 7–11 Feb 2005 (1♂), J. B. Sullivan (12-SRNP-13003) (USNM). Río Sarapiqui, 2 km SE Cariblanco, 700 m, 28 Mar 1992 (3♂), McCarthy & Powell (EME). Río Sarapiqui, 6 air km S San Miguel, 800 m, 7 Jun 1988 (1♂), J. Brown & J. Powell (EME). Guanacaste: Area de Conservacion Guanacaste: Sector Cacao, Sendero Nayo, 1090 m, 10.92446N, -85.46953W, 18 Nov 2006 (1♀), r.f. *Ardisia compressa*, H. Ramirez, em: 10 Dec 2006 (06-SRNP-36810) (USNM); 14 July 1999 (1♀), r.f. *Mysine coriacea*, D. Janzen, em: 22 Aug 1999 (99-SRNP-1154) (USNM); 14 Feb 2008 (1♀), r.f. *Billia hippocastanum*, H. Ramirez, em: 9 Mar 2008 (08-SRNP-35037) (USNM). Sector Cacao, Estacion Cacao, 1150 m, 10.92691N, -85.46822W, 2 Aug 2000 (1♀), r.f. *Trema micrantha*, M. Periera, em: 5 Sep 2000 (00-SRNP-10308) (USNM); 21 Jul 2009 (1♂), r.f. *Myrsine coriaceae*, H. Ramirez, em: [no data] (09-SRNP-36609). Sector Cacao, Sendero Circular, 1185 m, 10.92714N, -85.4668W, 19 Feb 2008 (1♀), r.f. *Pouteria exfoliata*, M. Peiiera, em: 22 Mar 2008 (08-SRNP-35082) (USNM); 19 Feb 2008 (1♂), r.f. *Persea americana*, H. Ramirez, em: 16 Mar 2008 (08-SRNP-35079) (USNM). Sector Cacao, Sendero Toma Agua, 1140 m, 10.92847N, -85.46680W, 4 Aug 1999 (1♂), r.f. *Solanum schlechtendalianum* (Solanaceae), M. Pereira, em: 3 Sep 1999 (99-SRNP-1300) (USNM). Sector Rincon Rain Forest, Sendero Albergue Crater, 980 m, 10.84886N, -85.3281W, 14 Mar 2012 (1♀), r.f. *Ardisia compressa*, G. Sihezar, em: 7 Apr 2012 (10-SRNP-1392) (USNM); 20 Mar 2010 (1♀), r.f. *Paullinia faginea*, G. Sihezar, em: 13 Apr 2010 (10-SRNP-1611) (USNM). Sector Pitilla, Sendero Nacho, 710 m, 10.98445N, -85.42481W, 27 Jan 2010 (1♂), r.f. *Eugenia basilaris*, P. Rios, em: 12 Feb 2010 (10-SRNP-30416) (USNM). Sector Pitilla, Sendero Orosilito, 900 m, 10.98332N, -85.43623W, 17 Apr 2005 (1♂), r.f. *Desmopis schippii*, M. Rios, em: 7 May 2005 (05-SRNP-31531) (USNM).

Etymology. *Anacrusis terrimccarthyae* from the upper slopes of Volcan Cacao is named to honor Terri McCarthy of Grand Rapids, Michigan, in recognition and in gratitude for her three decades of intense care for the Wege Foundation and its antecedents, extraordinary encouragement for the development of Area de Conservacion Guanacaste (ACG), decades of enthusiastic fund-raising to save and expand ACG forest, and believing in the ACG teachers that educate and fascinate upcoming generations.

Anacrusis piriferana (Zeller, 1877)

(Figs. 4, 9, 14, 19)

Grapholitha piriferana Zeller, 1877: 158. TL: Chiriqui, Panama.

Anacrusis piriferana; Clarke 1958: 28 (combination); Razowski & Becker 2011: 166 (revised status).

Anacrusis piriferana (= *stapiana*); Powell et al. 1995: 148 (synonymy); Brown 2005: 89.

Cacoecia geographica Meyrick, 1912: 678. TL: Palma Sola, Venezuela.

Anacrusis geographica (= *piriferana*); Clarke 1958: 28 (synonymy).

Anacrusis geographica (= *stapiana*); Powell et al. 1995: 148 (synonymy); Brown 2005: 89.

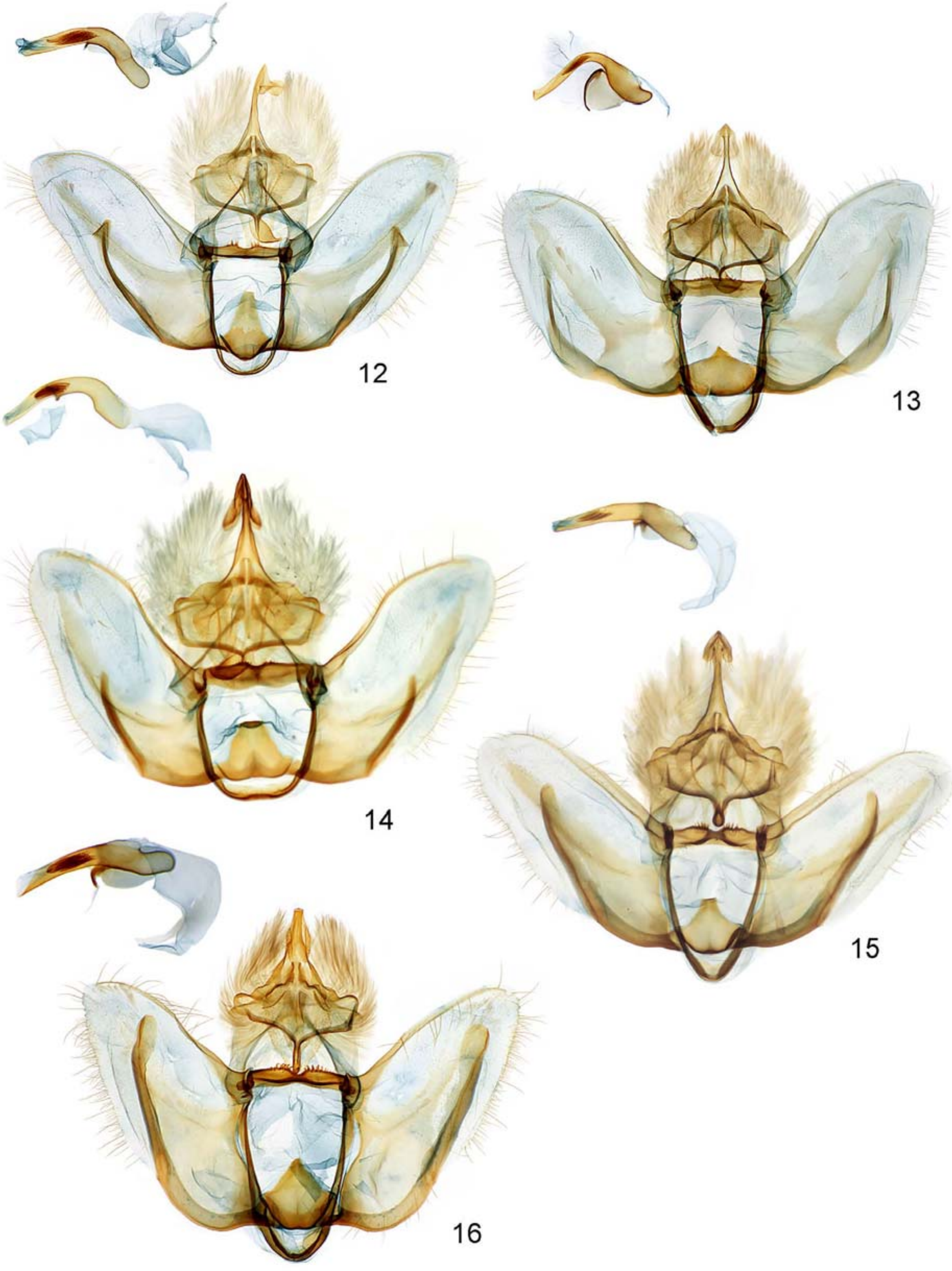
A small, divergent barcode cluster of specimens (about 7% divergent from the nearest other cluster) (Fig. 1) revealed distinct genitalia in both sexes. The male genitalia are identical to those of *Anacrusis piriferana* as illustrated by Clarke (1958) and Razowski & Becker (2011). We also examined a large number of field-collected specimens ranging from Costa Rica to Venezuela that are identical in facies and genitalia. A single field-collected specimen from French Guiana was DNA barcoded, revealing about 3% divergence from the cluster of *Anacrusis piriferana*. Its conspecificity with the latter is therefore questionable.

Diagnosis. Male. The male of *Anacrusis piriferana* (Fig. 4) is superficially nearly indistinguishable from all ACG *Anacrusis* except *Anacrusis turrialbae*. It shares the short patch of blunt-tipped scales of the hindwing cubital pecten with *Anacrusis terrimccarthyae* and *Anacrusis turrialbae*. The genitalia (Fig. 14) are distinguished from those of *Anacrusis terrimccarthyae* by the larger, usually divergent lobes of the distally-bent apical portion of the uncus; the short, angled (in basal 0.4), more strongly sclerotized sacculus that extends to about 0.5 valva length; and the distinctly bilobed transtilla.

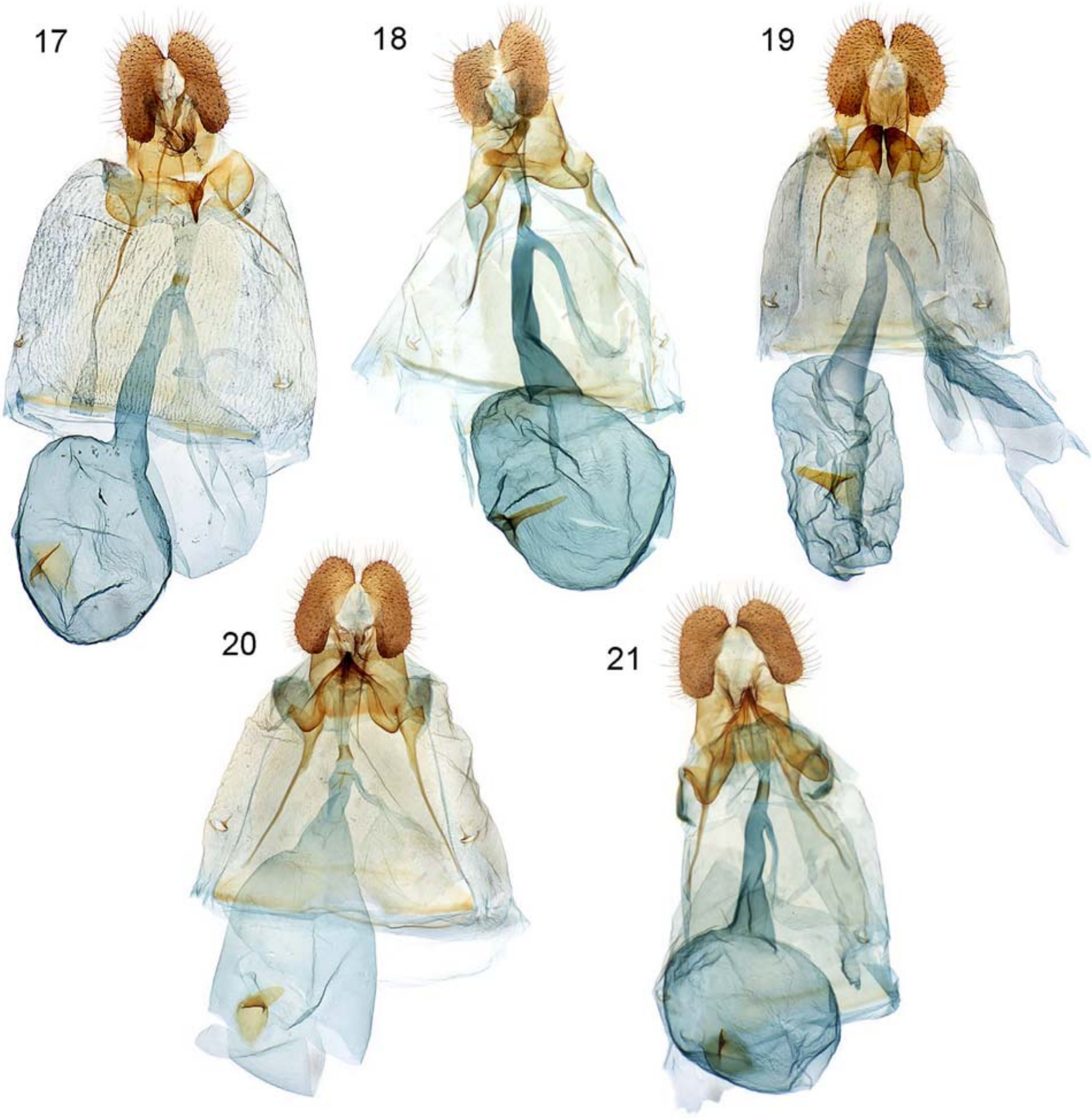
Female. The female of *Anacrusis piriferana* (Fig. 9) is superficially indistinguishable from that of *Anacrusis terrimccarthyae*, with a small circular brown patch in the subapical region narrowly outlined with white, a small white blotch at its outer edge, and the presence of one or two small dark brown dots in the middle of the subterminal area. The corethrogyne scales on the venter of A8 are pearly cream-white in the middle and gray laterally, which may be diagnostic. In the sterigma (Fig. 19), the lateroanterior lobes are short and round and the lateral arms are broad and comparatively shorter, weakly attenuating distally. The signum is broad, long, and thorn-like.

Barcode Data. There is a tight cluster of six individuals with almost no difference in barcodes (Fig. 1).

Geographic Distribution. Based on male and female genitalia, we assign specimens from Costa Rica, Colombia, and Venezuela (BMNH, EME, INBio, USNM) to this species. Two specimens from French Guiana (USNM) are conspicuously smaller than *Anacrusis piriferana* from elsewhere but are indistinguishable from putative conspecifics based on facies, male secondary features, and genitalia. However, sequence data from the more recently collected of the two show a slight divergence from the tight cluster of specimens from Costa Rica; therefore we suspect that the two specimens from French Guiana represent a closely related species.



FIGS. 12–16. *Anacrusis* male genitalia. **12.** *Anacrusis turrialbae* Razowski (USNM slide 137,460). **13.** *Anacrusis terrimccarthyae* Brown (USNM slide 137,569 and 137,465, capsule and phallus, respectively). **14.** *Anacrusis piriferana* (Zeller) (USNM slides 142,209 and 142,219, capsule and phallus, respectively). **15.** *Anacrusis nephrodes* (Walsingham) (USNM slide 137,463). **16.** *Anacrusis ellensatterleeae* Brown (USNM slides 142,268 and 141,886, capsule and phallus, respectively).



FIGS. 17–21. *Anacrusis* female genitalia. **17.** *Anacrusis turrialbae* Razowski (USNM slide 142,002). **18.** *Anacrusis terrimccarthyae* Brown (USNM slide 137,500). **19.** *Anacrusis piriferana* (Zeller) (USNM slide 137,459). **20.** *Anacrusis nephrodes* (Walsingham) (USNM slide 142,237). **21.** *Anacrusis ellensatterleeae* Brown (USNM slide 142,225).

This species was collected from 455 to 680 m elevation in ACG rain forest, placing it in the elevational band just below *Anacrusis terrimccarthyae*.

Host plants. *Anacrusis piriferana* is polyphagous, with larvae collected and reared from the following ACG plants: *Clethra mexicana* (Clethraceae), *Alchornea costaricensis* (Euphorbiaceae), *Pausandra trianae* (Euphorbiaceae), *Strychnos chlorantha* (Loganiaceae), *Conostegia xalapensis* (Melastomataceae), *Clavija costaricana* (Primulaceae), and *Paullinia grandifolia* (Sapindaceae).

Larva. Based on rearing notes from Janzen and Hallwachs (2013), the larva has a brown head and a green body, and rolls the soft new leaves of the host plant.

Discussion. *Anacrusis piriferana* (holotype ♂; TL: Panama) and its probable synonym, *geographica* (holotype ♂, without abdomen; TL: Venezuela), were synonymized with *Anacrusis stapiana* (Felder & Rogenhofer) (holotype ♀; TL: Brazil) by Powell et al. (1995), and that treatment was followed by Brown (2005). Unfortunately, the genitalia on the slide-mounted preparation of the holotype of *Anacrusis stapiana* do not belong to *Anacrusis*, and it is obvious that the wrong abdomen was glued to the holotype (fide J. Powell notes on the BMNH slide). Hence, comparisons cannot be made between the holotype of *Anacrusis stapiana* and females that are associated with males of *Anacrusis piriferana* based on barcode data. Consequently, there is no evidence that the two (i.e., the holotype male of *Anacrusis piriferana* and the holotype female of *Anacrusis stapiana*) represent opposite sexes of the same species. We remove *Anacrusis piriferana* (and *Anacrusis geographica*) from synonymy of *Anacrusis stapiana* for the following reasons: (1) there are subtle differences between the forewing patterns of female *Anacrusis piriferana* and the holotype of *Anacrusis stapiana* (i.e., the dark markings in the subterminal region of *Anacrusis piriferana* are usually represented by one or two dots, sometimes fused, whereas the marking in the same area of the holotype of *Anacrusis stapiana* is narrow and wedge-shaped); (2) we have seen no males of *Anacrusis piriferana* from Brazil; and (3) our ability to associate sexes of *Anacrusis* based on anything but barcodes would be guesswork. Hence, we treat *Anacrusis stapiana* as a taxon separate from *Anacrusis piriferana* until additional females matching the holotype of *Anacrusis stapiana* or males matching *Anacrusis piriferana* from Amazona are discovered and their genitalia compared.

Anacrusis nephrodes (Walsingham, 1914)
(Figs. 5, 10, 15, 20)

Tortrix nephrodes Walsingham, 1914: 276. TL: Chiriqui, Panama.
Anacrusis nephrodes; Powell et al. 1995: 148 (combination); Brown 2005: 89; Razowski & Becker 2011: 165.

All members of our largest barcode cluster of specimens (Fig. 1) are extremely similar in forewing pattern and identical in male and female genitalia. Females compare favorably with the holotype of *Anacrusis nephrodes*, and on this basis we assign our specimens to this species. We also assign to this species a number of field-collected specimens ranging from Guatemala to Panama that are identical in forewing pattern, male secondary features, and genitalia.

Diagnosis. Male. The male of *Anacrusis nephrodes* (Fig. 5) is superficially essentially indistinguishable from all ACG *Anacrusis* but *Anacrusis turrialbae*. It shares the long, slender, lanceolate-tipped scales of the hindwing cubital pecten with *Anacrusis ellensatterleeae*. The male genitalia (Fig. 15) are distinguished from those of *Anacrusis ellensatterleeae* by the distal portion of the uncus, which is divided into a pair of lateral processes forming a tent rather than undivided and forming a somewhat ovoid hood as in *Anacrusis ellensatterleeae*; by the weakly U-shaped lower (anterior) edge of the transtilla, which is straighter in *ellensatterleeae*; and by the shape of the large cornutus in the vesica.

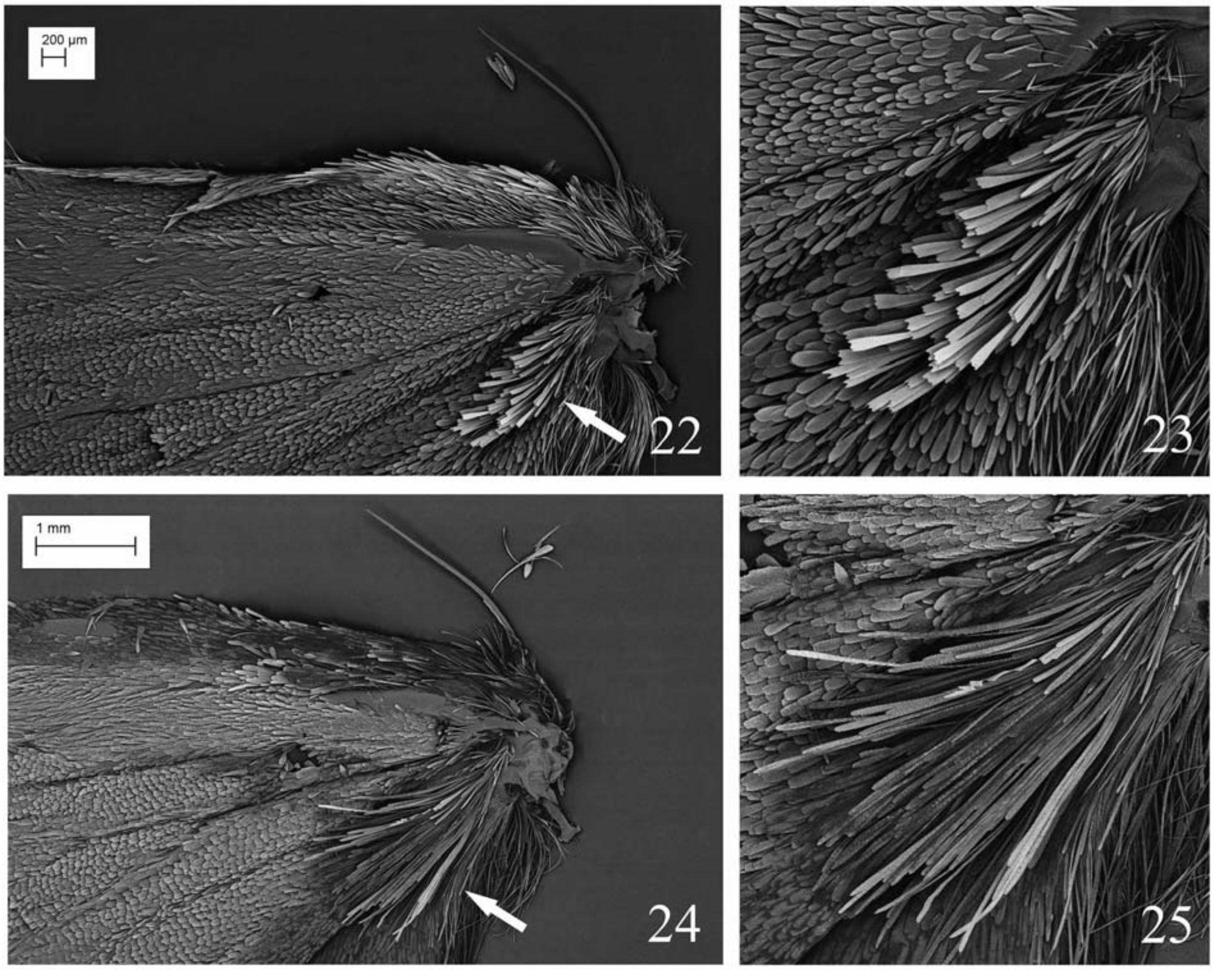
Female. The female of *Anacrusis nephrodes* (Fig. 10) is nearly indistinguishable from that of *Anacrusis ellensatterleeae*, with a small silver-white rounded dash at the outer edge of the forewing costal blotch. The large costal blotch has the margins more sharply defined, and rarely is there any white scaling accompanying the dark dots in the middle of the subterminal region. The corethrogyne scales on the venter of A8 are entirely beige. In the sterigma (Fig. 20), the lateroanterior lobes are angled subbasally, and the lateral arms are relatively short, somewhat triangularly expanded distally, with rounded and finely spined apices. The signum is flattened and blade-like rather than thornlike.

Barcode Data. The barcode data show a large, tight cluster of over 323 individuals with complete barcodes, and even shorter barcodes link within this larger cluster, distinct from the other four barcode (i.e., species) clusters. All haplotypes are within about 0.5% divergence.

Geographic Distribution. We assign specimens from Guatemala, El Salvador, Nicaragua, Costa Rica, and Panama (USNM, EME) to this species. In ACG and elsewhere in Costa Rica, this species is the most common *Anacrusis* in the low- to mid-elevation band of rain forest below the elevational band of *Anacrusis terrimccarthyae*.

Host plants. *Anacrusis nephrodes* is extremely polyphagous, with larvae collected and reared from the following ACG plants: *Justicia aurea* (Acanthaceae), *Tapirira brenesii* (Anacardiaceae), *Anaxagorea crassipetala* (Annonaceae), *Guatteria diospyroides* (Annonaceae), *Guatteria tonduzii* (Annonaceae), *Tabernaemontana alba* (Apocynaceae), *Dendropanax arboreus* (Araliaceae), *Vernonia patens* (Asteraceae), *Mansoa hymenaea* (Bignoniaceae), *Adelia triloba* (Euphorbiaceae), *Alchornea latifolia* (Euphorbiaceae), *Conceveiba pleiostemona* (Euphorbiaceae), *Inga umbellifera* (Fabaceae), *Pterocarpus hayesii* (Fabaceae), *Zygia longifolia* (Fabaceae), *Drymonia macrophylla* (Gesneriaceae), *Drymonia serrulata* (Gesneriaceae), *Paradrymonia decurrens* (Gesneriaceae), *Matudaea trinervia* (Hamamelidaceae), *Hernandia stenura* (Hernandiaceae), *Alfaroa guanacastensis* (Juglandaceae), *Beilschmiedia costaricensis* (Lauraceae), *Nectrandra hihua* (Lauraceae), *Nectandra umbrosa* (Lauraceae), *Ocotea insularis* (Lauraceae), *Ocotea puberula* (Lauraceae), *Mortoniodendron costaricense* (Malvaceae), *Trichospermum galeottii* (Malvaceae), *Cedrela odorata* (Meliaceae), *Guarea bullata* (Meliaceae), *Guarea kegelii* (Meliaceae), *Guarea rhopalocarpa* (Meliaceae), *Trichilia adolfi* (Meliaceae), *Trichilia martiana* (Meliaceae), *Siparuna thecophora* (Monimiaceae), *Clarisia mexicana* (Moraceae), *Sorocea affinis* (Moraceae), *Sorocea trophoides* (Moraceae), *Ludwigia leptocarpa* (Onagraceae), *Sobralia* sp. (Orchidaceae), *Bocconia frutescens* (Papaveraceae), *Piper amalago* (Piperaceae), *Piper arboreum* (Piperaceae), *Piper auritum* (Piperaceae), *Piper cenocladum* (Piperaceae), *Piper fimbriulatum* (Piperaceae), *Piper glabrescens* (Piperaceae), *Piper guanacostense* (Piperaceae), *Piper imperiale* (Piperaceae), *Piper phytolaccaefolium* (Piperaceae), *Piper reticulatum* (Piperaceae), *Piper sancti-felicis* (Piperaceae), *Piper* sp. (Piperaceae), *Piper tuberculatum* (Piperaceae), *Ardisia auriculata* (Primulaceae), *Ardisia calycosa* (Primulaceae), *Ardisia compressa* (Primulaceae), *Ardisia opegrapha* (Primulaceae), *Parathesis glabra* (Primulaceae), *Panopsis costaricensis* (Proteaceae), *Clematis haenkeana* (Ranunculaceae), *Faramea multiflora* (Rubiaceae), *Faramea stenura* (Rubiaceae), *Hamelia patens* (Rubiaceae), *Palicourea guianensis* (Rubiaceae), *Pentagonia donnell-smithii* (Rubiaceae), *Psychotria aggregata* (Rubiaceae), *Psychotria berteriana* (Rubiaceae), *Psychotria cyanococca* (Rubiaceae), *Psychotria elata* (Rubiaceae), *Psychotria lamarinensis* (Rubiaceae), *Psychotria officinalis* (Rubiaceae), *Psychotria remota* (Rubiaceae), *Psychotria racemosa* (Rubiaceae), *Rudgea cornifolia* (Rubiaceae), *Angostura granulosa* (Rutaceae), *Conchocarpus nicaraguensis* (Rutaceae), *Toxosiphon lindenii* (Rutaceae), *Zanthoxylum melanostictum* (Rutaceae), *Meliosma glabrata* (Sabiaceae), *Cupania glabra* (Sapindaceae), *Cupania juglandifolia* (Sapindaceae), *Cupania rufescens* (Sapindaceae), *Smilax spinosa* (Smilacaceae), *Smilax vanilliodora* (Smilacaceae), *Brugmansia candida* (Solanaceae), *Cestrum megalophyllum* (Solanaceae), *Cestrum racemosum* (Solanaceae), *Solanum aphyodendron* (Solanaceae), *Solanum arboreum* (Solanaceae), *Solanum schlechtendalianum* (Solanaceae), and *Callicarpa acuminata* (Verbenaceae).

Discussion. The primary question regarding the identity of this species is to which of our two slightly different (perhaps) *Anacrusis nephrodes*-like females is the holotype of *Anacrusis nephrodes* most similar. The majority of our reared specimens from Costa Rica have forewing features nearly identical to those of the holotype of *Anacrusis nephrodes* (TL: Panama), but the latter specimen is slightly redder, as in *Anacrusis ellensatterleeae*. However, the holotype of A. *nephrodes* lacks the subtle white edging of the subterminal dots characteristic of *Anacrusis ellensatterleeae*, suggesting that our common cluster is conspecific with *Anacrusis nephrodes*. Furthermore, *Anacrusis ellensatterleeae* occurs only on the very top of Volcan Cacao (above the distribution of *Anacrusis terrimccarthyae*), whereas *Anacrusis nephrodes* is omnipresent in low- to mid-lowland rain forest, below the distribution of *Anacrusis terrimccarthyae*. Because the lateral arms of the sterigma extend nearly perpendicular to the sterigma, they are distorted in every genitalia preparation. The female genitalia of the holotype of *Anacrusis nephrodes* are extremely flattened on the slide-mounted preparation; hence, it is difficult to interpret the characters. Nonetheless, we associate our large series of specimens with the holotype of *Anacrusis nephrodes* for the following reasons: (1) we have examined numerous examples of this phenotype with virtually identical genitalia over a wide geographic range in Central America (i.e., Guatemala to Panama), and the genitalia of the holotype are a slightly better match for our large series of *Anacrusis nephrodes* females than to the our small series of *Anacrusis ellensatterleeae* females; and (2) *Anacrusis nephrodes* is a common, widespread species, whereas *Anacrusis ellensatterleeae* appears to be less common, known primarily from a series reared from the top of Volcan Cacao in central ACG.



FIGS. 22–25. Cubital pecten of male hindwing. **22.** *Anacrusis turrialbae*. **23.** Close-up of *Anacrusis turrialbae*. **24.** *Anacrusis nephrodes.* **25.** Close-up of *Anacrusis nephrodes*.

Anacrusis ellensatterleeae Brown, **new species**

(Figs. 6, 11, 16, 21)

A small, divergent (>5%) barcode cluster of specimens (Fig. 1) revealed distinct genitalia in both sexes. In addition, two specimens from Puntarenas (1550 m) and one from Alajuela (1450 m) are associated with the barcode cluster based on male genitalia. We found no described material that matched these specimens.

Diagnosis. Male. The male of *Anacrusis ellensatterleeae* (Fig. 6) is superficially essentially indistinguishable from all ACG *Anacrusis* except *Anacrusis turrialbae*. It shares long, slender, lanceolate-tipped scales of the hindwing cubital pecten (Figs. 24, 25) with *Anacrusis nephrodes*. The male genitalia (Fig. 16) are distinguished from those of *Anacrusis nephrodes* by the distal portion of the uncus, which is undivided, forming a somewhat ovoid hood rather than a pair of lateral flanges forming a tent as in *Anacrusis nephrodes*; by the nearly straight lower (anterior) edge of the transtilla, which is more U-shaped mesally in *Anacrusis nephrodes*; and by the shape of the large cornutus in the vesica.

Female. The female of *Anacrusis ellensatterleeae* (Fig. 11) is superficially nearly indistinguishable from the female of *Anacrusis nephrodes*, with a small silver-white rounded dash at the outer edge of the forewing costal blotch. Although the differences are subtle, the large costal blotch of the forewing is slightly less defined, the overall ground color is slightly redder, and there usually are traces of white scaling accompanying the dark dot(s) in the middle of the subterminal region in *Anacrusis ellensatterleeae*. The corethrogyne scales on the venter of A8 are entirely beige. In the sterigma (Fig. 21), the lateroanterior lobes are angled subbasally as in *Anacrusis nephrodes*, and the lateral arms are comparatively longer with rounded, less spined, truncate apices. The signum is flattened and bladelike rather than thornlike.

Description. Male. *Head*: Vertex and upper frons rough scaled, maroon; lower frons smooth scaled, cream; labial palpus pale maroon on outer surface, paler on inner surface, all segments combined about 1.25 times diameter of compound eye, second segment very weakly upcurved, third segment nearly concealed by scaling of second; ocellus conspicuous. Antenna with scape, pedicel, and basal 6–8 segments of flagellum with maroon scales, becoming progressively paler toward distal end of antenna, with two rows of scales per flagellomere, sensory setae dense, length about 0.5–0.6 times width of flagellomere. *Thorax*: Anterior portion of prothorax and anterior base of tegula maroon, remainder slightly reddish fawn brown. Proleg with dense fascicle of long scales originating near trochanter, extending along femur (as illustrated in Brown 1990: fig. 5). Forewing length 10.5–13.0 mm (mean = 12.0; n = 7); forewing ground pale reddish brown, with faint, irregular, pale brown striations and irregular areas of paler overscaling; a large, triangular, maroon patch in middle of wing extending from costa, about 0.3–0.8 distance from base to apex, attenuating before dorsum; a large, darker maroon-brown sub-circular blotch occupying most of subterminal region, finely outlined with white, bulging inward near distal end of discal cell; a variable, ill-defined, pale bluish white spot between bulging part of subterminal blotch and outer edge of triangular patch. Fringe mostly concolorous with forewing ground. Hindwing uniformly pale gray brown, except for paler region near anal margin; cubital pecten a dense patch of long, lanceolate scales (Figs. 24, 25). Fringe pale reddish brown along outer margin, pale gray along lower and anal margins. *Abdomen*: Shiny pale gray dorsally, with some cream scales on venter; scales at distal end of abdomen and externally on genitalia slightly to conspicuously darker than on remainder of abdomen. Genitalia (Fig. 16) with tegumen short, broad; vinculum rather long; uncus broad at base, narrowed in middle, with expanded, undivided, hood-like process distally; socius broad in basal 0.5, digitate in distal 0.5, densely clothed in long scales; gnathos arms narrow, with hook-shaped process at mesial junction of arms; valva broadest at base, upturned, slightly attenuating toward apex, costa narrowly sclerotized to apex; sacculus mostly uniform in width, confined to ventral edge of basal 0.3 of valva, then upturned, diverging slightly from edge of valva, ending in a rounded tip; valva between base and sacculus weakly sclerotized; transtilla a transverse band with rounded concavity along posterior edge at middle, with small spines on posterior margin; juxta a broad, diamond-shaped plate, rounded basally, pointed dorsally at attachment point of phallus. Phallus gently curved, basal 0.5 broader, rounded at base, distal 0.5 uniformly narrow; vesica with fascicle of about 17–18 slender, asiculate, subbasally attached, deciduous cornuti, and a single broad, spindle-shaped cornutus.

Female. *Head and Thorax*: Essentially as described for male, except proleg without modified scaling and hindwing lacking dense scale patch at base of Cu. Forewing length 16.0–18.5 mm (mean = 17.0; n = 8); forewing ground pale reddish brown, with faint, irregular, pale brown striations; a brownish maroon triangular patch from costa about 0.25–0.80 distance from base to apex, with its apex just beyond lower edge of discal cell, middle of triangle with semicircular areas of pale brown along costa; small white arrowhead-shaped spot at outer margin of triangular patch; one to three small, black dots between CuA and M_2 midway between discal cell and termen, usually faintly and narrowly outlined with white; termen with conspicuous concavity in apical 0.4. Fringe concolorous with forewing ground in tornal region, darker red brown along concavity. Hindwing mostly gray brown, paler along outer margin, pale red brown in apical region. *Abdomen*: Gray brown dorsally, corethrogyne scaling of venter beige throughout. Genitalia (Fig. 18) with papillae anales oblong-ovate; apophyses anteriores slightly longer than posteriores; lateral arms of sterigma extremely long, flattened and attenuate distally; ductus bursae about 1.5 times as long as corpus bursae, gradually broadening toward corpus bursae, colliculum comparatively long; corpus bursae rounded, weakly punctuate with small bladelike signum.

Barcode Data. The barcode data show a tight cluster of 17 individuals with extremely limited differences (less than 0.2% divergence).

Geographic Distribution. This species is known from the series of 26 specimens reared from the top of Volcan Cacao, ACG (1080-1460 m, except for one specimen from 710 m), two specimens from Estacion Biologia Las Alturas (1550 m), and one specimen from the north slope of Volcan Poas (1450 m). It likely occurs at the same elevations on Volcan Orosi and Volcan Rincon de la Vieja in the same Cordillera Guanacaste.

Host plants. *Anacrusis ellensatterleeae* is polyphagous, with larvae collected and reared from the following ACG plants: *Saurauia montana* (Actinidiaceae), *Geonoma* sp. (Arecaceae), *Sphaeradenia occidentalis* (Cyclanthaceae), *Ocotea insularis* (Lauraceae), *Piper aequale* (Piperaceae), *Piper tenuimucronatum* (Piperaceae), *Ardisia nigropunctata* (Primulaceae), *Myrsine coriacea* (Primulaceae), *Coussarea caroliana* (Rubiaceae), *Hoffmannia longipetiolata* (Rubiaceae), *Notopleura tolimensis* (Rubiaceae), *Palicourea salicifolia* (Rubiaceae), *Meliosma glabrata* (Sabiaceae), *Billia rosea* (Sapindaceae), and *Smilax spinosa* (Smilacaceae).

Larva. The head is black, and the body is dark green with fine white hairs throughout. As is typical of most external feeding tortricids, the larvae roll the leaves of the host plant or tie together adjacent leaves to form a shelter.

Discussion. This species can be confused only with *Anacrusis nephrodes*. The differences between the two are discussed above.

Holotype ♂, Costa Rica, Guanacaste, Area de Conservacion Guanacaste, Sector Cacao, Sendero Cima, 1460 m, 10.93328N, -85.45729W, 8 Sep 1997, r.f. *Sphaeradenia occidentalis*, em: 23 Sep 1997 (97-SRNP-1822) (USNM).

Paratypes (9♂, 19♀). COSTA RICA: Alajuela: North slope Volcan Poas, 8 km N Vara Blanca, 1450 m, 25-26 Jul 1990 (1♂), S. Meredith & J. Powell (EME). Cartago: Orosi Tunnel Rd., P.N. Tapantí, 9.432N, -83.466W, 1475 m, 7–9 Jul 2008 (1♂), J. B. Sullivan (USNM). Guanacaste: Area de Conservacion Guanacaste: Sector Cacao, Sendero Derrumbe, 1220 m, 10.92918N, -85.46426W, 18 Apr 2002 (1♂), r.f. *Hoffmannia longipetiolata*, F. Quesada, em: 16 May 2002 (02-SRNP-9033) (USNM); 18 May 2000 (1♂), r.f. *Ocotea insularis*, M. Pereira, em: 10 Jun 2000 (00-SRNP-9529); 18 Jul 2007 (1♂), r.f. *Billia rosea* (Sapindaceae), M. Pereira, em: 21 Aug 2007 (07-SRNP-36233) (USNM); 24 Apr 2001 (1♀), r.f. *Coussarea caroliana*, M. Pereira, em: 17 May 2001 (01-SRNP-6734) (USNM); 11 Aug 2005 (1♀), r.f. *Ardisia nigropunctata*, H. Ramirez, em: 1 Sep 2005 (05-SRNP-35845) (USNM). Sector Cacao, Sendero Derrumbe, 1220 m, 10.92918N, -85.46426W, 20 Dec 2001 (1♀), r.f. *Saurauia montana*, M. Pereira, em: 7 Jan 2002 (01-SRNP-21522) (USNM); 1 Aug 2000 (1♀), r.f. unknown plant, M. Pereira, em: 18 Aug 2000 (00-SRNP-10254) (USNM); 29 Mar 2006 (1♀), r.f. *Coussarea caroliana*, M. Pereira, em: 6 May 2006 (06-SRNP-35136) (USNM); 6 Oct 2008 (1♀), r.f. *Palicourea salicifolia*, H. Ramirez, em: 31 Oct 2008 (08-SRNP-37075) (UNSM); 13 Aug 1997 (1♀), r.f. *Notopleura tolimensis*, R. Moraga, em: 15 Sep 1997 (97-SRNP-1655). Sector Cacao, Estacion Cacao, 1150 m, 10.92691N, -85.46822W, 10 Oct 2003 (1♂), r.f. *Piper tenuimucronatum*, M. Periera, em: 6 Nov 2003 (03-SRNP-23349) (USNM). Sector Cacao, Casa Fran, 1140 m, 10.93663N, -85.46685W, 5 Apr 1997 (1♀), r.f. *Meliosma glabrata*, G. Pereira, 28 Apr 1997 (97-SRNP-1026) (USNM). Sector Cacao, Sendero Circular, 1185 m, 10.92714N, -85.46683W, 18 Dec 1999 (1♀), r.f. *Piper aequale*, M. Pereira, em: 24 Jan 2000 (99-SRNP-17216) (USNM); 13 Mar 2000 (1♀), r.f. *Coussarea caroliana*, M. Pereira, em: 18 Mar 2000 (00-SRNP-9181) (USNM). Sector Cacao, Sendero Cima, 1460 m, 10.93328N, -85.45729W, 4 Feb 1997 (1♀), r.f. unknown plant, gusaneros, em: 20 Feb 1997 (97-SRNP-505); 17 Aug 1997 (5♀), r.f. *Sphaeradenia occidentalis*, R. Franco, em: [no date] (97-SRNP-1775), em: 18 Sep 1997 (97-SRNP-1776), em: 8 Sep 1997 (97-SRNP-1777), em: 21 Aug 1997 (97-SRNP-1778), em: 7 Sep 1997 (97-SRNP-1781) (USNM); 24 Aug 1997 (1♀), r.f. *Sphaeradenia occidentalis*, gusaneros, em: 9 Sep 1997 (97-SRNP-1807) (USNM); 8 Sep 2002 (1♀), r.f. *Geonoma* sp., M. Pereira, em: 7 Oct 2002 (01-SRNP-7722) (USNM); 15 Nov 2006 (1♂), r.f. *Smilax spinosa*, D. Garcia, em: 1 Jan 2007 (06-SRNP-36805) (USNM). Sector Cacao, Sendero Nayo, 1090 m, 10.92446N, -85.46953W, 5 Nov 2009 (1♀), r.f. *Myrsine coriacea*, H. Ramirez, em: 27 Nov 2009 (09-SRNP-36836) (USNM). Puntarenas: Estacion Biologia Las Alturas, 12 air km NE San Vito, 1550 m, 22-24

Jan 1993 (2♂), J. Powell (EME), J.Powell no. 93A24, em: 8 Feb 1993, r.f. understory plant.

Etymology. *Anacrusis ellensatterleeae* from the very top of Volcan Cacao is named to honor Ellen Satterlee of Grand Rapids, Michigan, in recognition and with gratitude for her three decades of intense care for the Wege Foundation and its antecedents, steadfast encouragement throughout the development of Area de Conservacion Guanacaste (ACG), decades of enthusiastic fund-raising to save, expand and grow ACG rain forest, and understanding the value of biodiversity education.

Diagnostics of Costa Rican *Anacrusis*

Facies. On the basis of forewing maculation, two "forms" of the male can be distinguished: an *Anacrusis turrialbae* form (including only *Anacrusis turrialbae*) and an *Anacrusis nephrodes* form (including the remaining four species). The four species of the *Anacrusis nephrodes* form can be separated into two groups of two each on the basis of the hindwing cubital pecten (Figs. 22–25): short, with blunt-tipped scales (in *Anacrusis terrimccarthyae* and *Anacrusis piriferana*) (Figs. 22, 23) and long, with lanceolate-tipped scales (in *Anacrusis nephrodes* and *Anacrusis ellensatterleeae*) (Figs. 24, 25). Within the latter two species pairs, males of the species cannot be separated reliably by facies; however, the genitalia of each are distinct.

On the basis of forewing maculation, two forms of the female can be separated: an *Anacrusis turrialbae* form (including *Anacrusis turrialbae*, *Anacrusis terrimccarthyae*, and *Anacrusis piriferana*) and an *Anacrusis nephrodes* form (including *Anacrusis nephrodes* and *Anacrusis ellensatterleeae*). The *Anacrusis turrialbae* form has an isolated, rounded maroon-brown patch narrowly outline by white near the costa about 0.6 the distance from the wing base to the apex that is lacking in the *Anacrusis nephrodes* form. Within the *Anacrusis turrialbae* form, *Anacrusis turrialbae* is distinguished by the absence of a small black dot (or dots) near the middle of the subterminal region. *Anacrusis terrimccarthyae* and *Anacrusis piriferana* are distinguished by subtle differences in the color of the corethrogyne scaling on abdominal segment eight: pearly cream-white throughout in *Anacrusis terrimccarthyae*; cream-white in the middle, and gray laterally in *piriferana*. In females of *Anacrusis ellensatterleeae* the dark dot(s) near the middle of the subterminal area usually are surrounded by a few white scales; in *Anacrusis nephrodes* they are surrounded by ground color. Also, the two regions of the large costal patch (i.e., large triangular and smaller semicircular) are less differentiated in *Anacrusis ellensatterleeae*, the latter of which has a slightly more reddish ground color. The shape of the rounded concavity of the forewing termen immediately below the apex of the forewing also may be of some diagnostic value. However, all of these features of the female forewing are subtle and variable.

Genitalia. The male genitalia of all five species are most easily distinguished by differences in the shape of the sacculus (Figs. 12–16). However, differences in the shapes of the uncus, gnathos, and phallus also provide convincing characters for species discrimination, and these are discussed above in the species diagnoses. All five species also can be distinguished by features of the female genitalia, but many of these are less obvious in slide-mounted preparations owing to artifacts from flattening. The length and shape of the lateral processes (arms) of the sterigma are species specific (Figs. 17–21).

Elevation. In ACG, *Anacrusis turrialbae* and *Anacrusis nephrodes* occur from the lowlands to intermediate elevations in rain forest, primarily below about 500 m elevation, with a few scattered records as high as 650 m. *Anacrusis periferana* has been collected over a narrow range from 455 to 680 m elevation. *Anacrusis terrimccarthyae* occupies the boundary between cloud forest (above) and intermediate elevation rain forest (below) from about 700 to 1220 m, immediately above the range of the previous three species. *Anacrusis ellenatterleeae* is known only from near the tops of Volcan Cacao and Volcan Poas at 1080-1550 m.

DNA barcodes. The 658 basepair section of the mitochondrial gene COI separates the taxa into five clusters. The outliers, other than the five *Anacrusis turrialbae*DHJ02, are due to normal variation in barcode clusters resulting from incomplete sequence data. Individuals from other countries do not always fit convincingly within the five clusters, and many of them may represent undescribed species.

Food plants

All five of these species of *Anacrusis* are unambiguously extreme generalists, feeding on many species of plants in many plant families. However, as is generally the case with ACG "generalists," some groups of potential food plants are conspicuously missing or rarely used (e.g., monocots, ferns, cycads, *Selaginella*, flowers, fruits, vines, herbs), and some common families are used very little (e.g., Fabaceae, Rubiaceae); furthermore, there are no dry forest records for ACG *Anacrusis*. In short, the very long lists of actual food plants for each species should not be interpreted as random or haphazard selections out of the total available to an ovipositing female or a wandering caterpillar (if they do). Far larger samples will be required to determine if each of the five "generalists" are using different sets of rain forest or cloud forest plants, as sometimes occurs in other species of ACG generalist caterpillars. While the numbers of records per species of food plant found by the inventory to date can be easily obtained by the summary data in Janzen and Hallwachs (2013), these numbers can only be interpreted in the context of collection intensity per species of plant, numbers of individuals of a plant species in a site, habitats examined differentially, distances above the ground, and seasonality of the ecosystem or habitat that is searched. These considerations will be eventually dealt with in ecological analyses of the caterpillars from the ongoing ACG inventory, but it would be both deceptive and irrelevant if they were simply listed here. However, it can be stated with confidence that all five species are truly extreme generalists, rather than each being a complex of specialists lumped under one name, as the inventory has discovered to be the case with some other ACG "generalists" (e.g., Burns et al 2008, Chacon et al 2013, Smith et al 2007, 2008).

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