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CHASING BUTTERFLIES IN MEDIEVAL EUROPE

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ABSTRACT. A survey of illuminated medieval manuscripts from Europe reveals depictions of several different methods used in the Middle Ages for catching butterflies. A discussion on the meaning and iconography of lepidopteran imagery in these manuscripts is presented.

Additional key words: Marginalia, Manuscripts, Lepidoptera, Iconography, Psyche

With the large-scale digitization of rare illuminated medieval manuscripts by libraries, museums and other institutions around the world, a new and unexpected online resource is rapidly becoming available for a least likely audience: entomologists. Although mostly of religious nature, the illuminated manuscripts produced during the Middle Ages (5th–15th century CE) are richly illustrated with scenes from daily lives of ordinary people, clerics, and royalty. The margins of these manuscripts are often ornamented with elaborate decorative illustrations, also known as "marginalia", incorporating a variety of natural elements such as flowers, birds, and other animals, including insects. Previous studies on illustrations of birds (Yapp 1982), dragonflies (Kern 2005) and snails (Hope 2013) in medieval manuscripts have shown that beside useful historical taxonomic information, insights can be gained from these sources on iconography and symbolism of living elements in medieval times. In this paper I will discuss some of the ways in which the lepidopterans may be understood in medieval iconography, and in particular in the context of religion and warfare. The time frame for the works selected in this paper is 1280–1540, and the selection contains images from modern-day Belgium, England, France, Italy, Netherlands, and Spain. The manuscripts include books of hours, breviaries, pontificals, ordinals, decretals, psalters, oratories, graduals, and other works of devotion. The images in this paper are all either in public domain or are reproduced here with permission.

Materials and Methods

Using various online databases and websites from European and North American institutions, I conducted searches for digitized medieval manuscripts made available courtesy of universities, religious colleges, municipal or national libraries, or other institutions. The quality of images and the ownership rights varied but all institutions were cooperative in providing permission to use and obtain higher quality images for research purposes upon request. Many of these institutions have built comprehensive online databases with descriptions of elements on every folio (page) of the manuscripts in their deposition, making it easy to search for key words (e.g. "butterfly") and focus only on pages where these images appear. Others, however, did not have such a cataloguing system and required checking each manuscript page by page for relevant imagery.

Among the hundreds of manuscripts surveyed, I found about 270 that contained lepidopteran imagery. There is no doubt that a more rigorous search will yield further material. In many of these manuscripts, the depicted lepidopterans are highly stylized and it is often difficult to even tell if an image is of a butterfly or a moth. Among the ones I came across, about 30 manuscripts included scenes where lepidopterans were shown in some kind of interaction either with humans, monkeys, putti (child-like winged nude beings), centaurs, or other fantastical creatures. Lepidopterans in these scenes were either being pursued, aimed at, or caught in one-way or another. The diversity of methods depicted by medieval illustrators to capture butterflies and moths was truly surprising, especially since the principal motivation behind these activities has remained largely unexplained. Here I provide example images of these medieval collecting methods.

Results

Although individual butterflies are common in marginal decorations, they rarely appear as background elements in other scenes. I found only one such instance in a Belgian Book of Hours[1] from early 16th century, where several butterflies are fluttering in a field with farmers working (Fig. 1). In a French Book of Hours[2] (1430), a butterfly seems to have startled a bearded man wearing a soft-peaked hat (Fig. 2). In another Book of Hours from England[3] (1450s), a hooded, bearded man is pointing a finger at a large, poorly drawn *Aglais urticae* (Fig. 3). In *"Bréviaire à l'usage de Besançon"* [4] (pre-1498), a putti is shaking a tree where a nicely drawn *Aglais urticae* is perched (Fig. 4). In a late 13th century Breviary from Burgundy, France[5], two woman are

FIGS 1-11: **1**) *Book of Hours*, 1525-1530, Belgium (Bruges), Pierpont Morgan Library, New York, MS M.1175, f. 9v; **2**) *Book of Hours*, 1430, France (Rennes), Pierpont Morgan Library, New York, MS M.0173, f. 16r; **3**) *Book of Hours*, 1440-1450, England (London?), Pierpont Morgan Library, New York, MS G.09, f. 12r; **4**) *Bréviaire à l'usage de Besançon*, Before 1498, Western France (Normandie), Besançon, Bibliothèque municipals, MS 0069, f. 485; **5**) *Belleville Breviary*, 1323-1326, Netherlands (Ghent), attributed to Jean Pucelle (Enlumineur), Bibliothèque Nationale Paris, MS lat. 10484, f. 24v; **6**) *Pontifical of Guillaume Durand*, 1390, France, Bibliothèque Sainte-Geneviève, Paris, MS 0143, f. 1; **7**) *Heures à l'usage de Bayeux*, 1430-1440, Western France (Normandie), Aurillac, Bibliothèque municipals, MS 0002, f. 4; **8**) *Heures à l'usage de Rouen*, 1460-1470, France (Rouen), Aix-en-Provence, Bibliothèque municipales, MS 0022, f. 139; **9**) *Piccolomini breviary*, 1475, Italy (Lombardy), Pierpont Morgan Library, New York, MS M.0799, f. 260v; **10**) *Catholic Church, Ordinal*, 1482, Spain, Houghton Library, Harvard University, Cambridge, Massachusetts, MS Typ 236, f. 1; **11**) *La Divina Commedia di Dante* (Dante and the Divine Comedy), 1430-1435, Italy, Bibliothèque Nationale, Paris, MS it. 74, f. 3v.

FIGS 12-19: **12**) *Book of Hours*, Use of Rome (the 'Golf Book'), 1540, Netherlands, The British Library Board, MS 24098, f. 24v; **13**) *Book of Hours*, 1495-1503, France (Rouen), Pierpont Morgan Library, New York, MS M.0261, f. 78v; **14**) *Bréviaire à l'usage de Langres*, after 1481, Eastern France (Bourgogne ?), Chaumont, Bibliothèque municipals, MS 0033, f. 119v; **15**) *Romance of Alexander*, 1338-1344, France (Flemish), attributed to various authors including Lambert le Tort, Alexandre de Bernai (de Paris), Jehan de Grise and others, Bodleian Library Oxford, England, MS Bodl. 264, pt. I, f. 44r; **16**) *Book of Hours*, Dominican use, 1458-1465, Italy, Houghton Library, Harvard University, Cambridge, Massachusetts, MS Typ 463, f. 97; **17**) *Decretals of Gregory IX with glossa ordinaria* (the 'Smithfield Decretals'), Last quarter of the 13th century or 1st quarter of the 14th century, Southern France (Toulouse?), The British Library, Royal MS 10 E IV, f. 91v; **18**) *Romance of Alexander*, 1338-1344, France (Flemish), attributed to various authors including Lambert le Tort, Alexandre de Bernai (de Paris), Jehan de Grise and others, Bodleian Library Oxford, England; MS Bodl. 264, pt. I, f. 41r; **19**) *Ormesby Psalter,* Mid 14th century, England (East-Anglia?), Bodleian Library, Oxford, England, MS Douce 366, f. 38r.

FIGS 20-28: **20**) *The Bird Psalter*, 1280-90, England, Fitzwilliam Museum, University of Cambridge, Cambridge England, MS 2-1954, f. 1r; **21**) *Partitiones Oratoriae*, *Topica, etc.* 1425-1430, Italy (Florence), The Beinecke Library, Yale University, New Haven, Connecticut, Marston MS 278, f. 1r; **22**) *Pontifical of Guillaume Durand*, 1390, France, Bibliothèque Sainte-Geneviève, Paris, MS 0143, f. 247v; **23**) *ibid*; MS 0143, f. 1; **24**) *Estoire del Saint Graal, La Queste del Saint Graal, Morte Artu*, 1315-1325, France, The British Library Board, Royal MS 14 E III, f. 89r; **25**) *The Queen Mary Psalter*, 1310-1320, England, The British Library, Royal 2B VII, f. 163v; **26**) *Horae* etc., 13th century, Belgium (Flanders), Trinity College Cambridge, England, MS B.11.22, f. 137v; **27**) *Romance of Alexander*, 1338-1344, France (Flemish), attributed to various authors including Lambert le Tort, Alexandre de Bernai (de Paris), Jehan de Grise and others, Bodleian Library Oxford, England, MS Bodl. 264, pt. I, f. 132v; **28**) *ibid*; MS Bodl. 264, pt. I, f. 135r.

FIGS. 29-36: **29**) *Le roman de la rose*, 1390, France, attributed to Guillaume de Lorris and Jean de Meung, Bodleian Library, Oxford, England, MS e Mus. 65, f. 11r; **30**) *Breviary*, 1350-1374, France (Paris), Pierpont Morgan Library, New York, MS M.0075, f. 111r; **31**) *Hours of Charlotte of Savoy*, 1420-1425, France (Paris), Pierpont Morgan Library, New York, MS M.1004, f. 133r; **32**) *Book of Hours*, 1418, France (Paris), Pierpont Morgan Library, New York, MS M.0919, f. 190v; **33**) *Romance of Alexander*, 1338-1344, France (Flemish), attributed to various authors including Lambert le Tort, Alexandre de Bernai (de Paris), Jehan de Grise and others, Bodleian Library Oxford, England, MS Bodl. 264, pt. I, f. 67r; **34**) *Psalter - Hours of Yolande de Soissons*, last quarter 13th century, France (Amiens), Pierpont Morgan Library, New York, MS M.0729, f. 346r; **35**) *Gradual*, 1350-1400, Italy, Houghton Library, Harvard University, Cambridge, Massachusetts; MS Typ 079, f. 1; **36**) *Omne Bonum (Ebrietas-Humanus)*, James Le Palmer, 1360-1375, SE England (London), The British Library Board, Royal MS 6 E VII, f. 67v.

depicted in an outing, one of whom is holding what seems like a surprisingly modern net (cover photo). Although this maybe interpreted as a fishing net, its true purpose remains unclear since the accompanying text is unrelated and there are no butterflies or fish illustrated in the page.

A good portion of the imagery that I found depicted people reaching for, chasing or having caught butterflies with their bare hands. The oldest of these is found in the *Beleville Breviary* [6] (1323–1326, Netherlands), where a monkey holds a well-drawn *Aglais urticae* in his hand (Fig. 5). In the *Pontifical of Guillaume Durand*[7] (France, 1390), a nude boy reaches to grab a white butterfly (Fig. 6). Similar scenes with humans, putti or other heavenly figures appear in the marginalia of several Books of Hours or Ordinals produced in France [8,9] (1430s; 1460s), Italy [10] (1475), and Spain[11] (1482, with a *Saturnia pyri*) (Figs. 7–10). On the front piece to a reproduction of Dante's "*La Divina Commedia*" produced in Italy[12] in the 1430s, a nude man is depicted on a tree reaching for a black butterfly or moth (Fig. 11). Nested within a wide marginal strip, the *Golf Book* [13] (Netherlands, 1540) and *The Breviary of Eleanor of Portugal*[14] (Belgium, 1510s, not shown) both show scenes of inconspicuous grey human figures chasing butterflies with bare hands and also with hats and medieval golf clubs (Figs. 12).

In a French Book of Hours [18] from 1495–1503, a nude man is depicted attempting to catch a butterfly with an object in his hand that could be either a large gray hat or a rock (Fig. 13). I also found two instances, both in manuscripts originating from France, of men depicted clubbing lepidopterans. One of these is from a French Breviary[16] produced after 1481 (Fig. 14), and the other is in the well-known "*Romance of Alexander*"[15] (1338–1344)(Fig. 15). In an Italian manuscript[17] from mid 15th century, a putto riding a peacock is aiming a spear at a highly stylized butterfly (Fig. 16).

In the *Decretals of Gregory IX* [19] (13th century), a man is attacking a butterfly with a large sword in his right hand and a small shield in left hand (Fig. 17). A similar image also appears in "*Romance of Alexander*" [15] (Fig. 18). But another more commonly depicted weapon against butterflies in medieval period is bows and arrows. Humans [20], centaurs [7,21], putti [22], and monkeys [7,23] have been depicted aiming at butterflies with bows and arrows, using various kinds of arrowheads (Figs. 19–24).

In *The Queen Mary Psalter* [32] (1310–1320), boys are seen playing with butterflies tied at the end of threads (Fig. 25). Several manuscripts include scenes with people, putti or monkeys attempting to catch butterflies with long-tailed hoods (a.k.a. *gugels*). The oldest of such images comes from a 14th century Flemish Book of Hours from Belgium [24] (Fig. 26). In *Romance of Alexander* [15], the margins of two separate pages are dedicated to depicting elaborate scenes with several men (Fig. 27) or women (Fig. 28) chasing butterflies with their hoods or bare hands, and some holding their hoods on the ground, evidently having caught one. In "*La Roman de La Rose*" [25] (France, 1390), two young maidens are depicted in a garden, one seated holding something in her hands, while the other is standing with outstretched left hand, right hand behind her holding a hood to strike a butterfly above her head (Fig. 29). Similar scenes also appear in a French Breviary [26] (1350–1374) as well as *The Hours of Charlotte of Savoy* [27] (1420–1425) (Figs. 30, 31). Hoods are also depicted as collecting tools being used by putti [28] as well as monkeys [15] (Figs. 32, 33). I also found two instances of nude men depicted attempting to catch a butterfly with a different, larger white item of clothing, possibly a cape or a cloak [29,30] (Figs. 34, 35). In *Omne Bonum* [31] (1360–1375), children are depicted playing with toys and chasing butterflies, with an unidentified item of clothing (Fig. 36).

DISCUSSION

Lepidopterans are very common elements in symbolism of societies worldwide. Within the limited scope of western art, Gagliardi (1976) describes 74 different symbolic contexts in which butterflies and moths may appear. Among these, the most prominent have to do with lepidopteran metamorphosis, a fascinating phenomenon that has captured the human imagination from the dawn of time. In Roman and Greek antiquity, the butterfly (*Psyche*) was a symbol of soul and transcendent immortal life after death ([Blatchford] 1889). In the ancient story of *Psyche and Cupid* (or Eros in Greek), best narrated by Roman writer Apuleius (2nd century CE), Psyche is an earthly woman whose beauty threatens Venus, the goddess of Love. Venus sends Cupid to take revenge, but Cupid falls in love with her. Venus banishes Psyche to the underworld but she comes back to life victoriously, and is granted immortality by Jupiter so that she can marry Cupid as an equal. Hence she symbolizes not only the image of the immortal soul, but the anguish and triumph of soul. The Greeks and Romans saw butterflies as personification of Psyche's death and resurrection cycle. In Greaco-Roman artifacts featuring scenes with Cupid and Psyche embracing or otherwise engaged in various amorous or entertaining activities, Cupid is always depicted with angelic, feathered wings like those of a bird, while Psyche has fragile, often highly stylized wings similar to those of a butterfly. In Roman seals from the 1st century, Cupid is sometimes depicted burning a butterfly with a torch, symbolizing the anguish of the soul in love (Platt 2007). In Greek artwork dating as far back as the 3rd century BCE, Eros is often pictured as a child rather than an adolescent (Stuveras 1969). Many of the scenes in the manuscripts I studied involve putti, the little winged children, shooting or otherwise catching butterflies. These putti may be justifiably interpreted as a representation of Cupid chasing his love, Psyche. The abundance of these scenes from an essentially pagan story in Christian religious manuscripts from medieval Europe is rather interesting and demonstrates the continued symbolic representation of butterflies well into the Middle Ages and beyond.

Moths are mentioned many times in the Bible, all in a negative context as pests of stored goods or cloths (e.g. Job 13:28; Psalms 39:11; Isaiah 51:8; Hosea 5:12; Matthew 6:19; James 5:2). Although some of the imagery presented here may be interpreted as depictions of frustrated people chasing away clothes moths, the negative attitude towards lepidopterans seems to have gradually changed over time, especially upon the introduction of silk to Europe in early 12th century. In fact, similar to the honeybee, the 'Silkworm' (*Bombyx mori*) was recognized as a useful insect and illustrated in detail in manuscripts dealing with silk production (Morge 1973). Entomology as a science, however, was rudimentary in medieval Europe, and the Greek philosopher Aristotle's biological works, written in 3rd century BCE, were the only source of zoological knowledge throughout the Middle Ages. Aristotle maintained that worms originated in woods or rotting meat, caterpillars in cabbage, and moths in clothes. Early biological observations during the 13th century—such as the works of Thomas Cantiprantanus (*Liber de Natura Rerum*, 1233–1248), Albertus Magnus (*De Animalibus*, 1255–1270) or Bartholomeus Anglicus (*De proprietatibus rerum*, mid-13th century)—were not free from the old Aristotelian dogma. They contained wildly incorrect assertions about insects; some calling butterflies 'flying worms' or 'small birds' (Morge 1973). Aristotle's now-obsolete theory of spontaneous generation (of living beings emerging from inanimate matter) was in fact still being taught in Europe in the mid-seventeenth century (Kern 2005). The limited scholarly activity and scientific interest in butterflies during the Middle Ages cannot adequately explain the abundance of these scenes in medieval manuscripts.

Lepidopterans make rare appearances in Christian artwork predating the 14th century, such as tapestries or paintings, but are generally absent from manuscripts. One of the oldest illuminated manuscripts, the Scottish "*Book of Kells*" from 800 CE (Trinity College Dublin, MS 58; not shown), includes two small moths hidden within the gothic calligraphy of the Chi-Rho page (Spangenberg 2010). From late 13th century onwards, butterflies begin to appear more frequently in the borders of European manuscripts. Some of the scenes involving butterflies in this period may be explained by the well-known religious symbolism during the Middle Ages (Panofsky 1955). In medieval iconography, monkeys represented mischief (Walker Vadillo 2013), snails may have represented humility (Hope 2013) or virginity (Ettlinger 1978), flies were symbols of death, evil or brevity of life on earth, and ladybugs the seven sorrows of the Virgin (Yanoviak 2013); scarabs represented sinners, bees were associated with virginity (Berenbaum 1995) or structure and hierarchy (Payne 1990); louse or fleas with plague and disease, and locusts with famine (Morge 1973). Butterflies maintained their status as the iconic representations of the soul. It has been argued that the combination of flies (symbol of death), dragonflies (symbol of flight and ascension) and butterflies (symbol of resurrection) in medieval marginalia is a representation of Christ (Hassig 1995).

The majority of these exquisite books were commissioned by the nobility and took several years to complete, and often involved several artists. They were prized possessions not only because of their religious content, but also as magnificent works of art. It is therefore worth noting some of the major pre-occupations of the nobility in medieval times: hunting and warfare. In the English "*Bird Psalter*" (1280–90), a bowman is shown aiming at a Snipe but also a white *Pieris* butterfly (Fig. 20). Scenes of hunting of birds and other animals abound in medieval marginalia, as this was a common activity among the nobles and royalty. However, weapons are more often portrayed in the context of warfare rather than hunting, reflecting the violent tenor of the age. Few regions of Europe or Asia remained untroubled by invasion, rebellion or civil war during the 13th and 14th century, resulting in a gradual change in the way armies were organized and battles conducted. For example, in 1337, just before the outbreak of the war with France, Edward III of England prohibited all sports except archery on punishment of death (Mortimer 2012). On every village green, young men became proficient in the use of longbows, and standards of archery soared. It is not far-fetched therefore to think that for these medieval warriors (as well as hunters) aspiring to improve their skills in archery or swordsmanship, tiny objects moving erratically in the air constituted the ultimate aiming target, and this may have been a routine part of fighter training in the Middle Ages. This practice was probably commonplace and continued even to modern times: Laubin & Laubin (1980) mention that modern American Indian boys practice aiming by shooting arrows at butterflies.

Whether a representation of the ephemeral beauty of nature or a religious symbol, butterflies and moths seem to have been a significant source of curiosity and contemplation for the medieval mind. Many of these butterflies were drawn from real models, which were perhaps captured by the illustrator or his aides in one way or the other; and one may presume that this activity itself somehow found its way into the margins of some of these illuminated books. The prolific use of insects in the margins of medieval manuscript may also have played a role in developing interest in empirical observations and changing attitudes towards nature, and formed the basis on which the first scientific naturalists—such as Thomas Muffet and Maria Sybilla Merian—started their work in the later centuries.

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31 Omne Bonum (Ebrietas-Humanus). James Le Palmer. 1360-1375, S.E. England (London). The British Library Board, Royal MS 6 E VII. **In public domain.**

32 *The Queen Mary Psalter,* 1310-1320, England. The British Library; Royal 2B VII. **In public domain.**

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A CRYPTIC NEW *JEMADIA* (HESPERIIDAE: PYRGINAE: PYRRHOPYGINI) FROM COSTA RICA AND PANAMA WITH A SUBTLY DISTINCTIVE COMBINATION OF BLUE RAYS AND WHITE BANDS

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ABSTRACT. "We have little doubt it is rightly referred to this species," wrote Godman and Salvin (1893: 262) about their only Panamanian specimen, a female from Calobre, in order to treat the South American *Jemadia hewitsonii* (Mabille, 1878) in their "Biologia Centrali-Americana. Insecta. Lepidoptera–Rhopalocera." Half a century later, Evans included her in a type series of the newly described subspecies *J. hewitsonii pater* Evans, 1951, which after 50 more years Burns elevated to species status. This female is neither *J. hewitsonii* nor *J. pater*, but a new species, possibly closest to South American *Jemadia ovid* Evans, 1951, **new status**. The new Central American *Jemadia*, repeatedly reared in the Caribbean rain forest of Costa Rica's Area de Conservación Guanacaste, is described here as *Jemadia suekentonmiller* Grishin, **sp. nov.**; and its facies, genitalia, and DNA barcodes are closely compared with those of various congeners. The twice-misplaced female is a paratype of *J. suekentonmiller* and is still the only known specimen from Panama.

Additional key words: cryptic species, biodiversity, caterpillars, skipper butterflies, genitalia, DNA barcodes, Area de Conservación Guanacaste.

Despite much work and some dedicated collecting, the Central American Hesperiidae fauna is still rich in surprises. In Nicaragua and Costa Rica, many phylogenetic groups that originated in South America currently appear to be at their northern distribution limits. Central American populations in some groups have become species that are often less common than their South American sister species and so morphologically similar to them (at least in facies) as to be cryptic (e.g., Grishin et al. 2013a).

Large series of specimens are desirable to study intraspecific variation and document interspecific differences. Abundant material from a long-term comprehensive inventory of the non-leaf miner species of Lepidoptera of Area de Conservación Guanacaste (ACG) in northwestern Costa Rica (Janzen et al. 2009, Janzen and Hallwachs 2011) is extraordinarily useful in this taxonomic effort. Because most of this material has been reared from wild-caught caterpillars, knowledge of their traits, foodplants, ecology, etc., greatly augments the usual data from adult morphology. Moreover, short sequences (ca. 654 bp) of mitochondial DNA coding for the C-terminal segment of cytochrome c oxidase subunit 1 (COI), and dubbed DNA barcodes, are routinely obtained for many specimens, adding molecular characters to those of morphology and biology. These DNA barcodes have been remarkable flags, both indicating possible new species and identifying recognized species (Hebert et al. 2004, Burns and Janzen 2005, Janzen et al. 2009, 2011, 2012, Burns et al. 2010, 2008, 2013, Grishin et al. 2013a, b).

While barcoding and more advanced DNA-based technologies are beginning to catch on in other areas of the Neotropics (Ratnasingham and Hebert 2007), traditional morphological comparisons are an integral part of species discovery and recognition of new ACG taxa in contrast to their closest relatives farther south. For instance, diligent and insightful analysis of facies and genitalia performed by Burns (Burns and Janzen 2001) detected a possible undescribed species of *Jemadia* E. Watson, 1893 on the basis of just three reared specimens, only one of which was male.

Comparison of over a dozen males and half a dozen females of this species available today supports Burns's conclusions. Moreover, comparison with the COI barcodes of other *Jemadia* species, many of which are South American and are from the same *Jemadia hewitsonii* species group, further strengthen the species-level status of this new taxon and place it further away from other *J. hewitsonii*-like species. Here, we formally describe this species and discuss its differences from other *J. hewitsonii* group taxa, both in facies and in male genitalia.

It should be noted that taxonomy of *J. hewitsonii* species group is currently uncertain. Further work on this group (and all Pyrrhopygini Mabille, 1877) is in progress and will soon be published by O. H. H. Mielke, E. Brockmann, and C. Mielke (pers. comm.). The purpose of this study is to describe a new species in the group and to show how to distinguish this new species from other taxa. Fortunately, the identity of taxa closest to the new species is quite clear. However, for completeness of comparison, we also illustrate facies and male genitalia of other distinct phenotypes in the *J. hewitsonii* group. Some of these taxa remain unnamed until the Mielke, Brockmann, and Mielke publication.

MATERIALS AND METHODS

Adult specimens used in this study are from the following collections: National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM); Natural History Museum, London, UK (BMNH); Museum für Naturkunde, Berlin, Germany (ZMHB); and American Museum of Natural History, New York, NY, USA (AMNH). All specimens reared from wild-caught caterpillars by the ACG inventory are so indicated with a specimen voucher code in the format yy-SRNP-x…, where "yy" are the last two digits of a year and "x…" is the serial number (1 to 5 digits long) of a specimen recorded for that year, e.g., 5289 or 22467. (A 6-digit code means that the adult specimen was wild-caught instead of reared.) This SRNP code can be sought on the inventory web site (Janzen and Hallwachs 2013) and soon, in general internet search engines. When they are reared, adults are on average slightly smaller than the wild-caught ones that usually populate museums.

For genitalia dissection, NVG used the following method (Robbins 1991): the abdomen was broken off, soaked for 40 minutes (or until ready) in 10% KOH at 60°C (or overnight at room temperature), dissected, and subsequently stored in a small glycerol-filled vial on the pin under the specimen. Genitalia and wing venation terminology follows Steinhauser (1981). Length measurements are in metric units and were made from photographs of specimens taken with a scale and magnified on a computer screen. Photographs of specimens and dry genitalia were taken by NVG with Nikon D200 and Nikon D800 cameras through a 105 mm f/2.8G AF-S VR Micro-Nikkor lens; dissected genitalia were photographed in glycerol with the Nikon D200 camera without the lens and through microscopes at 2× and 5× magnifications. Images were assembled and edited in Photoshop CS5.1. Genitalia photographs were taken in several focus slices and stacked in Photoshop to increase depth of field. DNA sequences were downloaded from GenBank <http://genbank.gov/> or BOLD <http://www.boldsystems.org/>, aligned by hand since they matched throughout their length without insertions or deletions, and analyzed using the Phylogeny.fr server at http://www.phylogeny.fr/ with default parameters (Dereeper et al. 2008). Many of these sequences have been reported in Janzen et al. (2011) and photos of specimens are available from the Area de Conservación Guanacaste (ACG) on-line database (Janzen and Hallwachs 2013) and BOLD database (Ratnasingham and Hebert 2007) to confirm or suggest identifications.

RESULTS AND DISCUSSION

Evans characterized *J. hewitsonii* by white-spotted patagia and the presence of a short discal "blue band" on the dorsal hindwing "from vein 7 [=Rs] to vein 3 [=Cu_1], placed above 2 oblique basal streaks" (Evans 1951: 52–53). This blue band, shaped more like a ray (indicated by arrows in Fig. 45), runs between the splits of two vein pairs: Rs with M_1 and M_3 with Cu_1 (yellow arrows in Fig. 45b), in most taxa spilling into the base of the cell M_3–Cu_1 (pink arrow in Fig. 45c) and possibly into the base of the cell Rs–M_1 (upper pink arrow in Fig. 45d). Evans (1951: 53) partitioned *J. hewitsonii* into five subspecies. He used the widths of the discal white band and a doublet of postdiscal spots on the forewing and the form and appearance of the submarginal band on the dorsal hindwing as the main characters to differentiate among the subspecies. The first and the northernmost subspecies, recorded from Panama, Colombia, and Venezuela, Burns later recognized as a distinct species, *J. pater* Evans, 1951, owing to the differences in genitalic valvae between it and other taxa (Burns and Janzen 2001). In a series of 73 type specimens of *J. pater* in the BMNH collection curated by Evans, only one, a female from Panama, has a shorter blue ray (running only from vein 6 [=M_1] to vein 4 [=M_3]) without either of the blue spots at the bases of M_3–Cu_1 and Rs–M_1 cells. In all other *J. pater* specimens we examined, the blue ray intrudes at least into the cell M_3–Cu_1. However, 19 ACG specimens of *Jemadia* lack the longer blue ray characteristic of *J. pater*; instead, this ray is invariably short and limited to the spaces between veins 6 and 4 and not between 7 and 3. Therefore, these specimens, called "*Jemadia* Burns01" in Janzen et al. (2011), do not key out to *J. hewitsonii* of Evans (1951). They are described here (with the aforementioned female from Panama) as a new species proposed previously without a formal scientific name by Burns and Janzen (2001) and differing from all other *J. hewitsonii* group taxa not only by wing patterns but also by male genitalia and, where known, DNA barcodes (over 5% difference).

Jemadia suekentonmiller Grishin, **new species**
(Figs. 1–14, 45a, 46, 47a, 48a–i, 49, 50 part, 51 part)

Description: Male (n=14, Figs. 1–2, 7–10, 45a, 51 part) – holotype forewing length = 26.5 mm. Forewing triangular, no costal fold; forewing dorsally black with a diagonal discal white band broken by dark veins into 3 spots: (1) trapezoidal, narrower towards costa spot in discal cell, (2) rectangular spot with uneven edges in Cu$_1$–Cu$_2$ cell, and (3) triangular spot with a more or less convex side in Cu$_2$–2A cell, with point of this spot not reaching 2A vein; the band medium broad: 2.5–4.5 times longer than wide; a doublet of thinner than the band white postdiscal spots in cells M$_2$–M$_3$ and M$_3$–Cu$_1$; a band of four white apical spots with edges aligned along a curve in cells between veins R$_3$ and M$_2$; white-blue basal band; marine blue postbasal band; a doublet of marine blue elongated spots posteriad and slightly basad of white discal band; submarginal band of marine blue spots in each cell between M$_2$ and 2A veins, the band continuous with the white apical spots and in contact with the lower of the postdiscal white spots along vein Cu$_1$; marine blue overscaling basad near costa, towards costa from the discal white band, and distad discal cell in some specimens; ventrally similar to dorsal, but paler and more violet in background color, especially basad; basal pale band vestigial, mostly as overscaling and spots (the extreme base of the wing bluish-white); postbasal band paler (almost white), less regular and more diffuse than on the upperside; discal band continuing as bluer spots towards costa to the middle of costal cell, no doublet of marine blue spots near tornus, just some violet overscaling along vein 2A and inner margin as an extension of submarginal marine band; prominent marine blue spot distad discal cell; fringe black. Hindwing narrow, triangular, almost lobed at tornus, termen slightly scalloped between veins Cu$_2$ and 2A, dorsally black with two pale-blue streaks from the base along Cu$_2$ and 2A veins, streaks longer than half of the wing, the first streak paler, almost white; marine-blue ray narrowing from the split of veins Rs and M$_1$ to the split of veins M$_3$ and Cu$_1$; postdiscal marine blue band thinly separated into spots by darker veins, band narrowing from vein Rs to vein 2A, entering cell 2A–3A as a spot offset basad; violet spot continuous with the band in Sc+R$_1$ cell; ventrally similar to dorsal, but the postdiscal marine blue band wider and from costa to anal margin; area along anal margin overscaled with marine blue; no streaks or discal ray, but the base from costa bluish-white, and two longitudinal bands (basal band paler) sometimes connected along vein 2A to form a narrow U, discal band from Sc+R$_1$ vein, poorly defined in Sc+R$_1$–Rs cell in some specimens; fringe mostly black, but white mediad in cells near tornus. Head and palpi black above with white-blue spots and bands; below each palp with a wide white longitudinal band continuing on cheeks and pectus, cheeks and pectus otherwise black; antennae black, nudum dark reddish-brown, 18–20 segments (n=5), collar with four blue-white spots, tegulae black with blue-white longitudinal band; thorax above with two marine blue longitudinal bands; abdomen above black with white-blue spots on each side in tergums' anterior, beneath black, white-banded at segments; legs black with white spots and bands. **Male genitalia** (Figs. 46, 47a, 51 part) – tegumen very short, with a pair of as long as tegumen caudal processes at the base of uncus, processes finger-shaped, directed posterodorsad; uncus more than twice longer than tegumen, dome shaped, divided into two arms, each arm thin and narrow apically and with a flat lateral lobe; gnathos poorly sclerotized and vestigial; saccus lever-shaped, directed dorsad, slightly bulbous at its apex, length as uncus; valva broad, ampulla-costa rounded, convex, without processes, but ampulla more sclerotized at the margin, cucullus more than half as long as the rest of the valva, almost rectangular, cucullus distal end is at about the same height as proximal end, cucullus dorsal margin weakly concave, finely dentate; distally, cucullus ventral margin bends dorsad almost at a right angle so that distal margin is nearly straight; sacculus as high as long, with small tooth at distal end of the dorsal margin, which is irregular and serrated anterior to the tooth; juxta very large (as long as phallobase), corner-shaped, bluntly triangular in lateral view, with several ridges; aedeagus about as long as tegumen plus uncus, boomerang-shaped, phallobase close to half of penis length, single triangular cornutus with irregular margin.

Female (n=7, Figs. 3–6, 11–14) – forewing length = 27 to 32 mm, similar to male, but larger, with more rounded, broader wings, outer margin of hindwings with a small, low lobe (absent in males) from M$_2$ vein to the middle of Cu$_1$-Cu$_2$ cell, nudum 22–25 segments (n=4). **Female genitalia** (Figs. 48a–i) – lamella antevaginalis strongly sclerotized, thick, broad-M-shaped in ventral view and U-shaped in posterior view, expanding into narrowing lateral lobes; lamella postvaginalis membranous and vestigial; antrum sclerotized, slightly wider than ductus bursae; ductus bursae with a weakly bulbous sclerotized enlargement around its middle, continuous with corpus bursae, together about 4 times sterigma length.

DNA barcodes: Barcode sequence of the holotype (voucher 04-SRNP-34396), GenBank accession GU161554, 658 base pairs:
AACTTTATATTTTATTTTTGGAATTTGAGCAGGAATAATTGGAA
CATCTCTTAGATTGCTAATTCGAACTGAATTAGGAACTCCTGA
ATCTTTAATTGGAGATGATCAAATTTATAATACTATTGTAACAGC
TCATGCATTTATTATAATTTTTTTTATAGTTATACCAATTATAATT
GGCGGATTTGGAAATTGACTAGTCCCCCTTATATTGGGAGCA
CCTGATATAGCTTTCCCTCGAATAAATAACATAAGATTTTGGTT
ATTACCCCCTTCATTAACCTTACTTATTTCAAGAAGTATCGTAG
AAAATGGTGCCGGAACTGGATGAACAGTTTATCCCCCCCTCT
CTTCTAATATCGCACACCAAGGAGCTTCTGTAGATTTAGCTAT
TTTTTCTTTGCATTTAGCTGGAATTTCATCAATTTTAGGAGCTA
TTAACTTTATTACAACAATTATCAATATACGAATTAAAAACCTAT
CTTTTGACCAAATACCATTATTTGTTTGAGCTGTAGGAATTACA
GCATTATTATTACTTTTATCACTGCCCGTATTAGCAGGAGCTAT
TACTATATTATTAACAGATCGAAATATCAATACTTCTTTTTTTGA
TCCCGCTGGAGGTGGAGATCCCATTTTATATCAACACTTATTT

We also determined barcode sequences of 13 paratypes. Seven of them (voucher codes/GenBank accessions: 10-SRNP-103600/HM884525, 05-SRNP-31969/GU151442, 04-SRNP-32358/GU161555, 04-SRNP-30754/DQ292573, 03-SRNP-21823/DQ292574, 03-SRNP-21528/DQ292575, 01-SRNP-9029/DQ292569) are identical to that of the holotype (except that 01-SRNP-9029 has a single undetermined base pair (bp) "N" within its sequence and is lacking 102 bp from the 3' end) and others show variation within a third of a percent: 1 bp difference (145 C, not T [numbering is from 1 to 658 for the holotype as a reference]) in five sequences (09-SRNP-30034/GU649882, 05-SRNP-31086/GU150502, 04-SRNP-56811/GU150503, 02-SRNP-13059/DQ292570, 00-SRNP-4482/DQ292571), and 2 bp difference (145 C, not T and 592 T, not A) in one (96-SRNP-12846/DQ292572). Several of these sequences lack some segments at the termini. All of these 14 sequences appear monophyletic on all the trees we have seen or built, and the closest available sequence to them is that of *J. pater*, different by 23 bp, which is over 5% (Fig. 50). Additional (and updated) information and neighbor-joining trees can be retrieved by searching the BOLD database (Ratnasingham and Hebert 2007) with the holotype sequence at <http://www.boldsystems.org/index.php/IDS_OpenIdEngine>.

Types: Holotype male has the following rectangular labels: white printed & hand-printed - || Voucher: D.H.Janzen & W.Hallwachs | DB: http://janzen.sas.upenn.edu | Area de Conservacion Guanacaste, || COSTA RICA. | 04-SRNP-34396 ||; yellow printed - || LEGS AWAY

FIGS. 1–44. *Jemadia* specimens. **1–12.** *J. suekentonmiller* type specimens (**1–2.** is the holotype, others are paratypes): Costa Rica: ACG, data in text, elaborated in Janzen & Hallwachs (2013), sexes and voucher codes are: 1–2. ♂ 04-SRNP-34396; **3–4.** ♀ 04-SRNP-32358; **5–6.** ♀ 04-SRNP-32840; **7–8.** ♂ 02-SRNP-13059 (genitalia Figs. 46i–m); **9–10.** ♂ 03-SRNP-21528; **11–12.** ♀ 04-SRNP-30754. Dorsal and ventral surfaces are shown on odd- and even-numbered figures, respectively. Labels are shown for some specimens between and around the views of a specimen. Labels are reduced by about 1/3 compared to specimens: smaller scale bar below one of the labels refers to labels, and larger scale bars refer to specimens. "F" indicates mirror image (left-right inverted). Pinholes and some other imperfections are digitally removed. Insets numbered with a corresponding figure number and "z" (for zoom) show the details of discal hindwing blue ray near the base of M_3–Cu_1 cell; M_3 on the right indicates where this vein reaches the edge of the inset; vertical gray bar is 1 mm; blue arrow points to an image the insert refers to, except 15z, which (for lack of space) is removed from the image of wings.

FIGS. 1–44 (continued). **13–14.** *J. suekentonmiller* paratype ♀, Panama: Calobre, leg. Arce, Godman-Salvin Collection 1912–23, BMNH(E) #1037694; **15–16.** *J. pater* [holo]type (as deduced by Mielke 2005) ♂, Colombia: Bogota region, BMNH(E) #982078; **17–18.** *J. pater* [para]type ♀, Venezuela, Hewitson Collection 79-69, BMNH(E) #1054222 (genitalia Fig. 48k); **19–20.** *J. pater* ♂ Panama: Darien Prov., Cana (Cerro Pirre), 7° 56'N 77° 43'W, 500 m, 15-Jul-1983, leg. G. B. Small, genitalia X-4830 J. M. Burns 2000 [USNM] (genitalia Fig. 47b); **21–22.** *J. ortizi* ♂ Venezuela: Mérida, S. P. Gabaldon Coll., genitalia X-4848 J. M. Burns 2000 [USNM] (genitalia Fig. 47f); **23–24.** *J. ovid* [holo]type ♂, Ecuador: Paramba, 3500 ft, Apr-1897, dry season, leg. Rosenberg, BMNH(E) #982977; **25–26.** *J. ovid* [para]type ♀, Ecuador: Paramba, leg. Rosenberg, BMNH(E) #1054224 (genitalia Fig. 48j); **27–28.** *J. ovid* ♂ Ecuador: Pichincha Prov., Alluriquín, 700 m, Aug-1973, leg. N. R. Venedictoff, genitalia X-4832 J. M. Burns 2000 [USNM] (genitalia Fig. 47g). Images of BMNH specimens on all figures are copyright Trustees of the Natural History Museum, London; used with permission.

FIGS. 1–44 (continued). **29–30.** *J.* cf. *albescens* Röber, 1925 ♂, Ecuador: "Environs de Loja", 1890, E. T. Owen collection, genitalia X-4839 J. M. Burns 2000 [USNM] (genitalia Fig. 47j); **31–32.** *J.* cf. *albescens* ♀, Ecuador: Zamora, 3000-4000 ft, leg. O. T. Baron, BMNH(E) #1037689; **33–34.** *J.* cf. *albescens* ♀, Brazil: Rondônia, 62 km S Ariquemes, Fazenda Rancho Grande, 10.53°S, 62.80°W, 165 m, {19–29}-Sep-1996, leg. B. Harris, genitalia NVG121102-39 [USNM] (genitalia Figs. 48l–n); **35–36.** *J. hewitsonii* [syn]type ♂, Brazil: Amazonas, Hewitson Collection 79-69, type H 54, BMNH(E) #982976, round "Type" and square labels are shown in dorsal and ventral views; **37–38.** *J.* cf. *hewitsonii* ♂, Peru: Pebas, "Amazones", 1880, leg. M. de Mathan, BMNH(E) #1037693 (genitalia Fig. 47k); **39–40.** *J.* cf. *hewitsonii* ♂, Brazil: Amazonas, São Paulo de Olivença, Mar-1962, leg. J. Kesselring, genitalia vial H210 prep. S. S. Nicolay [USNM] (genitalia Fig. 47l); **41–42.** *J.* cf. *hewitsonii* ♂, Brazil: Matto Grosso, Cuiabá, genitalia X-4854 J. M. Burns 2000 [USNM] (genitalia Fig. 47m); **43–44.** *J.* cf. *hewitsonii* ♀, Bolivia: Santa Cruz de la Sierra, 1905/6, leg. J. Steinbach, BMNH(E) #1054212.

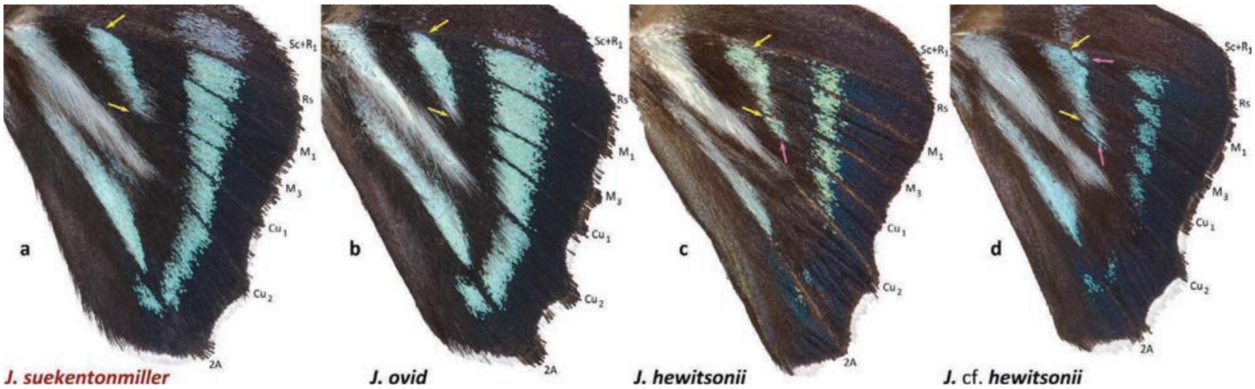


FIG. 45. Discal blue ray on dorsal hindwing of *Jemadia* males. Three observed ray types are shown: **b.** no patches of blue scales at either base of Rs–M_1 cell and M_3–Cu_1 cell (specimen Figs. 27–28); **c.** blue spot at the base of M_3–Cu_1 cell, no spot at the base of Rs–M_1 cell (specimen Figs. 35–36); **d.** blue spots at both cell bases (specimen Figs. 39–40). Veins are labeled along the outer margin. Pink arrows point at spots, yellow arrows point at the splits between Rs and M_1 veins and between M_3 and Cu_1 veins. **a.** *J. suekentonmiller* ray is of a type shown in **b**, i.e., no spots at either base (specimen Figs. 9–10). Images not to scale, but rescaled to be similar in size and are edited to digitally remove wear and imperfections in specimens.

| FOR DNA ||; red printed - || HOLOTYPE ♂ | *Jemadia* | *suekentonmiller* | Grishin ||. Holotype data: Costa Rica: Area de Conservación Guanacaste, Guanacaste Province, Sector Pitilla, site Sendero Cuestona, 10.99455 -85.41461, 640 m, collected on 12-VIII-2004 as pupa on *Casearia arborea* (Salicaceae) by Calixto Moraga, adult eclosed 08-Sep-2004, voucher code 04-SRNP-34396. Since the holotype is from a wild-caught pupa, its size is more in line with the norm for the species, and not reduced as for most adults reared from caterpillars. **Paratypes:** 13 ♂♂ and 7 ♀♀. Costa Rica, Area de Conservación Guanacaste: Guanacaste Province, Sector Pitilla, reared from caterpillars feeding, or collected as pupae, on *Casearia arborea* (Salicaceae), plus one adult: site Estacion Pitilla, 10.98931 -85.42581, 675 m: 1♂ collected as adult on 17-III-2005, voucher code 05-SRNP-31086; 1♀ collected on 16-VI-1996 as antepenultimate instar, adult eclosed on 21-IX-1996, genitalia No. X-4821 J. M. Burns 2000, voucher code 96-SRNP-12846; site Loaiciga, 11.01983 -85.41342, 445 m: 1♂ collected on 29-X-2003 as preantepenultimate instar, adult eclosed on 03-IV-2004, voucher code 03-SRNP-21528; 1♀ collected on 19-VI-2004 as antepenultimate instar, adult eclosed on 04-X-2004, voucher code 04-SRNP-33566; site Sendero Cuestona, 10.99455 -85.41461, 640 m: 1♂ collected on 08-VIII-2004 as pupa, adult eclosed on 01-IX-2004, voucher code 04-SRNP-34305; 1♀ collected on 04-II-2004 as last instar, adult eclosed on 31-III-2004, voucher code 04-SRNP-30754; site Sendero Evangelista, 10.98680 -85.42083, 660 m: 1♂ collected on 23-XI-2000 as preantepenultimate instar, adult eclosed on 10-IV-2001, genitalia No. X-5050 J. M. Burns 2001, voucher code 00-SRNP-4482; 1♂ collected on 06-I-2001 as penultimate instar, adult eclosed on 15-II-2001, genitalia No. X-5883 J. M. Burns 2004, voucher code 01-SRNP-9029; site Sendero Laguna, 10.9888 -85.42336, 680 m: 1♂ collected on 31-V-2005 as antepenultimate instar, adult eclosed on 26-IX-2005, voucher code 05-SRNP-31969; 1♀ collected on 19-V-2004 as preantepenultimate instar, adult eclosed on 12-X-2004, genitalia NVG121102-38, voucher code 04-SRNP-32840; site Sendero Memos, 10.98171 -85.42785, 740 m: 1♂ collected on 06-I-2009 as antepenultimate instar, adult eclosed on 16-III-2009, voucher code 09-SRNP-30034; 1♀ collected on 28-IV-2004 as preantepenultimate instar, adult eclosed on 15-X-2004, voucher code 04-SRNP-32358; 1♂ site Sendero Mismo, 10.98758 -85.41967, 680 m collected on 12-XI-2003 as preantepenultimate instar, adult eclosed on 31-III-2004, voucher code 03-SRNP-21823; 1♂ site Sendero Paleta, 11.00434 -85.41646, 570 m, collected on 23-VIII-2004 as pupa, adult eclosed on 30-VIII-2004, voucher code 04-SRNP-34735; 1♂ site Sendero Rotulo, 11.01355 -85.42406, 510 m, collected on 13-VII-2002 as last instar, adult eclosed on 13-VIII-2002, genitalia No. X-5884 J. M. Burns 2004, voucher code 02-SRNP-13059; 1♂ site Sendero Trichoptera, 10.98571 -85.41869, 655 m, collected on 14-XII-2004 as antepenultimate instar, adult eclosed on 10-IV-2005, voucher code 04-SRNP-56811; 1♀ collected as adult, genitalia No. X-4822 J. M. Burns 2000, voucher code 98-RIOS-171; 1♂ Alajuela Province: Sector Rincon Rain Forest, site Leiva (Potrero Chaves), 10.939 -85.322, 433 m, collected as adult on 02-IV-2010, leg. J. D. Turner & N. Turner, voucher code 10-SRNP-103600; 1♂ Cartago Province: 3 km WNW of Grano de Oro, 9° 49' 24"N 83° 29' 06"W 1100 m, collected as adult on 15-IV-2006, leg. I. & M. Nakamura, K. Nishida & R. Alverado. 1♀ Panama: [Veraguas Province, 25 km NE of Santiago,] Calobre, [8° 16'N, 80° 49'W per Selander & Vaurie (1962)] [leg.] Arcé, specimen No. BMNH(E) #1037694.

Deposition of types: Holotype is in the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM). Two paratypes (09-SRNP-30034 & from Panama: Calobre) are in the Natural History Museum, London, UK (BMNH). Two paratypes (04-SRNP-34305 & 04-SRNP-33566) are deposited in the McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida, Gainesville, FL (MGCL). One paratype (from Costa Rica: Cartago Prov.) is in Ichiro Nakamura collection. All other paratypes are in USNM.

Type locality: COSTA RICA: Area de Conservación Guanacaste, Guanacaste Province, Sector Pitilla, site Sendero Cuestona, GPS: 10.99455 -85.41461, elevation 640 m.

Etymology: Burns and Janzen (2001) wrote: ". . . the northernmost member of the *J. hewitsonii* species complex . . . is . . . in the rainforest of the ACG . . . and . . . more adults are desired before formal description of this apparent differentiate." The adults are now available, and this spectacular butterfly is named in honor of Susan Miller and Kenton Miller (RIP), in recognition of their 48 years of intense advocacy, planning, legitimizing, and mentoring the national parks of the world, and, specifically, recommending and planning the founding of Parque Nacional Santa Rosa in 1971 (today Sector Santa Rosa), the initial seed of Area de Conservacion Guanacaste (ACG), and mentoring and inspiring Alvaro Ugalde and Mario Boza to found the national park system of Costa Rica. Without their efforts, all known ACG forest habitat for this butterfly would long ago have been logged and agroscaped.

Distribution and phenology: Currently, this rain forest species is known from Costa Rica (Guanacaste, Alajuela and Cartago provinces) and Panama (Veraguas province), and has been reared in Costa Rica to eclose in February, March, April and August, September, October (Janzen and Hallwachs 2013), and two free-flying adults have been collected in March and April. The reasons for peaks and troughs in its phenology are unclear.

Diagnosis: This species belongs to *Jemadia*, because it possesses all the characters of the genus as given in the Evans identification key (1951: 3–4) and is particularly similar to other *J. hewitsonii* group taxa (all treated by Evans as subspecies). COI barcode sequences have been obtained for most species of *Jemadia*, including its type species, *Jemadia hospita* (Butler, 1877) (Fig. 50). The difference between the DNA barcodes of *J. suekentonmiller* and *J. hospita* is close to 10%, and is about the same as differences in many other *Jemadia* species pairs, e. g., *J. hospita* and *J. fallax* (Mabille, 1878) (Fig. 50). Although DNA sequence information about *Jemadia* is still very scarce, it is significant that the tree shown in Fig. 50 agrees very well with morphological evidence (Figs. 1–48, 51 and Warren et al. (2013) with photographs of other species), and that there is no indication of introgression or hybridization between species. Reliable groupings in the tree agree with the structure of Evans's (1951) identification key, e.g., all *J. hewitsonii* group taxa form a monophyletic group. Moreover, each of two pairs of species that are next to each other in his key, i.e., *J. hospita* (in which Evans included *J. pseudognetus* (Mabille, 1878) as a subspecies) plus *J. sosia* (Mabille, 1878) and *J. menechmus* (Mabille, 1878) plus *J. scomber* H. Druce, 1908, comprises sister taxa in the tree (Fig. 50).

The new species belongs to the *Jemadia hewitsonii* group by phenotype and by its position in the DNA barcode NJ tree. Taxa in this group can be distinguished from other *Jemadia* by the white-spotted collar and by the dorsal pattern of the hindwing, which consists of: **(a)** two pale streaks along veins Cu_2 and 2A from the base to at least half of the wing, the first streak paler and the second one bluer; **(b)** short discal blue ray constrained between veins Rs and Cu_1 and directed from the split of veins Rs and M_1 towards the split of veins M_3 and Cu_1; **(c)** postdiscal blue band approximately following the contour of hindwing outer margin. In other *Jemadia* species groups, either the pale streaks along veins Cu_2 and 2A are absent or short and discal ray is very long, reaching 2A vein; or the discal ray is absent (Fig. 45).

The new species is distinguished from all other taxa in the *J. hewitsonii* group by the combination of the following characters (the first two are likely diagnostic for facies): **(1)** discal blue ray on dorsal hindwing is short, only between M_1 and M_3 veins, blue scales do not invade bases of cells Rs–M_1 and M_3–Cu_1 (Fig. 45a); **(2)** discal white band on forewing is rather broad, 2.5–4.5 times longer than width (Figs. 1–14); **(3)** postdiscal blue band on dorsal hindwing is medium to broad, developed in all cells between veins Rs and 3A (Figs. 1–14); **(4)** cucullus distal end is at about the same height as proximal end (Figs. 46a, i, 47a); **(5)** cucullus dorsal margin is only slightly concave, more finely dentate; **(6)** cucullus ventral margin distally bends dorsad almost at a right angle and at the distal end deviates only slightly from a straight vertical line, thus cucullus appears most rectangular of all *J. hewitsonii* group species; **(7)** dorsolateral process (one on each side) off the distal end of tegumen is long, finger-like; **(8)** phallobase is short, about half of the penis length; **(9)** dorsal margin of sacculus near the apical tooth is dentate and irregular, not smooth and ending in a single prominent tooth; **(10)** saccus slightly bulbous at the apex (for genitalia characters see Figs. 46, 47a). These characters are illustrated in Fig. 51.

Interestingly, *J. suekentonmiller* shares most of these characters (all except 2, 5, 6 & 10) with *Jemadia ovid* Evans, 1951, **new status**, described as a subspecies of *J. hewitsonii* (Fig. 51). Both *J. suekentonmiller* and *J. ovid* have a short discal blue ray (character 1, Figs. 46a, b, yellow arrows) and well-defined postdiscal blue bands (character 3, Figs. 46a, b) on dorsal hindwing, cucullus distal end the same height as proximal end (character 4, Figs. 46a, g); long tegumen processes (character 7, Figs. 46a, g, pointed to by a brown arrow); short phallobase (character 8, Figs. 46a, g, measurements indicated by green marks and ratios shown in green numbers); and several teeth at the dorsal margin of sacculus (character 9, Figs. 46a, g, shown as insets "z"). Preliminary analysis of female genitalia (Fig. 48) shows that both the new species and *J. ovid* are characterized by narrower lamella antevaginalis near the antrum than that of both *J. pater* and *J.* cf. *hewitsonii*. While we did not obtain DNA sequences of *J. ovid*, we suspect that these extensive phenotypic similarities indicate that *J. suekentonmiller* is its Central American sister. Because of these similarities with the new species, as thus different from all other *J. hewitsonii* group taxa (*J. pater* and *J. ortizi* included), we treat *J. ovid* as a distinct species rather than a subspecies, in-line with the conclusions of Burns and Janzen (2001) who wrote: "Consideration of the color-pattern characters . . .,

FIG. 46. Male genitalia of *Jemadia suekentonmiller*. Genital capsule of paratypes, Costa Rica: ACG, data in text. Genitalia Nos. and voucher codes: **a–h.** X-5883 J. M. Burns, 01-SRNP-9029; **i–m.** X-5884 J. M. Burns, 02-SRNP-13059 (specimen Figs. 5–6). Views: **a, i.** left lateral; **b.** dorsolateral; **c, m.** lateroventral; **d.** dorsal; e. ventral; **f, j.** posterolateral; **g, k.** posterior; **h, l.** anterior. Specimens are in USNM.

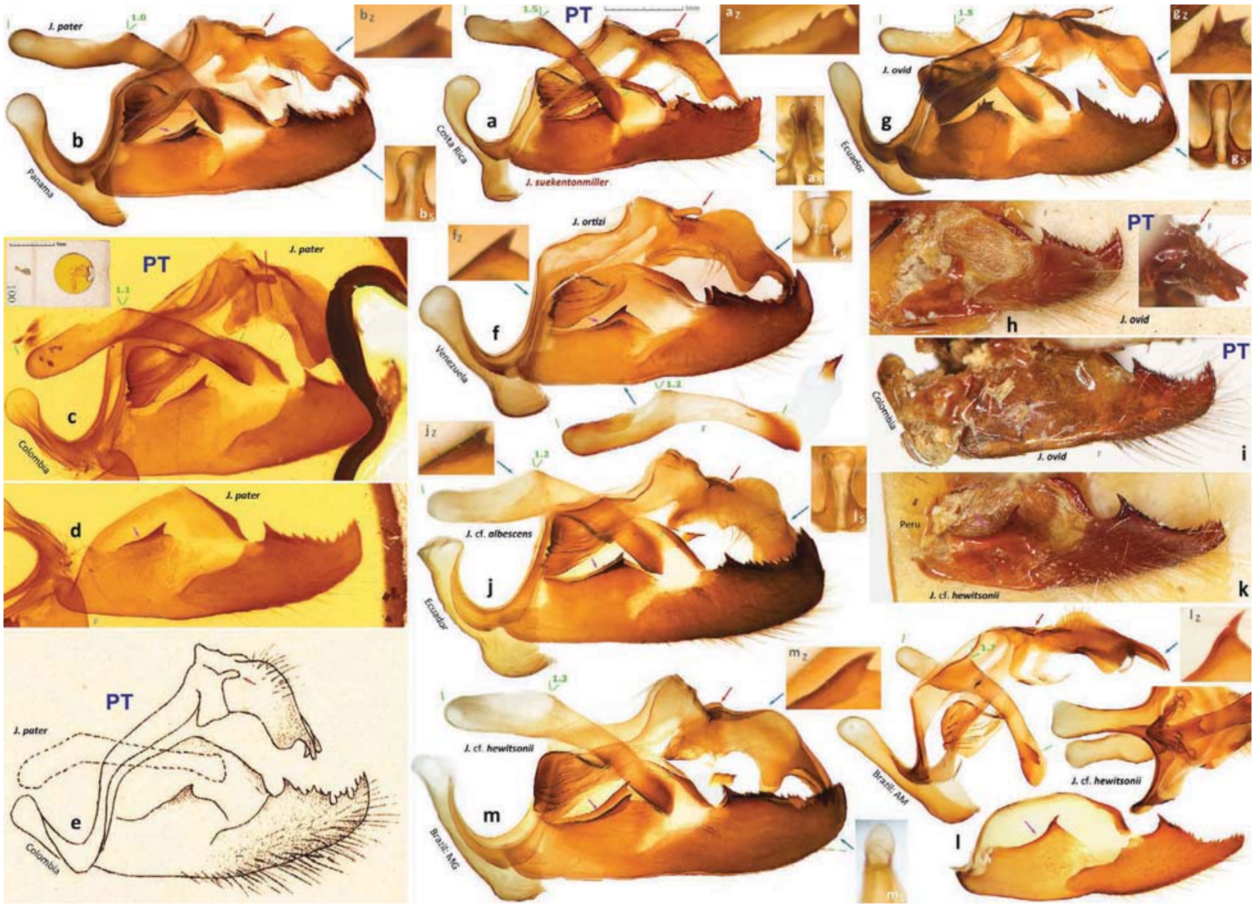


FIG. 47. Male genitalia of *Jemadia* hewitsonii group species. **a.** *J. suekentonmiller* n. sp. paratype, Costa Rica: ACG, voucher code 00-SRNP-4482, data in text, genitalia No. X-5050 J. M. Burns 2001 [USNM]; **b.** *J. pater*, Panama: Darien Prov., Cana (Cerro Pirre), 7° 56'N 77° 43'W, 500 m, 15-Jul-1983, leg. G. B. Small, genitalia No. X-4830 J. M. Burns 2000 [USNM] (specimen Figs. 19–20); **c–d.** *J. pater*, [para]type, Colombia: Bogota, Druce Collection, Godman-Salvin Collection 1912–23, genitalia mini-slide No. 100, specimen No. BMNH(E)#1037686 [BMNH]: **c.** complete genitalia without the left valva, inset shows mini-slide with genitalia and a scale bar for it; **d.** interior view of left valva, flipped to facilitate comparisons; **e.** *J. pater*, Colombia, illustration of genitalia shown in **c–d.** from Godman & Salvin (1893: pl. 74, fig. 9, as *J. hewitsonii*), note incorrect proportions of penis compared to **c–d**; **f.** *J. ortizi*, Venezuela: Mérida, S. P. Gabaldon Coll., genitalia No. X-4848 J. M. Burns 2000 [USNM], penis shown below (specimen Figs. 21–22); **g.** *J. ovid*, Ecuador: Pichincha Prov., Alluriquín, 700 m, Aug-1973, leg. N. R. Venedictoff, genitalia No. X-4832 J. M. Burns 2000 [USNM] (specimen Figs. 27–28); **h–i.** *J. ovid*, [para]type, Colombia: "Env. Bogotá", 1918, leg. Frere Apollinaire-Marie, BMNH(E)#1037687 [BMNH]: **h.** interior view of valva, inset shows dorsolateral view of uncus; **i.** lateral view of valva and saccus; **j.** *J.* cf. *albescens*, Ecuador: "Environs de Loja", 1890, E. T. Owen collection, genitalia No. X-4839 J. M. Burns 2000 [USNM] (specimen Figs. 29–30); **k.** *J.* cf. *hewitsonii*, Peru: Pebas, "Amazones", 1880, leg. M. de Mathan, BMNH(E) #1037693 [BMNH], interior view of valva (specimen Figs. 37–38); **l.** *J.* cf. *hewitsonii*, Brazil: Amazonas, São Paulo de Olivença, Mar-1962, leg. J. Kesselring, genitalia vial H210 prep. S. S. Nicolay [USNM], lateral view of genital ring with tegumen, uncus, gnathos, saccus and penis are on top left, interior view of valva at the bottom, and a section of ventral view showing saccus, part of penis and vinculum is on the right (specimen Figs. 39–40); **m.** *J.* cf. *hewitsonii*, Brazil: Matto Grosso, Cuiabá, genitalia No. X-4854 J. M. Burns 2000 [USNM] (specimen Figs. 41–42). **a–b, f–g, j, m**. is complete genital capsule in left lateral view, preparations in glycerol; **h–i, k**. are dry mounts glued to carton cards. Insets numbered with a corresponding figure number and "z" (for zoom) show 3x magnified details of the tooth on sacculus, blue arrow points to an image the insert refers to. Insets numbered with a corresponding figure number and "s" (for saccus) show ventral view of saccus apex, scale is the same as in other images and blue arrow points to an image the insert refers to. Brown arrow points at a distal process of tegumen, magenta arrow points at a curvature of the sacculus margin, green ticks demarcate the lengths of phallobase and penis and a number in green is the ratio of penis length to phallobase length. "F" indicates mirror image (left–right inverted). Images of BMNH specimens are copyright Trustees of the Natural History Museum, London; used with permission.

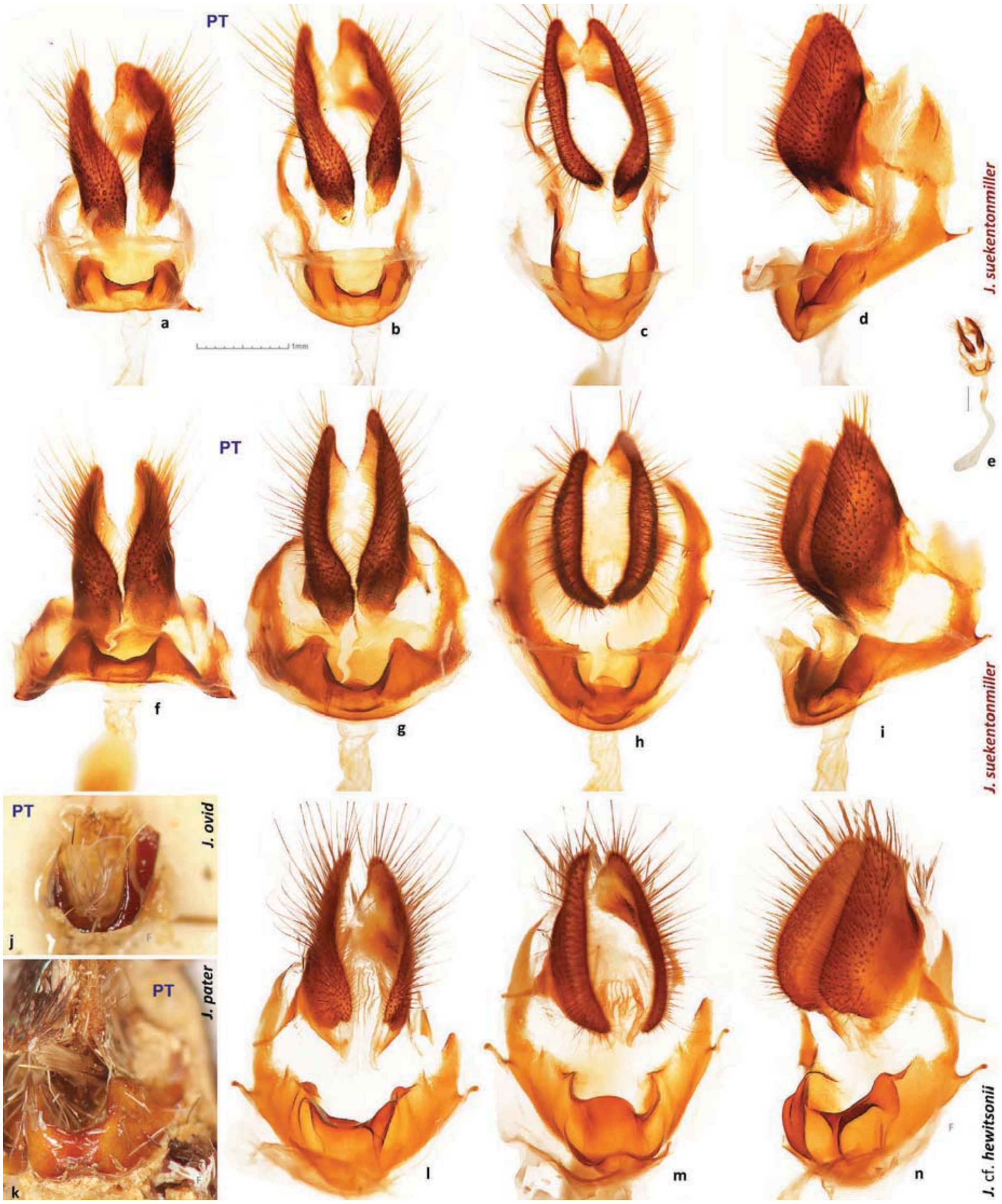


Fig. 48. Female genitalia of *Jemadia hewitsonii* group species. **a–i.** *J. suekentonmiller* n. sp. paratypes, Costa Rica, ACG, data in text, genitalia Nos. and voucher codes: **a–e.** X-4821 J. M. Burns, 96-SRNP-12846 and **f–i.** X-4822 J. M. Burns, 98-RIOS-171; **j.** *J. ovid* [para]type, Ecuador: Paramba, leg. Rosenberg, BMNH(E) #1054224 (specimen Figs. 25–26); **k.** *J. pater* [para]type, Venezuela, Hewitson Collection 79-69, BMNH(E) #1054222 (specimen Figs. 17–18); **l–n.** *J.* cf. *hewitsonii*, Brazil: Rondônia, 62 km S Ariquemes, Fazenda Rancho Grande, 10.53°S, 62.80°W, 165 m, {19–29}-Sep-1996, leg. B. Harris, genitalia NVG121102-39 [USNM] (specimen Figs. 33–34). Views: **a, f,** ventral; **b, g, l.** posteroventral; **c, h, j, m.** posterior; **d, i, n.** ventrolateral; **k.** lateroventral; **e.** reduced image of complete genitalia, scale shows 1 mm. **j.** is dry genitalia glued to carton card; **k.** is shown in situ, the end of abdomen with genitalia exposed, others are wet preparations stored in glycerin. "F" indicates mirror image (left-right iverted). Images of BMNH specimens are copyright Trustees of the Natural History Museum, London; used with permission.

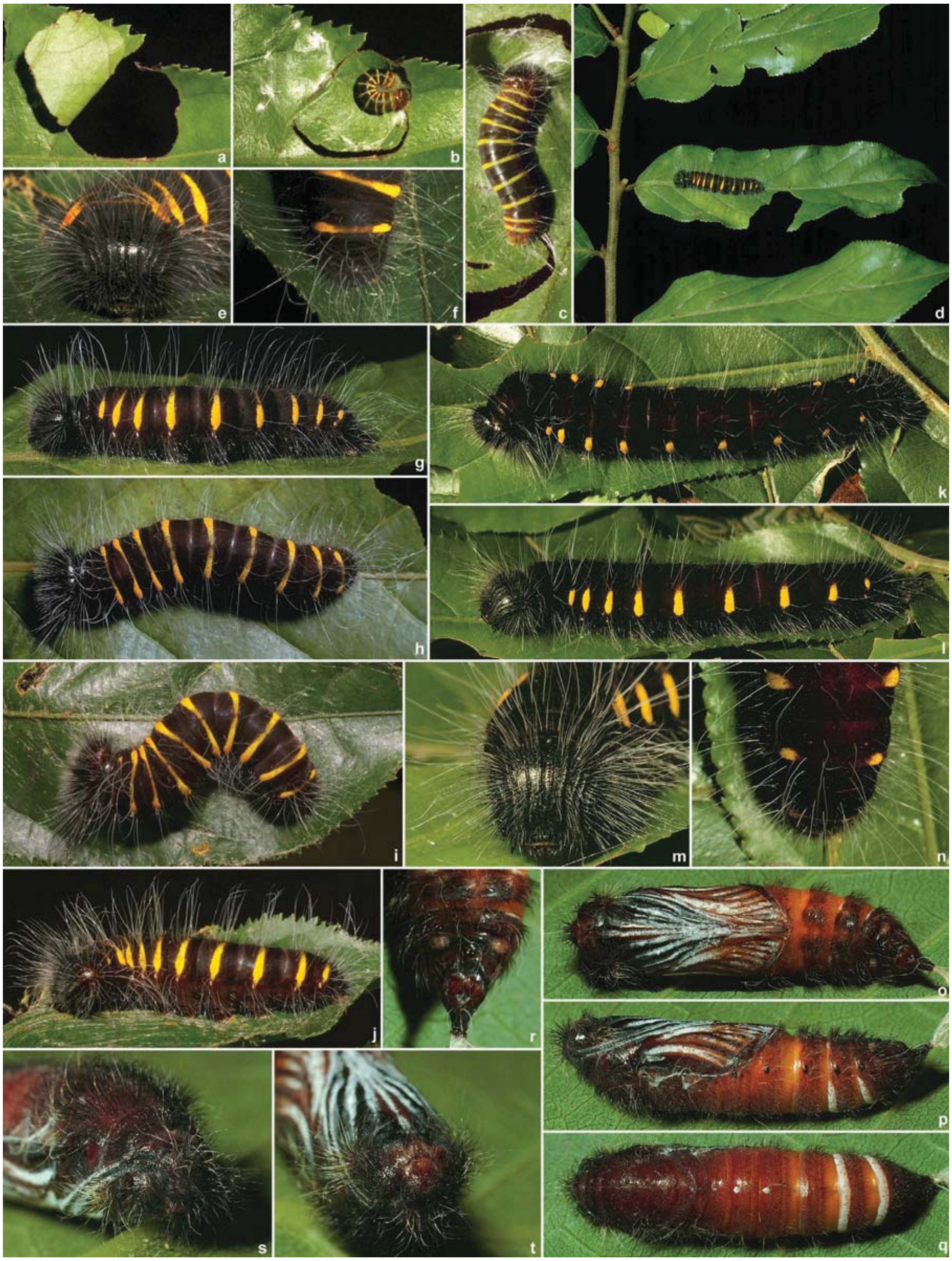
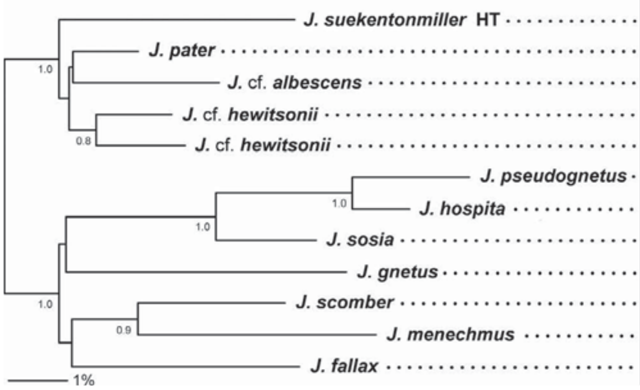


FIG. 49. Immature stages of *Jemadia suekentonmiller*. Costa Rica: ACG: **a–n.** caterpillars: **a–c.** early, **d–j.** penultimate, and **k–n.** ultimate instars; **o–t.** pupa. **a.** leaf shelter, opened in **b; e, m.** head in anterior view, posterior end in: **f, n.** dorsal and **r.** ventral views. Lengths of immatures: **b.** 5 mm, **c.** 8 mm, **e–f, i–j.** 27 mm, **d, g–h.** 29 mm, **k–n.** 55mm, **o–t.** 41 mm. Images **c, e–f, m–n** are magnified and **d** is reduced compared to the rest; **h** is a mirror image. Voucher codes: **a–b, e–f, i–j.** 05-SRNP-41483; **c.** 11-SRNP-31480; **d, g–h.** 03-SRNP-21528; **k–n.** 01-SRNP-9029; **o–t.** 02-SRNP-13059; data in text or in Janzen & Hallwachs (2013), together with additional information.



	1	2	3	4	5	6	7	8	9	10	11	12
1	–	**34**	**41**	**38**	**40**	73	67	65	66	56	70	61
2	**5.2**	–	23	19	20	64	58	47	47	44	54	45
3	**6.3**	3.5	–	28	28	71	68	54	57	54	63	53
4	**5.8**	2.9	4.3	–	**18**	64	60	50	55	43	58	44
5	**6.1**	3.1	4.3	**2.8**	–	64	58	48	55	49	60	51
6	11.2	9.8	10.9	9.8	9.8	–	**19**	37	64	67	72	73
7	10.2	8.9	10.4	9.2	8.9	**2.9**	–	32	58	63	63	66
8	9.9	7.2	8.3	7.6	7.3	5.7	4.9	–	58	51	56	51
9	10.1	7.2	8.7	8.4	8.4	9.8	8.9	8.9	–	54	57	56
10	8.6	6.7	8.3	6.6	7.5	10.2	9.6	7.8	8.3	–	**41**	48
11	10.7	8.3	9.6	8.9	9.2	11.0	9.6	8.6	8.7	**6.3**	–	53
12	9.3	6.9	8.1	6.7	7.8	11.2	10.1	7.8	8.6	7.3	8.1	–

FIG. 50. DNA-derived data. DNA barcode distance matrix is shown on the right and a BioNJ (Dereeper et al. 2008) distance tree corresponding to it is on the left. The scale bar corresponding to about 1% difference is placed below the tree. Fourteen reported *Jemadia suekentonmiller* sequences (Janzen et al. 2011) are nearly identical in sequence and differ from each other by not more than 2 nucleotides (0.3%), thus only the holotype is included in the tree. All sequences used in the tree are the same length of 654 bp. Bootstrap support values of above 0.75 are shown by each node in the tree, nodes without a number represent unreliable groupings. Data for specimens: GenBank accessions, where available (two letters followed by six digits, http://genbank.gov/), and voucher codes (with "SRNP" from Janzen & Hallwachs (2013), others from BOLD database (Ratnasingham & Hebert 2007)) are given first: **1.** *J. suekentonmiller* holotype: GU161554, 04-SRNP-34396, Costa Rica: Area de Conservación Guanacaste, Guanacaste, Sector Pitilla, Sendero Cuestona, 10.99455 -85.41461, 640 m, collected on 12-Aug-2004 as pupa by Calixto Moraga; **2.** *J. pater*: N/A, HESP-EB 02 778, Ecuador: Pastaza, Puyo, 10 de Agosto, Palora 3, -1.5 -77.58, 1000, 19-Aug-2011; **3.** *J.* cf. *albescens* (*J. hewitsonii albescens* sensu Evans, 1951): GU662084, HESP-EB 00-402, Peru: San Martin, Rioja-Pedro Ruiz, -5.4 -77.4, 1400 m, 10-Nov-2003; **4.** *J.* cf. *hewitsonii*: JN278044, HESP-EB 02084, Brazil: Para, Belem, 50 km E-NO from Belem, Santo Antonio do Taua, -1.0908 -48.0745, {20–27}-Oct-2009; **5.** *J.* cf. *hewitsonii*: N/A, BC-OM 37.188, Brazil: Rio de Janeiro, Barra do Sao Joao, 17-Oct-1986, leg. K. Brown; **6.** *J. pseudognetus*: JGU150506, 05-SRNP-4395, Costa Rica: Area de Conservación Guanacaste, Alajuela, Sector San Cristobal, Puente Palma, 10.9163 -85.37869, 460 m, collected on 30-Jul-2005 as penultimate instar by Gloria Sihezar; **7.** *J. hospita*: HM394394, HESP-EB 00 282, Bolivia: La Paz, Caranavi-Corioco, -16.0 -67.35, 1400 m, 01-Oct-2008; **8.** *J. sosia* (sensu Evans, 1951): GU662267, HESP-EB 00 246, Peru: San Martin, "Mina de Sal", 1900 m, 01-Jun-2007; **9.** *J. gnetus*: N/A, HESP-EB 02 624, Ecuador: Pastaza, Puyo, 10 de Agosto, -1.23 -77.52, 1000 m, 13-Jan-2011; **10.** *J. scomber*: HM394769, HESP-EB 01 028, Peru: Huanuco, Tingo Maria, -9.17 -75.59, 650 m; **11.** *J. menechmus*: HM422905, HESP-EB 00-403, Bolivia: La Paz, Caranavi, -15.5 -67.33, 750 m; **12.** *J. fallax*: GU662256, HESP-EB 00 230, Ecuador: Napo, Misahualli/Lita, -1.02 -77.4, 01-Jul-2008. The tree shown is unrooted and a confident position of the root could not be obtained. The tree is bent (i.e. the "["-shaped branch that does not necessarily imply the root position, is placed) to segregate *J. hewitsonii* group sequences (1 through 5) from the rest. Percent difference and the number of different nucleotides are shown below and above the diagonal in the matrix, respectively. Values corresponding to differences between sister species (two *J.* cf. *hewitsonii* sister species, *J. pseudognetus* vs. *J. hospita,* and *J. scomber* vs. *J. menechmus*) and between *J. suekentonmiller* and other *J. hewitsonii* group sequences are shown in bold font.

coupled with comparison of . . . genitalia . . . , suggests that several closely related species, rather than subspecies, comprise a *Jemadia hewitsonii* species complex."

The new species can be distinguished from *J. ovid* by its wider forewing discal band, whose width in *J. ovid* is less than a quarter of its length (character 2, Figs 1–14 vs. 23–28, *ovid* also has a very narrow, mostly streak-like, in males, postdiscal doublet of spots, Fig. 51); narrower postdiscal blue band on hindwings and this band is the broadest in *J. ovid* of all *J. hewitsonii* group taxa; less concave and finer dentate dorsal margin of cucullus, which is deeply concave and distally coarser dentate in *J. ovid* (character 5, Figs. 47a, g, h, i); cucullus being more rectangular in shape rather than more rounded distally in *J. ovid* (character 6, Figs. 47a, g, h, i); saccus looking more bulbous apically, but appearing narrower in *J. ovid* (character 10, Figs. 47a, g, insets "s").

The next closest species is *J. pater*, which is probably sympatric with *J. suekentonmiller* in Panama (Fig. 51). These two species share the width of the discal forewing white band (not as narrow as in *J. ovid*, character 2, Figs. 1–14 vs. 15–20); cucullus ends being at about the same height (character 4); and slightly bulbous saccus (character 10, Figs. 46a, b, insets "s"). However, seven remaining characters differ between them. Notably, *J. pater* has longer discal blue ray on dorsal hindwing (between veins Rs and Cu_1) and narrower postdiscal blue band; more concave and coarsely dentate dorsal margin of cucullus; more rounded distal end of cucullus, almost turning anteriad at the distal end; shorter process on tegumen; longer phallobase; and smooth dorsal margin of sacculus (Figs. 15–20, 48b–e). Recently described *J. ortizi* Orellana, [2010] is very similar to *J. pater* (Fig. 51), but is characterized by darker palpi and foretarsi (Fig. 22), which are white in *J. suekentonmiller*;

FIG. 51. Visual keys to species in the *Jemadia hewitsonii* group. **a.** *J. suekentonmiller* (paratypes, genitalia are of a different specimen); **b.** *J. ovid;* **c.** *J. pater;* **d.** *J. ortizi;* **e.** *J.* cf. *albescens;* **f.** *J. hewitsonii* (wings and head are of a syntype); **g.** *J.* cf. *hewitsonii.* Only dorsal side of wings is shown (males), inset shows ventral side of head and chest (not of the same specimen for **c**). Lateral view of male genitalia is illustrated below the wings (not the same specimens for **a** and **f**). Wings are to scale, genitalia are scaled approximately to match each other in size. Aedeagus for **d** and right valva for **f** are shown detached. Two characters deemed to be most reliable in separating *J. suekentonmiller* are in red font. Wing patterns and genitalia are variable, therefore not all characters shown may hold in all specimens.

even more concave than in *J. pater* distal margin of cucullus, whose distal end is higher than the proximal end (Fig. 48f); and saccus that is even more bulbous at its apex (Fig. 48f inset "s"). Therefore *J. ortizi* appears to be even more distinct from the new species than is *J. pater*.

Other taxa in the *J. hewitsonii* group and unnamed phenotypes, differ by a larger number of characters, both in facies and genitalia, and are illustrated in Figs. 29–44, 45c–d, 47j–m, 48i–n, 50 (part), 51 (part) for comparison. Their taxonomy remains uncertain to us, but interesting differences in genitalia are observed, including, among others, the shape of cucullus and proportions of penis (compare Figs. 47j, k, l, and m), and sacculus dorsal margin (pointed at with pink arrow in Fig. 47). Interestingly, the proportions of penis (with shorter phallobase) are similar to those of *J. suekentonmiller* in some of these taxa (e.g., Fig. 47l). Further work on this group is in progress (O. Mielke, E. Brockmann, and C. Mielke, pers. comm.).

Immatures and foodplants (Fig. 49): In ACG, and probably elsewhere, *J. suekentonmiller* is highly host-specific, with all 68 wild-caught caterpillars having been found feeding on mature foliage of ACG rain forest *Casearia arborea* (Salicaceae). While these caterpillars were 1–4 m above the ground, there may be some in higher foliage not inspected for caterpillars. All *C. arborea* inspected for these caterpillars were growing on road-forest or abandoned pasture-forest edges, a microhabitat that is a facsimile of the margins of natural disturbance sites. While ACG is rich in species of *Casearia*, thousands of caterpillar capture records indicate that *J. suekentonmiller* eats only this one, and does this almost entirely in one band of intermediate elevation rain forest about 25 km long and 1–2 km wide, from the area of Estacion Biologica Pitilla in Sector Pitilla to Estacion Caribe in Sector Rincon Rain Forest (see Sector maps at http://www.acguanacaste.ac.cr/).

The first instar caterpillars are parasitized by an undescribed likely host-specific species of *Ogmoelachertus* Schauff, 2000 (Hymenoptera: Eulophidae), and the 2nd–4th instar caterpillars are parasitized by an undescribed likely host-specific species of *Casinaria* Holmgren, 1859 (Hymenoptera: Ichneumonidae). The last instar caterpillars are parasitized by an undescribed species of ACG rain forest *Houghia* Coquillett, 1897 (Diptera: Tachinidae) that specializes in attacking Pyrrhopygini.

The striking black and yellow ringed-to-dotted caterpillar color pattern (Fig. 49) places this hairy caterpillar among a large complex of similarly-colored mimics being described and analyzed elsewhere, in the same spirit as those with false eye spots (Janzen et al. 2010). The semi-hairy pupa ornamented with dark colors and fragmented white waxy overlay, standard for ACG Pyrrhopygini pupae, rather than the false eye spots commonly encountered decorating other ACG Hesperiidae pupae (e.g., Janzen et al. 2010), is probably mimicking a rotting and fungus-rich pupa, the consumption of which would be decidedly hazardous to the health of a foraging bird.

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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

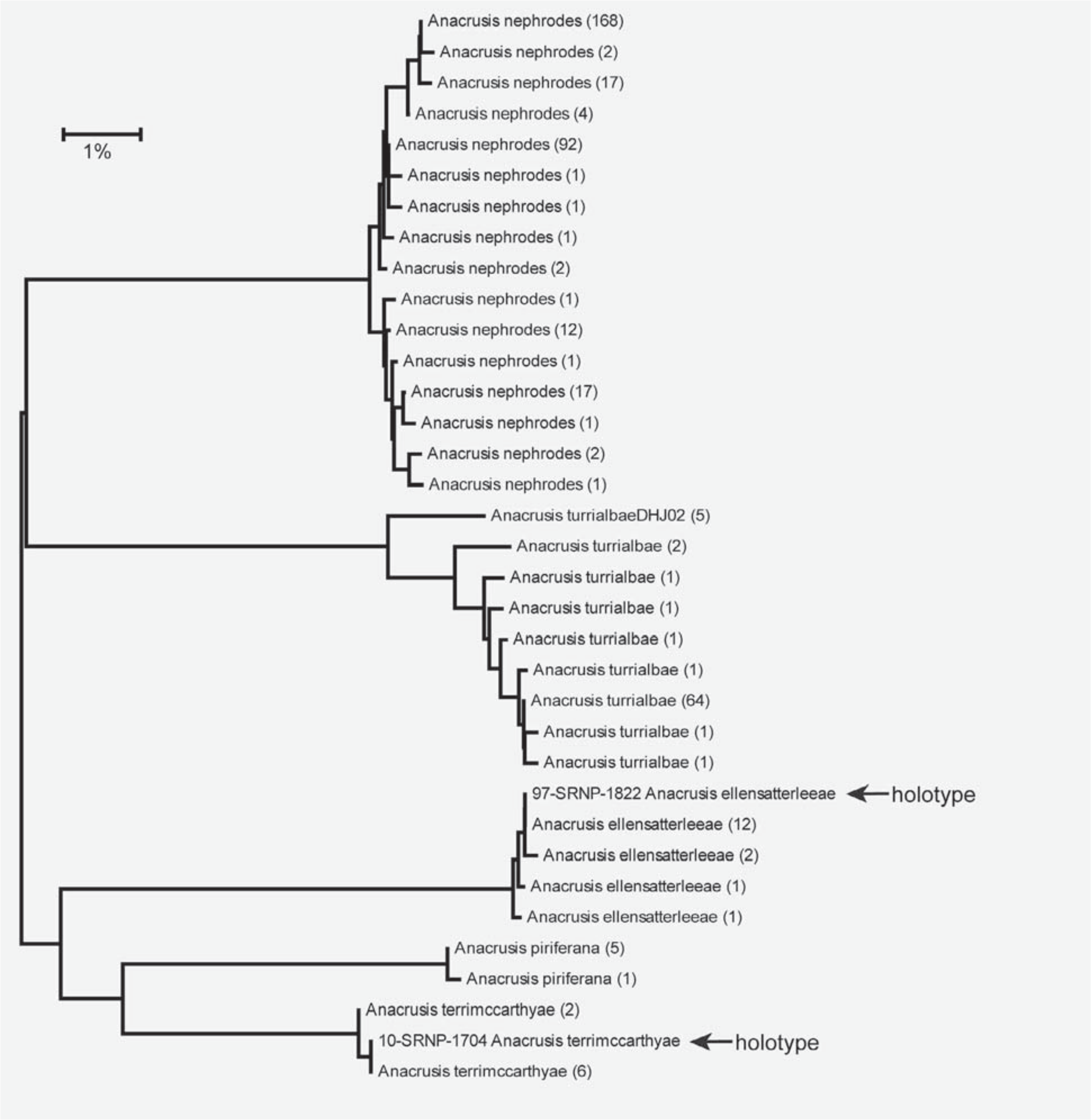


FIG. 1. Neighbor-joining tree based only on ACG *Anacrusis* COI sequences for complete (658 bp) DNA barcodes [not all specimens included].

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.

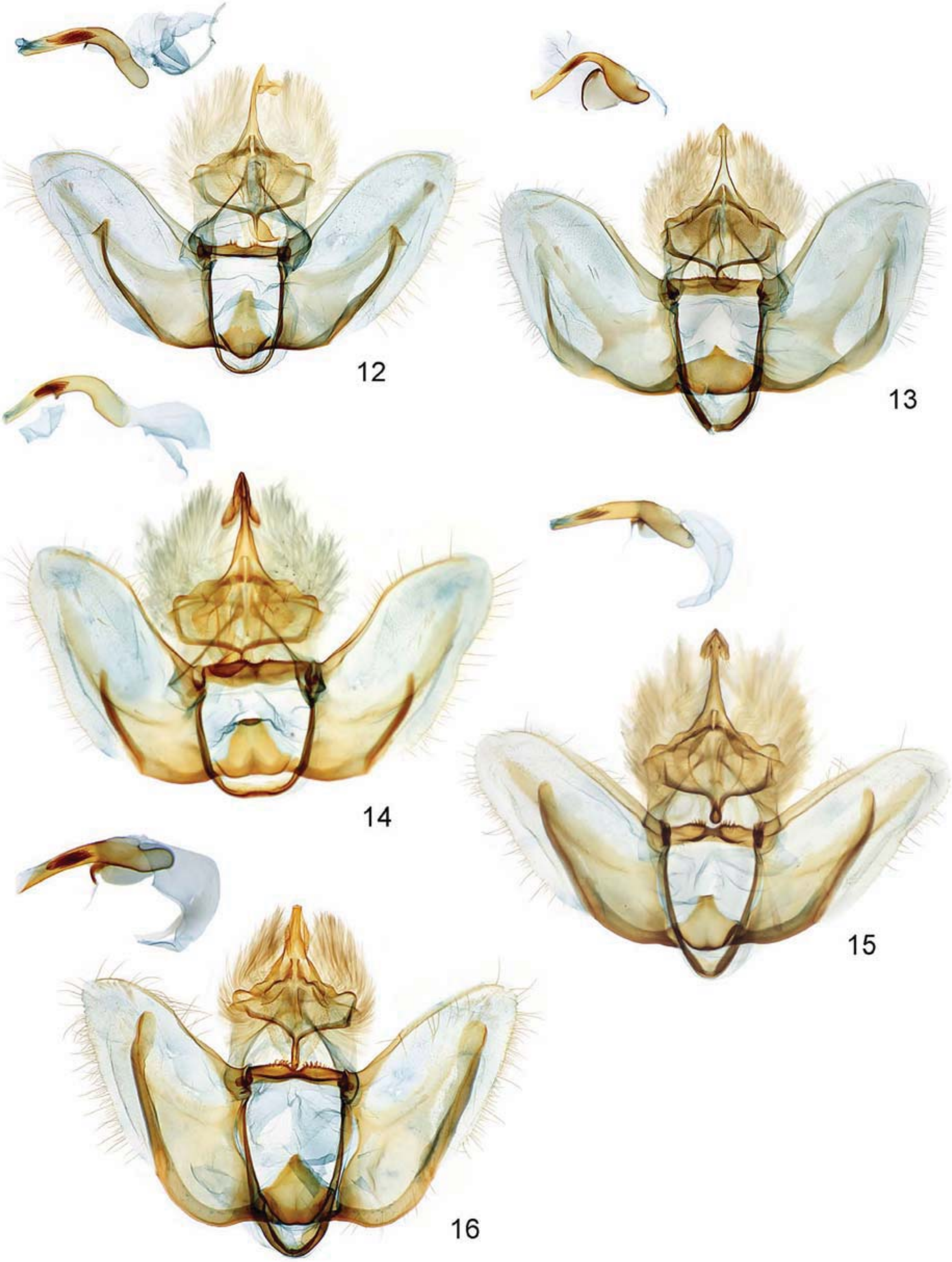
A small, divergent barcode cluster of specimens (about 7% divergent from the nearest other cluster) (Fig. 1) revealed distinct genitalia in both sexes. The male genitalia are identical to those of *Anacrusis piriferana* as illustrated by Clarke (1958) and Razowski & Becker (2011). We also examined a 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.

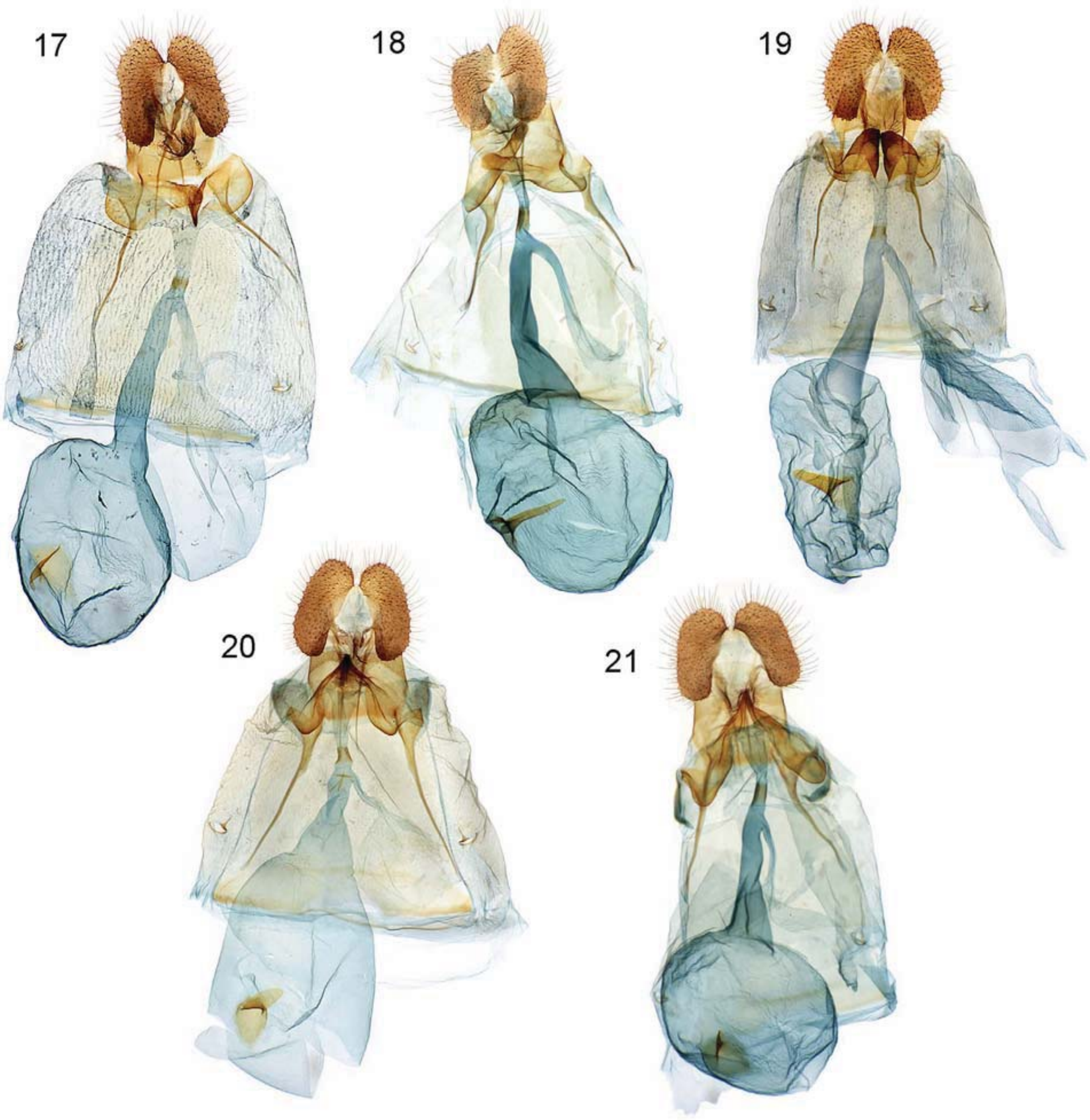
Female. The female of *Anacrusis piriferana* (Fig. 9) is superficially indistinguishable from that of *Anacrusis terrimccarthyae*, with a small circular brown patch in the subapical region narrowly outlined with white, a small white blotch at its outer edge, and the presence of one or two small dark 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.

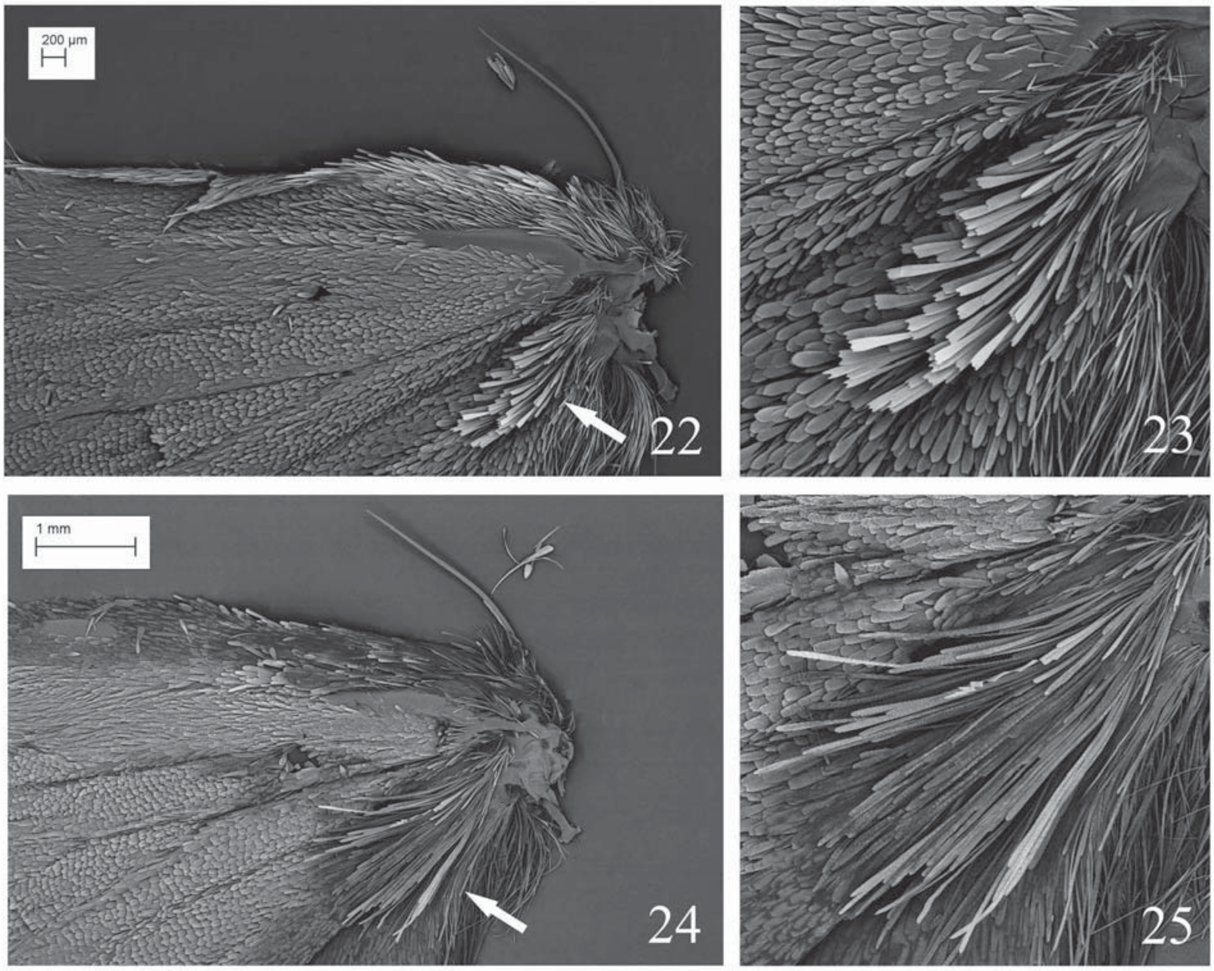
Female. The female of *Anacrusis nephrodes* (Fig. 10) is nearly indistinguishable from that of *Anacrusis ellensatterleeae*, with a small silver-white rounded dash at the outer edge of the forewing costal blotch. The large costal blotch has the margins more sharply defined, and rarely is there any white 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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POPULATION BIOLOGY AND BEHAVIOR OF THE IMPERILED *PHILOTIELLA LEONA* (LYCAENIDAE) IN SOUTH CENTRAL OREGON

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ABSTRACT. The sole known metapopulation of *Philotiella leona* on the Mazama Tree Farm (MTF) and adjacent areas of the Winema National Forest (WNF) in the Antelope Desert of Klamath County, Oregon was surveyed and studied during 2011–2013. The flight period extended from mid-June to mid-late July or early August (35–47 days) with higher temperatures in 2013 associated with the shortest period. Populations of *P. leona* based on Pollard walk counts were 4–5 X greater at 4 MTF sites than a WNF site. Populations appeared to be twice as large in 2011 than 2012 or 2013. Greatest numbers were seen in late June-early July with a gradual decline thereafter. Flight activity was meandering and low to the ground and mostly occurred after midday, as did mating and oviposition. Nectaring was observed on 9 plant species with *Eriogonum umbellatum* most favored. A mark, release and recapture (MRR) study was conducted at one location (~ 0.4 ha) in the MTF with 214, 95 and 105 adults marked in 2011, 2012 and 2013, respectively. Recapture rates of 5.1, 5.3 and 9.5%, respectively, indicated longevity of up to 14 days and yielded population estimates of 61-4515 individuals. Greatest populations of *E. spergulinum* and *P. leona* appear to be centered on cleared slash/burn sites (like the MRR site) which are linked by trails and tracks. Conservation of *P. leona* may depend on the periodic creation of trail-linked slash/burn sites which appear to function as sites for sub-populations of a metapopulation.

Additional key words: metapopulation, flight period, nectaring, population size, mark, release, recapture

Leona's little blue butterfly, *Philotiella leona* Hammond and McCorkle, is arguably the most restricted and endangered butterfly species in the United States. Discovered in 1995, *P. leona* appears to be restricted to less than 32 km² in the Antelope Desert of south central Oregon approximately 16 km east of Crater Lake (Fig. 1) (Hammond and McCorkle 1999, Pyle 2002, Warren 2005, Miller and Hammond 2007, Ross 2008, 2009, Matheson et al. 2010, James 2012). It appears to be a highly specialized species occupying a volcanic ash and pumice ecosystem, dependent upon a similarly specialized larval host plant, Spurry buckwheat, *Eriogonum spergulinum* A. Gray. (Fig. 2). *Eriogonum spergulinum* and *P. leona* occur primarily in openings of Lodgepole pine (*Pinus contorta* Douglas) forest. *Philotiella leona* is currently being considered for listing under the Endangered Species Act (Matheson et al. 2010). Apart from brief and fragmentary notes presented by Hammond and McCorkle (1999), Ross (2008, 2009) and Matheson et al. (2010), little is known of the ecology of *P. leona*. James (2012) provided detailed observations on the life history of *P. leona*. This paper provides information on the population biology and behavior of *P. leona* obtained during three flight seasons.

FIG. 1. Map of Oregon showing location of the known habitat of *Philotiella leona*, approximately 16 km east of Crater Lake.

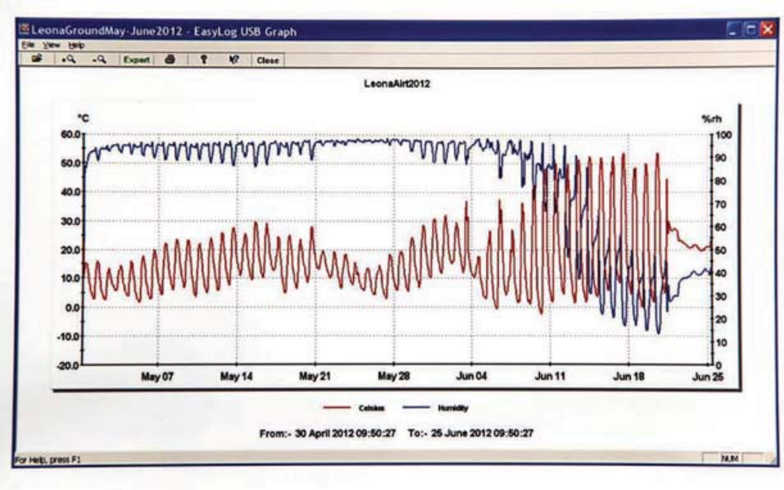
MATERIALS AND METHODS

Population census and observations on behavior. Field work was conducted during May-August 2011–13 in the known habitat of *P. leona*, private land owned by the Mazama Tree Farm (MTF) and adjacent areas of the Winema National Forest (WNF) in the Antelope Desert of Klamath County, Oregon. On the first visit (May 27–28 2011, pre-flight period) 5 locations were surveyed and established as separate sites for studies on *P. leona* populations. Sites were chosen on the basis of being open and having abundant Spurry buckwheat (*Eriogonum spergulinum*) seedlings. Sites were separated by 0.5–2.5 km with 4 on MTF (sites A, B, C, E) and 1 (D) on WNF land. At each site, two ~ 0.8 km transect or walk lines were identified that followed tracks or trails (Fig. 3). During the flight period each transect was walked by one or two observers at a pace of ~ 1.6 km/hr. On all occasions walks were conducted in sunshine between 1000–1700 h in temperatures of 21–30 ºC. During each walk observations on behavior

FIGS. 2–5. **2.** Spurry Buckwheat (*Eriogonum spergulinum*), host plant of *Philotiella leona* **3.** A track used for 'Pollard walk' population census of *P. leona* with the Crater Lake volcano in the background. **4.** Cleared slash/burn site used for mark, release and recapture study with abundant *E. spergulinum* (pink-red ground cover). **5.** Marked *P. leona* nectaring on *P. hispidus* immediately following release.

(flight, nectaring, roosting, courtship, mating, oviposition) of *P. leona* and the number of adults seen along the trail/track and ~ 5 m on each side, were recorded. This monitoring technique is based on the 'Pollard transect walk' for butterflies described by Pollard (1977). Occasionally, adults were netted (and released) to confirm sex and wing condition but in most instances status was assigned from observation only. Duration of walks varied from 25–35 minutes. Additional observations on behavior made between walks were also recorded.

Mark, release and recapture study. A mark, release and recapture (MRR) study was conducted each year in a 3888 m^2 (~ 0.4 ha) area near Site E. This area was a disturbed and cleared slash/burn site following tree harvest that occurred at least 5 years previously. *Eriogonum spergulinum* was abundant at the site (Fig. 4). In 2011, 7 visits at intervals of 2–14 days were made for MRR and 4 visits (6–9 day intervals) were made in 2012. The relative scarcity of recaptures in 2011 and 2012 prompted use of a shorter interval (24h) between MRR dates in 2013. At each visit one person spent 1–1.5 hours (1200–1400 h) collecting all the *P. leona* adults seen in the MRR area. Butterflies were placed in gauze covered plastic cylinder containers (12 cm × 13 cm) in a cooler and after the collection period were examined, marked and released at the center of the MRR area. Butterflies were allowed to disperse naturally from the opened containers. The sex and wing condition (worn, medium-worn and fresh) of each individual was recorded. Butterflies with no sign of wear or fading were classed as fresh. Faded and/or torn wings characterized worn individuals and individuals without substantial wear but lacking brightness of fresh butterflies were classed as medium-worn. Butterflies were marked by hand using fine point "Sharpies"® in 8 colors (red, blue, green, brown, black, yellow, pink, orange). Marks consisted of a series of 1–3 different colored dots placed on the ventral surface of the left hind wing, giving each individual a unique identity (Fig.



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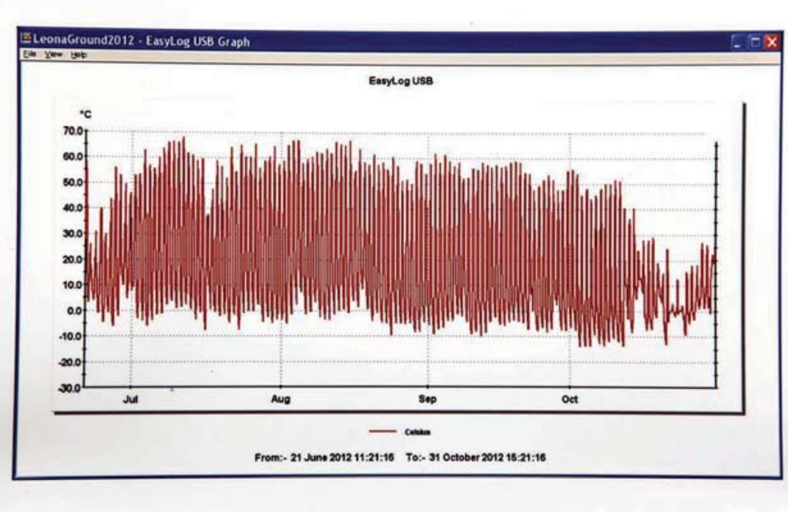

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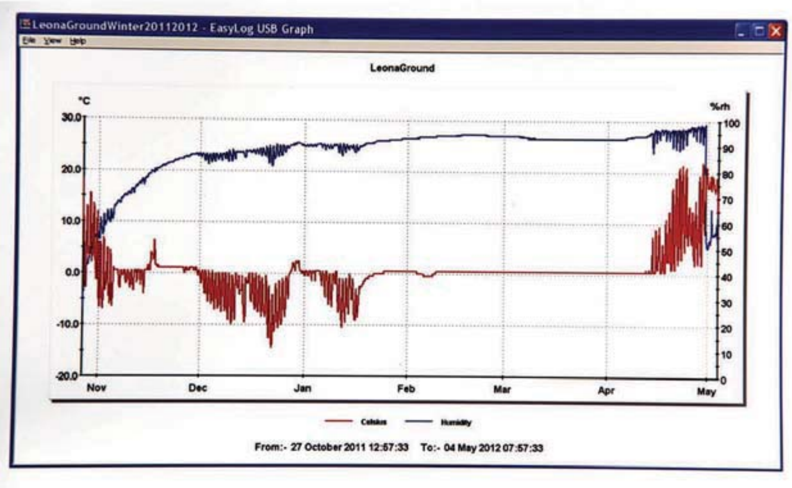

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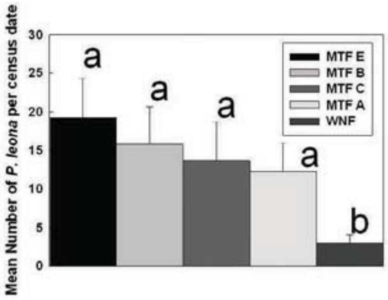
FIGS. 6–8. **6.** Daily soil (0.5 cm below ground) temperatures and relative humidities likely experienced by *P. leona* pupae prior to commencement of the flight period at MTF (June 15) in 2012. **7.** Daily temperatures recorded by a logger exposed to direct sunlight (13 cm above ground) at the MTF from June 21 to October 31 2012 **8.** Daily soil (0.5 cm below ground) temperatures and relative humidities likely experienced by overwintering pupae of *P. leona* at MTF from October 27 2011 to May 4 2012.



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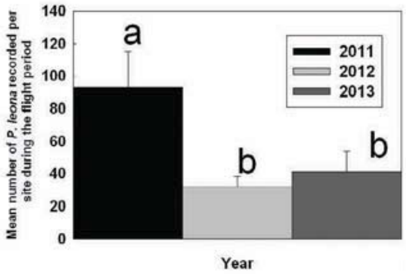

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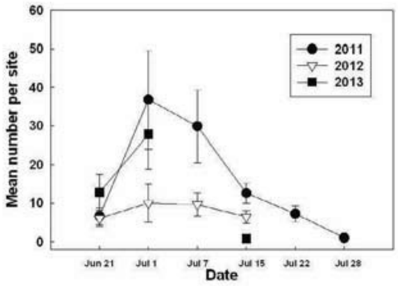

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FIGS. 9–11. **9.** Mean number of *P. leona* adults sighted per census date at the Mazama Tree Farm (MTF) and Winema National Forest (WNF) Pollard walk sites during June-July 2011-13. A different letter above a column indicates a significant difference (P < 0.011). **10.** Mean number of *P. leona* adults recorded per Pollard walk site during flight periods 2011–13. A different letter above a column indicates a significant difference (P < 0.031). **11.** Seasonal abundance of *P. leona* during 2011–13 as indicated by mean number recorded per Pollard walk site on each date. Data not obtained for July 7 in 2013 and July 22 and 28 in 2012 and 2013. Vertical bars represent standard errors.

5). Marked butterflies appeared unaffected behaviorally by the marks or process of marking and showed normal flight, courtship and nectaring behavior after release. MRR data in 2011 and 2012 were analyzed using Jolly's stochastic method which provides estimates of population size when three or more successive samples are taken (Jolly 1965). A simple Lincoln Index (Lincoln 1930) was used to analyze the two sets of two samples taken in 2013.

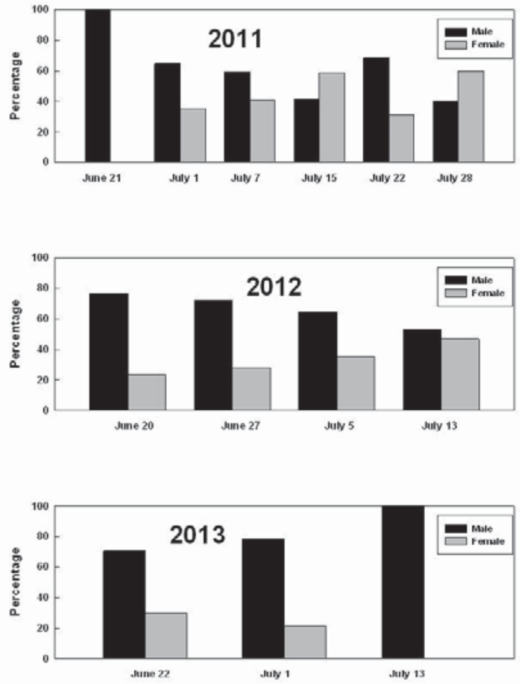

FIG. 12. Sex ratio of *P. leona* recorded on Pollard walks during each season.

Climate data. A climate data logger (Lascar electronics, Erie, PA USA, model EL-USB-2) was placed 1.5 m above the ground within the shade of a MTF Lodgepole pine tree, recording hourly ambient temperature and relative humidity from May to September in 2011 and 2012. In 2013, logistics prevented on-site climate data collection, and ambient temperature data for May-September were obtained from Chemult (Station MCHUO3 Weather Underground.com), ~ 15 km NE of the MTF. Temperature in direct sunlight (13 cm above the ground) was recorded hourly by a data logger at the MRR site from June 21–October 31 2012. Temperature and relative humidity 0.5 cm below ground level (data logger buried in soil) was recorded during August-September 2011 and October 27 2011 to June 20 2012. Temperatures in direct sunlight and on the ground provide an insight to the conditions experienced by basking adults, developing eggs/larvae and diapausing pupae at or just below the soil surface.

Data analysis. Population census data were analyzed using one way ANOVA on ranks and Holm-Sidak multiple comparison procedures.

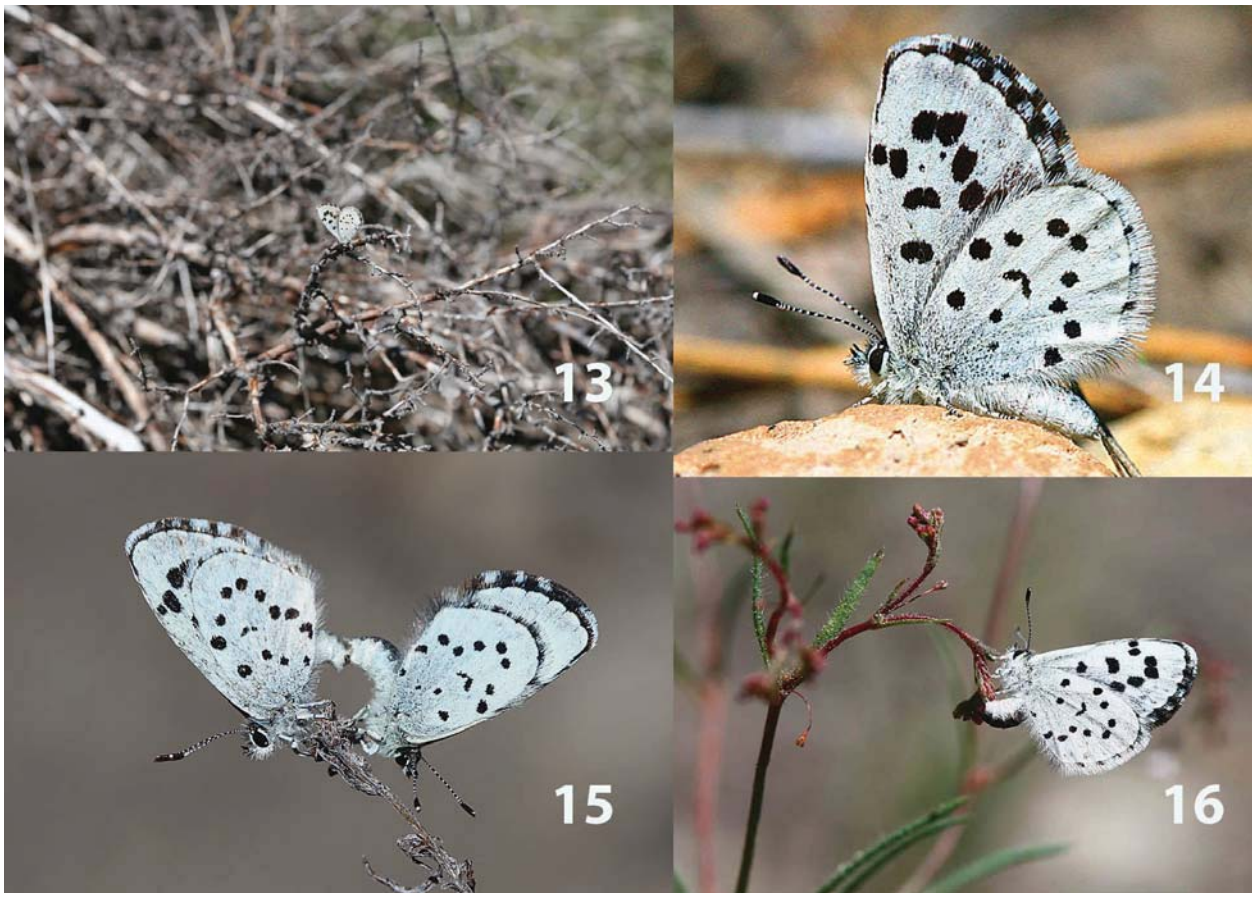

FIG. 13–16. 13. Typical overnight and morning roost of *P. leona* on bare twigs of low-growing plants. 14. *Philotiella leona* roosting on a warm stone on the ground. 15. *Philotiella leona* mating on bare twig close to the ground 16. *Philotiella leona* ovipositing on flower buds of *E. spergulinum*.

RESULTS

Flight period. *Philotiella leona* is univoltine with a flight period extending from mid-June to late July or early August (Table 1). The flight period in 2013 was shorter (35 d) than in 2011 (47 d) or 2012 (45 d). Mean daily maximum temperature for the first 30 days of the flight period in 2013 was 2–2.8 °C greater than in 2011 or 2012 with more days having maxima > 30 °C (Table 1). *Philotiella leona* eclose from ground level pupae (James 2012) and soil temperatures in 2012 showed a rapid warming from around 10 °C in early May to >30°C in early June (Fig. 6). Eclosion occurred soon after soil temperature daily maxima reached 50 °C and relative humidity fell below 90% (Fig. 6). By the end of the flight period in late July, most of the *E. spergulinum* host plants had senesced and it is likely that most larval development had been completed (James 2012) and the majority of the population was in the pupal stage. Pupae oversummer and overwinter on or perhaps just below the soil surface and are exposed to extreme temperatures ranging from 68 °C down to -5 °C (Figs. 7–8). Snow cover during January-April 2012 maintained temperatures at 0 °C (Fig. 8).

Population census. *Philotiella leona* populations based on Pollard walk counts were significantly larger at MTF sites than at the WNF site ($P < 0.011$) (Fig. 9). There was no significant difference between numbers at the MTF sites ($P > 0.05$). The overall population was significantly greater in 2011 than in 2012 or 2013 ($P < 0.031$) with no significant difference between the latter years ($P > 0.05$) (Fig. 10). In all years, greatest numbers were seen on the second survey date (June 21–July 1) with a gradual decline thereafter (Fig. 11).

Sex ratio. Combining all years and census dates we recorded 556 (66.7%) males and 277 (33.3%) females. Males were particularly dominant early in the flight period, suggesting some degree of protandry and females only outnumbered males twice during the 3 years (July 15 and 29 2011) (Fig. 12).

Nectaring. *Philotiella leona* was observed nectaring

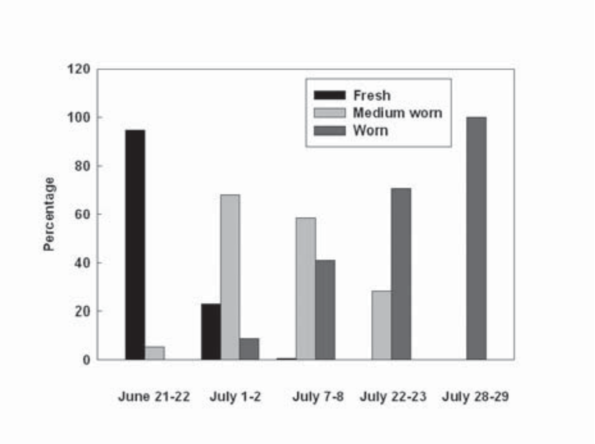

FIG. 17. Wing condition of *P. leona* during mark, release and recapture sampling at site E during 2011–2013.

on 9 flowering plants including the larval host plant *E. spergulinum* (Table 2). From 276 records, most nectaring occurred on Sulfur buckwheat (*Eriogonum umbellatum* Torr.) (32.6%) and Opposite-leaved tarweed (*Hemizonella minima* A. Gray) (23.9%). On June 26 2011 a male was observed visiting 67 *H. minima* flowers (10-20 seconds/flower) during 12 minutes.

Roosting. *Philotiella leona* spent much time roosting particularly before 1100 h despite sunshine and ambient temperatures of 10–20 °C. Most roosting occurred on the ground or on bare twigs of low-growing shrubs like *E. umbellatum* and *Purshia tridentata* (Pursh) (Bitterbrush) (Fig.13). Roosting *P. leona* were never found on green vegetation. Ground roosters usually chose warm stones or small rocks in direct sunlight (Fig. 14). In July 2012 the mean daily maximum temperature recorded in direct sunlight 13 cm above the ground was 58.5 ± 1.2 °C (range 37-68 °C) (Fig. 7). On June 23 2011 two males were observed roosting on the ground for 2 h (1030–1230 h, ambient temp. 15–20 °C).

Flight/courtship/mating. The flight of *P. leona* is typically low to the ground and meandering. Flight higher than 1m above the ground was rarely seen. Most flight activity occurred from midday to 1600 h. Early in the flight period males were frequently seen flying around *E. spergulinum* patches, presumably searching for females. Male-male interactions were frequent with individuals swirling around each other for ~ 10 seconds before breaking off. Five male-female courtship events were observed on June 22 and July 7, two resulted in mating. Two of the courtship events involved the pair in an upward spiral reaching heights of up to 7 m before descending to ground level but no mating occurred. The two successful matings followed high speed chases just above ground level for 10–15 seconds before the female alighted on a bare twig low to the ground with copulation taking place within 10 seconds. If disturbed, the female carried the male in flight. A total of 6 mating pairs were observed during the study, all on bare twigs and in the afternoon (1400–1600 h) (Fig. 15). Twenty one ovipositing females were observed, all in late June and early July. Most egg laying (86%) occurred during the afternoon (1200–1600 h). All eggs were laid on unopened flower buds of *E. spergulinum* (Fig. 16).

Mark, release and recapture study. A total of 414 *P. leona* (65.5 % female, 34.5% male) were marked during this study and 25 (6%) were recaptured overall. However, recaptures were greater in 2013 (9.5%) when a shorter interval (1 day) between sampling dates was used compared to 2–9 days in 2011 and 2012 (5.1–5.3%). The greatest period between marking and recapture was 14 days for a male marked on July 8 2011. Seven butterflies were recaptured 7–8 days after marking in 2011 and 2012. Population estimates for *P. leona* adults in the MRR area ranged from 61–4515 individuals (Tables 3–4). The population peaked in early July in all years. Individuals caught during June 21–23 were newly eclosed and mostly in fresh condition in all years. In the first week of July the majority of butterflies were in medium-worn condition but by July 22 the majority were worn (Fig. 17).

DISCUSSION

The data presented here constitute the first detailed study on important aspects of the population biology and behavior of *P. leona*. Previous information on the incidence and abundance of *P. leona* has been fragmentary and largely anecdotal with no direct data on population size and/or trends from year to year (Ross, 2008, 2009, Johnson, 2010, Matheson et al. 2010). The data presented here, obtained over three seasons, will serve as a reference point for future studies on population size and trends. The five monitoring sites used in this study span the center of the known distribution of *P. leona* at the MTF. The sole WNF site used is adjacent to MTF land.

The flight period of *P. leona* commenced during the second or third week of June with dates when first adults were seen ranging from June 10 to June 17. Adults eclose from pupae on the ground which experience rapid warming and drying during the month or so before eclosion. Ambient temperatures during the flight period in 2013 were greater than in the previous two years which appeared to result in a shorter flight period with the population disappearing by mid July instead of late July or early August. Senescence of the host plant of *P. leona*, *E. spergulinum* was also more rapid in 2013. Temperatures experienced by *P. leona* (both adults and immature stages) and host plants in direct sunlight in late June and July are very high (50–70ºC) and likely result in rapid development of eggs and larvae. James (2012) showed larval development takes only 10–12 days at 25–27 ºC. Oviposition and larval development can only occur on buds and flowers of *E. spergulinum* (James 2012) and the period when these plant parts are available appears to be limited to the flight period of *P. leona*. Thus, it appears likely that development of larvae is completed by the end of the adult flight period. Pupae are likely formed on or close to the ground (James, 2012) and are exposed to extremely hot (68 º C) and cold (-5 º C) temperatures although snow cover in winter minimizes exposure to extreme cold. Soil moisture content is high during November–June.

Populations of *P. leona* throughout this study appeared to be 4–5 times larger on the commercial tree farm land than at the adjacent national forest site. The reasons for this are unclear although the national forest land is generally less open than the tree farm land which has experienced extensive tree-harvesting over past decades. *Eriogonum spergulinum*, the host plant of *P. leona*, requires open habitat and is an early successional species establishing rapidly in recently cleared land, appearing to thrive in areas with burnt log piles. The abundance of *E. spergulinum* and *P. leona* appears to be greatest at slash/burn sites. A Google Earth™ image of part of the *P. leona* MTF habitat clearly shows the number and extent of clearings containing slash/burn piles within the tree farm (Fig. 18). These clearings harbor population concentrations of *P. leona* which are likely population centers making up the metapopulation occupying the 32 km² range of *P. leona*.

The abundance of *P. leona* in 2011, as indicated by numbers of adults seen during Pollard walk counts and the population estimates derived from the MRR study, was more than double that seen in 2012 and 2013. Although the 2011 flight period was cooler than in 2012 and 2013, it is unclear whether it was this that caused greater abundance. Population monitoring over a greater number of seasons is needed to determine the range of abundance levels and whether any trends are apparent. The phenology of abundance was similar in the three years with greatest numbers seen early in the flight period in late June and early July, declining during July. A male-dominated sex ratio was apparent from both Pollard walk and MRR data. This may have been caused by females avoiding male harassment by spending more time roosting, thus less easily detected or caught. James (2012) concluded that the sex ratio of *P. leona* was 'relatively balanced' but this was based on 2011 data only in which male dominance was reduced compared to the following 2 years (Fig. 12). The wing condition of individuals determined in the MRR study showed the expected clear progression from fresh to worn during the flight period.

The flight behavior of *P. leona* was characteristically low to the ground, meandering and difficult to track. Much of the flight activity was centered on and around patches of *E. spergulinum* host plants, males seeking mates and females ovipositing. Nectaring was a predominant activity with the sulfur buckwheat, *Eriogonum umbellatum*, a very important nectar source. Roosting on bare twigs or on the ground was also a characteristic behavior, often for extended periods during morning hours.

The MRR study showed that it is feasible to mark *P. leona* despite their small size (1.3–1.9 cm wingspan). Marking did not appear to interfere with post-release behavior. It is unknown whether marking caused increased mortality due to increased visibility. No

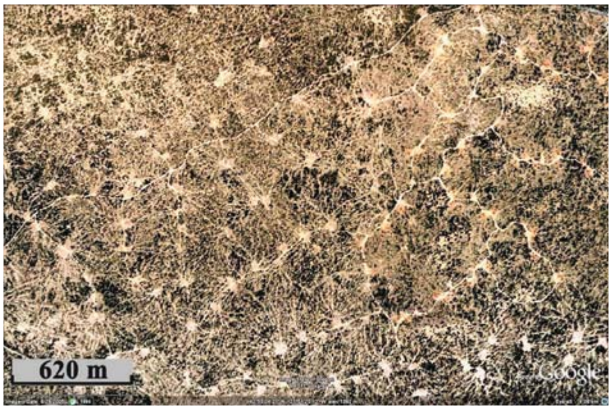

FIG. 18. A section of the Mazama Tree Farm showing multiple cleared slash and burn sites and associated trails (GoogleEarth™). The cleared sites host the densest populations of *E. spergulinum* and *P. leona*.

FIG. 19. *Eriogonum spergulinum* growing along a track in the Mazama Tree Farm

TABLE 1. Estimated flight periods for *P. leona* in 2011–13 and daily maximum temperature data.

Year	Estimated flight period	Mean daily maxima ºC for first 30 days of flight period	Number of days in first 30 days with maxima ºC > 30 ºC
2011	June 17-August 3	23.7	0
2012	June 15-July 30	24.5	4
2013	June 10-July 15	26.5	8

TABLE 2. Nectaring records for *P. leona* obtained on Pollard walks during 2011–13.

Plant Species	2011	2012	2013	Total (%)
Eriogonum umbellatum	34	24	32	90 (32.6)
Hemizonella minima	64	1	1	66 (23.9)
Cistanthe umbellatum	17	15	0	32 (11.6)
Plagiobothrys hispidus	12	19	0	31 (11.2)
Machaeranthera canescens	15	5	11	31 (11.2)
Eriogonum spergulinum	7	5	8	20 (7.2)
Packera cana	2	0	1	3 (1.1)
Gayophytum diffusum	2	0	0	2 (0.8)
Phacelia hastata	1	0	0	1 (0.4)
All Plants	154	69	53	276 (100)

TABLE 3. Mark, release and recapture data for *P. leona* in a 3888 m^2 area at site E during June-July 2011 and 2012. Population estimates derived by using Jolly's stochastic method.

2011 Date	**No. in 1 hr search**	**Caught**	**Marked**	**Recaptured (%)**	**Estimated population**
June 23	14	21	21	-	-
July 1	59	59	50	1	301
July 6	75	105	86	1	4515
July 8	52	39	27	6	215
July 22	21	21	19	1	242
July 24	13	11	9	2	61
July 29	2	2	2	0	-
Total (all dates)		258	214	11 (5.1)	
2012 Date					
June 21	19	34	30	-	
June 27	16	19	15	4	90
July 6	25	51	50	1	2600
July 13	13	11	0	0	-
Total (all dates)		105	95	5 (5.3)	

TABLE 4. Mark, release and recapture data for *P. leona* in a 3888 m^2 area at site E during June–July 2013. Population estimates derived by using the Lincoln index.

2013 Date	**No. in 1 hr**	**Caught**	**Marked**	**Recaptured (%)**	**Estimated population**
June 21	38	19	19	-	-
June 22	36	27	18	7	73
July 1	51	35	35	0	-
July 2	53	40	33	3	467
Total (all dates)		121	105	10 (9.5)	

instances of avian predation were observed during the 3 years of study suggesting perhaps that this source of mortality is generally low for this tiny butterfly. Recapture rates were low even with a short (24 h) interval between marking and re sampling (~ 10%). However, a 24 h interval did improve the recapture rate over that obtained with 2–8 day intervals (~5%). Low recapture rates may indicate death or emigration of individuals or their dilution within an increasing population. Fifty three per cent of recaptures in 2011 and 2012 were made 7–14 days after marking. This suggests longevity of adult *P. leona* can extend to 2 weeks but clearly more information is needed on the average length of life. If emigration is occurring then it may take place along the trails and tracks that connect cleared slash/burn population sites as shown in Fig. 18. No attempt was made in this study to sample butterflies along the trails and tracks emanating from the MRR site. These corridors are also heavily colonized by *E. spergulinum* (Fig. 19). Such sampling should be conducted in future MRR studies and may shed light on dispersal behavior of *P. leona* and therefore provide an insight on the maintenance of isolated populations within the metapopulation of *P. leona*. The population estimates derived in this study indicate *P. leona* populations in a small (~ 0.4 ha) but highly favorable habitat (open, abundance of host plants, nectar sources) may be large containing a few thousand individuals. The relatively low number of recaptures combined with uncertainty as to how well *P. leona* individuals redistribute within the MRR area after release, suggest caution in interpreting these population estimates. The population estimates of 4515 and 2600 on July 6 2011 and 2012, respectively, seem high but the estimates obtained on most other dates (61–467), appear reasonable and consistent. If we assume all cleared slash/burn sites on the MTF (~100) contain similar-sized populations of *P. leona*, then using a conservative estimate of 200 butterflies/site, the entire metapopulation of *P. leona* may consist of ~ 20,000 individuals. Although all of the slash/burn sites we visited during 2011–13 (~ 20) supported *P. leona* populations, a comprehensive survey needs to be conducted to determine actual occupancy of all the sites. Long term survival of the discrete populations that form a metapopulation requires at least some mixing of individuals between populations. Effective dispersal of butterflies from sites with declining populations is necessary to ensure local extinctions do not significantly affect the size and viability of the metapopulation. As favored open sites develop (from logging), dispersal of individuals from nearby centers should exploit the new habitats and establish new populations.

Although the greatest population densities were seen at the cleared slash/burn sites, *P. leona* is not confined to them. The Pollard walks conducted in this study along tracks and trails revealed significant populations in these areas as well. The numerous tracks and trails that cover the MTF may be extremely important conduits for *P. leona* moving between cleared site population centers. Continued maintenance of good-sized populations of *P. leona* at the MTF may be dependent on the continued existence of a large number of cleared sites and track/trail linkage between them. Continuance of a commercial logging operation on this land, at the levels conducted over the past few decades, may be crucial for conservation of *P. leona*. The current population levels of *P. leona* may actually be a consequence of commercial logging and creation of suitable habitat for *E. spergulinum*. There are some open areas within the MTF that appear never to have supported trees. *Philotiella leona* is present in these areas but at comparatively low population densities. It is possible that these areas represent the ancestral condition of limited suitable habitat and consequent low population densities of *E. spergulinum* and *P. leona*. Although the population density of *P. leona* on the adjacent National Forest land appears to be substantially lower than on the MTF, this perhaps could be rectified using tree management and harvesting protocols similar to those used on the MTF. Opening up more cleared areas with slash/burn piles on all areas of the National Forest land where it meets MTF land, may allow dispersal and shifting of high density MTF populations into National Forest land.

This study provides a good platform for future population research on *P. leona*. Such studies incorporating Pollard walks and MRR should be conducted annually to provide a better understanding of the evolving status of *P. leona* at the MTF. Data on population dynamics and underlying factors can ultimately be used to develop land and forest management strategies that are compatible with the long term survival of this imperiled species.

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AN UPDATED CHECK LIST OF THE COCHYLINA (TORTRICIDAE, TORTRICINAE, EULIINI) OF NORTH AMERICA NORTH OF MEXICO INCLUDING GREENLAND, WITH COMMENTS ON CLASSIFICATION AND IDENTIFICATION

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ABSTRACT. We present an updated list of the members of the subtribe Cochylina (Tortricidae) in North America north of Mexico. We summarize the proposed changes in the classification since the end of 1978. We propose revised status for two genera, *Rolandylis* Gibeaux, 1985 and *Thyraylia* Walsingham, 1897. We propose eleven revised combinations: *Saphenista parvimaculana* (Walsingham, 1879), unplaced Cochylina *omphacitis* (Meyrick, 1912) [*Cochylis*], unplaced Cochylina *voxcana* (Kearfott, 1907) [*Phalonia*], *Thyraylia bana* (Kearfott, 1907), *Thyraylia rhodites* (Meyrick, 1912), *Thyraylia bunteana* (Robinson, 1869), *Thyraylia discana* (Kearfott, 1907), *Thyraylia cricota* (Meyrick, 1912), *Thyraylia gunniana* (Busck, 1907), *Thyraylia hollandana* (Kearfott, 1907), and *Thyraylia nana* (Haworth, [1811]). We propose four revised combinations: *Rolandylis fusca* Pogue, 2001, *Rolandylis maiana* (Kearfott, 1907), *Rolandylis catalonica* Gibeaux, 1985, *Rolandylis virilia* Pogue, 2001; and three new synonymies: *Aethes ziscana* Kearfott with *A. bomonana* (Kearfott), *Henricus edwarsiana* (Walsingham) with *H. contrastana* (Kearfott), and *Phtheochroa pecosana* (Kearfott, 1907) with *Phtheochroa cartwrightana* (Kearfott, 1907). The described fauna includes 20 genera and 137 species, yet it is likely that this region of North America includes two to three times that many species; at least six new genera are defined, but not yet formally described.

Additional key words: Cochylidae, Cochylini, *Rolandylis*, *Saphenista*, *Thyraylia*, *Phtheochroa*, new synonymy, new combination

The most comprehensive, contemporary list of the North American members of the family "Cochylidae" was provided by Powell (1983) in his contribution to the Check list of the Lepidoptera of America North of Mexico (Hodges et al. 1983). In 1986, a PhD thesis completed by Michael Pogue at the University of Minnesota provided a thorough review of the classification of the North American fauna at the generic level, including manuscript descriptions of several new genera and many new combinations. The phylogenetic analysis portion of the thesis was published by Pogue and Mickevich (1990), but the descriptive and taxonomic portions were not. As a consequence, the nomenclatural changes and descriptions were not "formally" proposed, and the new names and actions remained unavailable. Brown (2005) compiled the first list of Cochylini worldwide, and his treatment of the North American fauna basically followed that developed by Pogue (1986). The new genera recognized by Pogue (1986) were identified as "Cochylini new genus 1," "Cochylini new genus 2," and so forth in order to provide a more meaningful taxonomic framework for the fauna, i.e., this action seemed a better alternative to leaving the associated species "unplaced."

Taxonomic changes proposed by Razowski (2009, 2011), Metzler & Albu (2013), and others over the last decade resulted in the generic reassignments of many species. Many of the changes proposed by Pogue (1986) were formalized through various publications (e.g., Pogue 2001, Brown 2005), and new species were added to the faunal list through introduction (e.g., *Agapeta zoegana*) (Powell et al. 2000) or description of the native fauna (e.g., Metzler & Forbes 2012, Brown 2013, Metzler & Albu 2013). In a phylogenetic analysis of Tortricidae based entirely on molecular data, Regier et al. (2012) revealed that Cochylini are a monophyletic lineage embedded within the larger Euliini and should be treated as the subtribe Cochylina until further evidence contradicts this proposed change in classification. Because so much information has accumulated since Powell (1983), we deem it advisable to recap the current list of species from North America and their generic assignments.

MATERIALS AND METHODS

Consistent with the Moths of North America (MONA) project, we treat the fauna of Canada, the United States, and Greenland. This geographical region is ca. 99% congruent with the Nearctic ecozone. Notable differences are the southern tip of peninsular Florida, which is Neotropical, and most of central Mexico south to approximately 18° north latitude, which is considered Nearctic.

We examined the original descriptions and genital preparations of all species of Cochylina that might be found within the study region. Whenever possible, we examined genitalia of types with the proviso that not all types are extant. If types are not available, we examined the genitalia of specimens overwhelmingly considered to be conspecific. In some cases, a judgment of generic assignment seemed to be a matter of convenience rather than based on scientific facts, thus a few species are considered unplaced pending more evidence. We know from experience that many species cannot be placed to genus without examination of the genitalia, thus our conservative approach is justified. While we recognize it is inconvenient to have species names without generic assignments, it would introduce imprecision to pretend we have information not available. Combinations without merit will not help settle the confusion in Cochylina classification.

We examined the literature for species descriptions and revised generic assignments published subsequent to Brown (2005). We followed the most recently published combinations, although as more species are examined and described, the combinations are subject to change.

Most of the new genera recognized (but not formally described) by Pogue (1986) and subsequently used by Brown (2005) are retained for stability in the classification. We emphasize that the manuscript names in Pogue (1986) are not published, we do not publish them here, and they are not available. We use original orthography in the spelling of species names.

For ease of use, and because the phylogeny of Cochylina is uncertain, the genera and synonyms are listed in alphabetical order, and the species and synonyms are listed in alphabetical order within each genus. We created an index to genus and species names. Detailed literature references to the original description, type locality, and disposition of type specimen(s) can be found in Brown (2005) and Gilligan et al. (2012). Not all misspellings from the literature are included here. Brown (2005) should be consulted for variations of species names found in much of the literature. We did not attempt to find all spellings previously used. Footnotes provide details for the placement of certain taxa subsequent to Pogue (1986) and indicate areas of ambiguity or disagreement that require further investigation.

RESULTS

List of genera and associated species from North America north of Mexico and Greenland

Cochylina Guenée, 1845 (sensu Regier et al. 2012)

Aethes Billberg, 1920
- *Argyridia* Stephens, 1852
- *Chlidonia* Hübner, [1825]
- *Chrosis* Guenée, 1845
- *Cirriaethes* Razowski, 1962, subgenus
- *Coecaethes* Obraztsov, 1943, subgenus
- *Dapsilia* Hübner, [1825]
- *Loxopera* Walsingham, 1900 (emendation of *Lozopera*)
- *Lozopera* Stephens, 1829
- *Phalonia* Hübner, [1825]
- *Phelonia*; Stephens, 1834 (misspelling of *Phalonia*)
  - **angulata** (Robinson, 1869)
  - **angustana** (Clemens, 1860)
    - *augustana*; (Powell, 1983) (misspelling of *angustana*)
    - *dorsimaculana* (Robinson,1869)(unnecessary replacement name for *angustana*)
  - **argentilimitana** (Robinson, 1869)
    - *labeculana* (Robinson, 1869)[1]
  - **atomosana** (Busck, 1907)
  - **baloghi** Sabourin & Metzler, 2002
  - **biscana** (Kearfott, 1907)
    - *giscana* (Kearfott, 1907)
    - *ixeuta* (Meyrick, 1912) (unnecessary replacement name for *biscana*)
  - **bomonana** (Kearfott, 1907)
    - *cyamitis* (Meyrick, 1912) (unnecessary replacement name for *bomonana*)
    - *cyanitis* Razowski, 2000 (misspelling of *cyamitis*)*fabicola* (Meyrick, 1912) (unnecessary replacement name for *ziscana*)
    - *ziscana* (Kearfott, 1907), **new synonym**[2]
  - **deutschiana** (Zetterstedt, 1839)
    - *chalcana* (Packard, 1866)
    - *fuscostriana* Razowski, 1997 (misspelling of *fuscostrigana*)
    - *fuscostrigana* (Clemens, 1864)
    - *lutulentana* (Herrich-Schäffer, 1856)
    - *murciana* Caradja, 1916
  - **fernaldana** (Walsingham, 1879)
  - **floccosana** (Walker, 1863)
    - *confusana* (Robinson, 1869)
    - *flaccosana*; (Powell, 1983) (misspelling of *floccosana*)
  - **heleniana** Razowski, 1997
  - **intactana** (Walsingham, 1879)
  - **interruptofasciata** (Robinson, 1869)

aureana (Busck, 1907)
sublepidana (Kearfott, 1907)
louisiana (Busck, 1907)
matheri Sabourin & Miller, 2002
matthewcruzi Sabourin & Vargo, 2002
monera Razowski, 1886 (nominal species is extra-limital)
ssp. *septentrionalis* Razowski,1997 (described from Canada)
mymara Razowski, 1997
obliquana (Kearfott, 1907)
obliquna; Razowski, 2000 (misspelling of *obliquana*)
patricia Metzler, 2000
promptana (Robinson, 1869)
rana (Busck, 1907)
funesta (Meyrick, 1912) (unnecessary replacement name for *rana*)
razowskii Sabourin & Miller, 2002
rutilana (Hübner, [1814]) (nominal species is extra-limital)
ssp. *canadiana* Razowski, 1997 (described from Canada)
interruptana (Klemensiewicz, 1907)
purpurella (Coquebert de Montbret, 1801) [nomen oblitum]
roridana (Mann, 1867)
ssp. *tatricana* (Adamszewski, 1936) (extra-limital)
seriatana (Zeller, 1875)
sexdentata Sabourin & Miller, 2002
smeathmanniana (Fabricius, 1781)
achromata (Skala, 1936)
biviana (Duponchel, 1842)
fabricana Hübner, [1796]
obsoletella (Dufrane, 1955)
scissana (Walker, 1863)
sonorae (Walsingham, 1884)
spartinana (Barnes & McDunnough, 1916)
terriae Sabourin & Miller, 2002
vachelliana (Kearfott, 1907)
westratei Sabourin & Miller, 2002

Agapeta Hübner, 1822
Aapeta Anonymous, 1990 (misspelling of *Agapeta*)
Agapete Hübner 1825 (misspelling of *Agapeta*)
Euxanthis Hübner, [1825]
Apapeta Razowski, 1977
Xanthosetia Stephens, 1829
Xanthosetia Stephens, 1829 (unnecessary redescription)
zoegana (Linnaeus, 1767)
brunneocycla Razowski, 1961
ferrugana (Haworth, [1811])

Cochylidia Obraztsov, 1956
subroseana (Haworth, [1811])
derosana Razowski, 1960
flammeolana (Tengström, 1848)
phaleratana (Herrich-Schäffer, 1847) (uninominal)
ssp. *roseotincta* Razowski, 1960 (extra-limital)
rubroseana (Stephens, 1829)

Cochylis Treitschke, 1829
Acornutia Obraztsov, 1944
Brevicornutia Razowski, 1960
Chochylis Duponchel, 1836 (misspelling of *Cochylis*)
Cochylichroa Obraztsov & Swatschek, 1958
Conchlis Razowski, 2011 (misspelling of *Conchylis*)
Conchyli Sodoffsky, 1837 (misspelling of *Cochylis*)
Longicornutia Razowski, 1960
Neocochylis Razowski, 1960 (described as a subgenus of *Cochylis*) (extra-limital)
Paracochylis Razowski, 1960 (described as a subgenus of *Cochylis*) (extra-limital)
Pontoturania Obratzsov, 1943
arthuri Dang, 1984
aurorana (Kearfott, 1907)[3]
avita Razowski, 1997
bucera Razowski, 1997
carmelana (Kearfott, 1907)
obispoana (Kearfott, 1907)
caulocatax Razowski, 1984
dormitoria Razowski, 1997
dubitana (Hübner, 1796)
ambiguana (Frölich, 1828)
baseirufana (Bruand, 1850)
formonana (Kearfott, 1907)[4]
myrinitis (Meyrick, 1912) (unnecessary replacement name for *formonana*)
hoffmanana (Kearfott, 1907)[3]
baryzela (Meyrick, 1912) (unnecessary replacement name for *toxcana*)
hofmanana Razowski, 1997 (misspelling of *hoffmanana*)
magnaedoeagana Gibeaux, 1985[5]
marloffiana (Busck, 1907)
nonlavana (Kearfott, 1907)
telifera (Meyrick, 1912) (unnecessary replacement name for *zoxcana*)
toxcana (Kearfott, 1907)
zoxcana (Kearfott, 1907)
hospes (Walsingham, 1884)[3]
parallelana (Walsingham, 1879)
paralellana (Razowski, 1964)(misspelling of *parallelana*)
ringsi Metzler, 2000[7]

- **temerana** (Busck, 1907)[3]
  - *cincinnatana* (Kearfott, 1907)
- **transversana** (Walsingham, 1879)8
- **viscana** (Kearfott, 1907)[3]
  - *peganitis* (Meyrick, 1912) (unnecessary replacement name for *viscana*)
- **yinyangana** Metzler, 2012

- **Eugnosta** Hübner, [1825][9]
  - *Argyrolepia* Stephens, 1829
  - *Carolella* Busck, 1939[10]
  - *Pharmacis* Hübner, 1823
  - *Safra* Walker, 1863
  - **argyroplaca** (Meyrick, 1931)
  - **beevorana** (Comstock, 1940)
  - **bimaculana** (Robinson, 1869)[11]
  - **brownana** Metzler & Forbes, 2012
  - **busckana** (Comstock, 1939)
  - **deceptana** (Busck, 1907)
  - **erigeronana** (Riley, 1881)
  - **mexicana** (Busck, 1907)
  - **sartana** (Hübner, 1823)11
  - **willettana** (Comstock, 1939)

- **Eupinivora** Brown, 2013
  - **ponderosae** Brown, 2013

- **Gynnidomorpha** Turner, 1916
  - *Pierca* Razowski, 1977 (misspelling of *Piercea*)
  - *Piercea* Filipjev, 1940
  - **romonana** (Kearfott, 1908)[12]
    - *officiosa* (Meyrick, 1912) (unnecessary replacement name for *romonana*)

- **Henricus** Busck, 1943
  - *Heinrichia* Busck, 1939
  - *Irazona* Razowski, 1964[13]
  - **cognata** (Walsingham, 1914)
  - **comes** (Walsingham, 1884)
  - **contrastana** (Kearfott, 1907)
    - *edwardsiana* (Walsingham, 1884), **new synonym**[4, 14]
  - **fuscodorsana** (Kearfott, 1904)
  - **infernalis** (Heinrich, 1920)
    - *brevipalpata* McDunnough, 1944
  - **macrocarpana** (Walsingham, 1895)
  - **umbrabasana** (Kearfott, 1908)

- **Lorita** Busck, 1939
  - **baccharivora** Pogue, 1988
  - **scarificata** (Meyrick, 1917)
    - *abornana* Busck, 1939

- **Phalonidia** Le Marchand, 1933
  - *Brevisociaria* Obraztsov, 1943
  - *Platphalonidia* Razowski, 1985
  - **basiochreana** (Kearfott, 1907)[4]
  - **elderana** (Kearfott, 1907)[4]
    - *helonoma* (Meyrick, 1912) (unnecessary replacement name for *elderana*)
  - **felix** (Walsingham, 1895)[15]
  - **latipunctana** (Walsingham, 1879)[16]
  - **lepidana** (Clemens, 1860)[16]
    - *plummeriana* (Busck, 1907)[16]
    - *schwarziana* (Busck, 1907)[16]
    - *zaracana* (Kearfott, 1907)[16]
  - **memoranda** Razowski, 1997
  - **ontariana** Razowski, 1997
  - **straminoides** (Grote, 1873), **revised status**[16, 17]

- **Phtheochroa** Stephens, 1829
  - *Arce* Joannis, 1919
  - *Durrantia* Razowski, 1960 (described as a subgenus of *Hysterosia*) (extra-limital)
  - *Hysterosia* Stephens, 1852
  - *Idiographis* Lederer, 1859
  - *Parahysterosia* Razowski, 1960 (described as a subgenus of *Hysterosia*) (extra-limital)
  - *Phteochroa* Caradja, 1926 (misspelling of *Phtheochroa)*
  - *Ptheochroa* Razowski, 1964 (misspelling of *Phtheochroa)*
  - *Propira* Durrant, 1914
  - *Trachysmia* Guenée, 1845
  - **aegrana** (Walsingham, 1879)
  - **aureoalbida** (Walsingham, 1895)
  - **baracana** (Busck, 1907)
    - *tiscana* (Kearfott, 1907)
    - *vigilans* (Meyrick, 1912) (unnecessary replacement name for *tiscana*)
  - **birdana** (Busck, 1907)
  - **canariana** (Barnes & Busck, 1920)
  - **cartwrightana** (Kearfott, 1907)
    - *pecosana* Kearfott, 1907, **new synonym**[18]
  - **fulviplicana** (Walsingham, 1879)
    - *fermentana* (Meyrick, 1912)(unnecessary replacement name for *komonana*)
    - *homanana* (Kearfott, 1907)
    - *komonana* (Kearfott, 1907)
    - *refuga* (Meyrick, 1912) (unnecessary replacement name for *homonana*)
  - **huachucana** (Kearfott, 1907)
  - **modestana** (Busck, 1907)
  - **perspicuana** (Barnes & Busck, 1920)
  - **riscana** (Kearfott, 1907)
    - *vincta* (Meyrick, 1912) (unnecessary replacement name for *riscana*)

terminana (Busck, 1907)
merrickana (Kearfott, 1907)
villana (Busck, 1907)
vitellinana (Zeller, 1875)
vulneratana (Zetterstedt, 1839)
exsulana (Lederer, 1855)
meinki (Amsel, 1932)
niponica (Kawabe, 1982) (misspelling of *nipponica*)
ssp. *nipponica* (Matsumura, 1931) (extra-limital)
waracana (Kearfott, 1907)
dicax (Meyrick, 1912) (unnecessary replacement name for *waracana*)

Platphalonia Razowski, 2011
albertae (Razowski, 1997)[19]
campicolana (Walsingham, 1879)[16, 19]
dangi (Razowski, 1997)[19]
lavana (Busck, 1907)[16, 19]
magdalenae Metzler & Albu, 2013
plicana (Walsingham 1884)[16, 19]

Rolandylis Gibeaux, 1985, **revised combination**[20]
"Clothoa" (unavailable name)[21]
fusca Pogue, 2001, **revised combination**[22]
maiana (Kearfott, 1907), **revised combination**[22]
catalonica Gibeaux, 1985, **revised combination**[5, 22]
virilia Pogue, 2001, **revised combination**[22]

Rudenia Razowski, 1985
leguminana (Busck, 1907)

Saphenista Walsingham, 1914
nomonana (Kearfott, 1907)
voluntaria (Meyrick, 1912) (unnecessary replacement name for *nomonana*)
parvimaculana (Walsingham, 1879), **new combination**[23]
saxicolana (Walsingham, 1879)

Spinipogon Razowski, 1967
resthavenensis Metzler & Sabourin, 2002
thes Razowski & Becker, 1983

Thyraylia Walsingham, 1897 **revised status**[24]
Thyralia Walsingham 1914 (misspelling of *Thyraylia*)
bana (Kearfott, 1907), **new combination**
rhodites (Meyrick, 1912) (unnecessary replacement name for *bana*)
bunteana (Robinson, 1869), **new combination**
discana (Kearfott, 1907), **new combination**
cricota (Meyrick, 1912) (unnecessary replacement name for *discana*)
gunniana (Busck, 1907), **new combination**
hollandana (Kearfott, 1907), **new combination**
nana (Haworth, [1811]) **new combination**[29]
albidana (Walker, 1866)[6]
altocorsicana (Petry, 1904)
carneana (Guenée, 1845)
cruentana (Guenée, 1845)
ochreoalbana (Walker, 1863)
pallidana (Herrich-Schäffer, 1847) (uninomial) (nomen nudum)
pallidana (Herrich-Schäffer, 1851)
pumillana (Herrich-Schäffer, 1847) (uninomial) (nomen nudum)
winniana (Kearfott, 1905)

Cochylini new genus [1] - "Atroposia" (unavailable name)[21]
oenotherana (Riley, 1881)

Cochylini new genus [2] - "Cagiva" (unavailable name)[21]
cephalanthana (Heinrich, 1921)

Cochylini new genus [3] - "Cybilla" (unavailable name)[21]
hubbardana (Busck, 1907)

Cochylini new genus [4] - "Honca" (unavailable name)[21]
grandis (Busck, 1907)

Cochylini new genus [5] - "Nycthia" (unavailable name)[21]
pimana (Busck, 1907)
yuccatana (Busck, 1907)

Cochylini new genus [6] - "Poterioparvus" (unavailable name)[21]
wiscana (Kearfott, 1907)
acropeda (Meyrick, 1912) (unnecessary replacement name for *wiscana*)

Cochylina unplaced[25]
baboquivariana Kearfott, 1907 [Tortrix]
dilutana Walsingham, 1879 [Cochylis]
foxcana Kearfott, 1907 [Phalonia]
liquida Meyrick, 1912 [Phalonia] (unnecessary replacement name for *foxcana*)
fulvotinctana Walsingham, 1884 [Conchylis]
glaucofuscana Zeller, 1875 [Conchylis]
imitabilis Razowski, 1997 [Platphalonidia][26]
punctadiscana Kearfott, 1908 [Phalonia][27]
voxcana Kearfott, 1907 [Phalonia][28]

Alphabetical list of species, their synonyms, and their associated genera from North America north of Mexico.

Aapeta (misspelling of *Agapeta*)
abornana, Lorita
achromata, Aethes
Acornutia (synonym of *Cochylis*)
acropeda, Cochylina new genus ^{6} ("*Poterioparvus*")
aegrana, Phtheochroa
Aethes
Agapeta
Agapete (misspelling of *Agapeta*)
albertae, Platphalonia
albidana, Cochylis
altocorsicana, Cochylis
ambiguana, Cochylis
angulatana, Aethes
angustana, Aethes
Apapeta
Arce (synonym of *Phtheochroa*)
argentilimitana, Aethes
Argyridia (synonym of *Aethes*)
Argyrolepia (synonym of *Eugnosta*)
argyroplaca, Eugnosta
arthuri, Cochylis
atomosana, Aethes
“Atroposia" (Cochylina new genus 1) (unavailable name)
augustana, Aethes
aureana, Aethes
aureoalbida, Phtheochroa
aurorana, Cochylis
avita, Cochylis
baboquivariana, Cochylina unplaced
baccharivora, Lorita
baloghi, Aethes
bana, Thyraylia
baracana, Phtheochroa
baryzela, Cochylis
baseirufana, Cochylis
basiochreana, Phalonidia
beevorana, Eugnosta
bimaculana, Eugnosta
birdana, Phtheochroa
biscana, Aethes
biviana, Aethes
bomonana, Aethes
Brevicornutia (synonym of *Cochylis*)
brevipalpata, Henricus
Brevisociaria (synonym of *Phalonidia*)
brownana, Eugnosta
brunneocycla, Agapeta
bucera, Cochylis
bunteana, Thyraylia
busckana, Eugnosta
“Cagiva" (Cochylina new genus 2) (unavailable name)
campicolana, Platphalonia
canadiana, Aethes
canariana, Phtheochroa
carmelana, Cochylis
carneana, Cochylis
Carolella (synonym of *Eugnosta*)
cartwrightana, Phtheochroa
catalonica, Rolandylis
caulocatax, Cochylis
cephalanthana, Cochylina new genus 2 ("Cagiva")
chalcana, Aethes
Chlidonia (synonym of *Aethes*)
Chochylis (mispelling of *Cochylis*)
Chrosis (synonym of *Aethes*)
cincinnatana, Phalonidia
Cirriaethes (synonym of *Aethes*)
“Clothoa” (synonym of *Rolandylis*)
Cochylichroa (synonym of *Cochylis*)
Cochylidia
Cochylina unplaced
Cochylis
Coecaethes (synonym of *Aethes*)
cognata, Henricus
comes, Henricus
Conchlis (misspelling of *Cochylis*)
Conchyli (misspelling of *Cochylis*)
Conchylis (misspelling of *Cochylis*)
confusana, Aethes
contrastana, Henricus
cricota, Thyraylia
cruentana, Cochylis
cyamitis, Aethes
cyanitis, Aethes
“Cybilla” (Cochylina new genus 3) (unavailable name)
dangi, Platphalonia
Dapsilia (synonym of *Aethes*)
deceptana, Eugnosta
derosana, Cochylidia
deutschiana, Aethes
dicax, Phtheochroa
dilutana, Cochylina unplaced
discana, Thyraylia
dormitoria, Cochylis
dorsimaculana, Aethes
dubitana, Cochylis
Durrantia (synonym of *Phtheochroa*)
edwardsiana, Henricus
elderana, Phalonidia
erigeronana, Eugnosta
Eugnosta
Eupinivora
Euxanthis (synonym of *Agapeta*)
exsulana, Phtheochroa
fabicola, Aethes
fabricana, Aethes
felix, Phalonidia
fermentata, Phtheochroa
fernaldana, Aethes
ferrugana, Agapeta
flaccosana, Aethes
flammeolana, Cochylidia
floccosana, Aethes
formonana, Cochylis
foxcana, Cochylina unplaced
fulviplicana, Phtheochroa
fulvotinctana, Cochylina unplaced
funesta, Aethes
fusca, Rolandylis
fuscodorsana, Henricus
fuscostriana, Aethes

fuscostrigana, Aethes
giscana, Aethes
glaucofuscana, Cochylina unplaced
grandis, Cochylina new genus 4 ("Honca")
gunniana, Thyraylia
Gynnidomorpha
Heinrichia (synonym of *Henricus*)
heleniana, Aethes
helonoma, Phalonidia
Henricus
hoffmanana, Cochylis
hofmanana, Cochylis
hollandana, Thyraylia
homanana, Phtheochroa
“Honca" (Cochylina new genus 4) (unavailable name)
hospes, Cochylis
huachucana, Phtheochroa
hubbardana, Cochylina new genus 3 ("Cybilla")
Hysterosia (synonym of *Phtheochroa*)
Idiographis (synonym of *Phtheochroa*)
imitabilis, Cochylina unplaced
infernalis, Henricus
intactana, Aethes
interruptana, Aethes
interruptofasciata, Aethes
Irazona (synonym of *Henricus*)
ixeuta, Aethes
komonana, Phtheochroa
labeculana, Aethes
latipunctana, Phalonidia
lavana, Platphalonia
leguminana, Rudenia
lepidana, Phalonidia
liquida, Cochylina unplaced
Longicornutia (synonym of *Cochylis*)
Lorita
louisiana, Aethes
Loxopera (synonym of *Aethes*)
Lozopera (synonym of *Aethes*)
lutulentana, Aethes
macrocarpana, Henricus
magdalenae, Platphalonia
magnaedoeagana, Cochylis
maiana, Rolandylis
marloffiana, Cochylis
matheri, Aethes
matthewcruzi, Aethes
meincki, Phtheochroa
memoranda, Phalonidia
merrickana, Phtheochroa
mexicana, Eugnosta
modestana, Phtheochroa
monera, Aethes
murciana, Aethes
mymara, Aethes
myrinitis, Cochylis
nana, Thyraylia
Neocochylis (synonym of *Cochylis*)
niponica, Phtheochroa
nipponica, Phtheochroa
nomonana, Saphenista
nonlavana, Cochylis
“Nycthia" (Cochylina new genus 5)
obispoana, Cochylis
obliquana, Aethes
obliquna, Aethes
obsoletella, Aethes
ochreoalbana, Cochylis
oenotherana, Cochylina new genus 1 ("Atroposia")
officiosa, Gynnidomorpha
omphacitis, Cochylina unplaced
ontariana, Phalonidia
pallidana, Cochylis
Paracochylis (synonym of *Cochylis*)
Parahysterosia (synonym of *Phtheochroa*)
paralellana, Cochylis
parallelana, Cochylis
parvimaculana, Saphenista
patricia, Aethes
pecosana, Phtheochroa
peganitis, Cochylis
perspicuana, Phtheochroa
phaleratana, Cochylidia
Phalonia (synonym of *Aethes*)
Phalonidia
Pharmacis (synonym of *Eugnosta*)
Phelonia (synonym of *Aethes*)
Phteochroa (misspelling of *Phtheochroa*)
Phtheochroa
Pierca (synonym of *Gynnidomorpha*)
Piercea (synonym of *Gynnidomorpha*)
pimana, Cochylina new genus ^{5} ("Nycthia")
Platphalonia
Platphalonidia (synonym of *Phalonidia*)
plicana, Platphalonia
plummeriana, Phalonidia
ponderosae, Eupinivora
Pontoturamia (synonym of *Cochylis*)
“Poterioparvus” (Cochylina new genus 6) (unavailable name)
promptana, Aethes
Propira (synonym of *Phtheochroa*)
Ptheochroa (misspelling of *Phtheochroa*)
pumillana, Cochylis
punctadiscana, Cochylina unplaced
purpurella, Aethes
rana, Aethes
razowskii, Aethes
refuga, Phtheochroa
resthavenensis, Spinipogon
rhodites, Thyraylia
ringsi, Cochylis
riscana, Phtheochroa
Rolandylis
romonana, Gynnidomorpha
roridana, Aethes
roseotincta, Cochylidia
rubroseana, Cochylidia
Rudenia
rutilana, Aethes
Safra (synonym of *Eugnosta*)
Saphenista
sartana, Eugnosta
saxicolana, Saphenista
scarificata, Lorita
schwarziana, Phalonidia

scissana, Aethes
septentrionalis, Aethes
seriatana, Aethes
sexdentata, Aethes
smeathmanniana, Aethes
sonorae, Aethes
spartinana, Aethes
Spinipogon
straminoides, Phalonidia
sublepidana, Aethes
subroseana, Cochylidia
tatricana, Aethes
telifera, Cochylis
temerana, Cochylis
terminana, Phtheochroa
terriae, Aethes
thes, Spinipogon
Thyralia (misspelling of *Thyraylia*)
Thyraylia
tiscana, Phtheochroa
toxcana, Cochylis
Trachybyris (synonym of *Eugnosta*)
Trachybyrsis (synonym of *Eugnosta*)
Trachysmia (synonym of *Phtheochroa*)
transversana, Cochylis
umbrabasana, Henricus
vachelliana, Aethes
vigilans, Phtheochroa
villana, Phtheochroa
vincta, Phtheochroa
virilia, Rolandylis
viscana, Cochylis
vitellinana, Phtheochroa
voluntaria, Saphenista
voxcana, Cochylina unplaced
vulneratana, Phtheochroa
waracana, Phtheochroa
westratei, Aethes
willettana, Eugnosta
winniana, Cochylis
wiscana, Cochylina new genus 6 ("Poterioparvus")
Xanthosetia (synonym of *Agapeta*)
yuccatana, Cochylina new genus 5 ("Nycthia")
zaracana, Phalonidia
ziscana, Aethes
zoegana, Agapeta
zoxcana, Cochylis

DISCUSSION

The taxonomy of the subtribe Cochylina is poorly known. Although the number of described species worldwide increases every year, mostly as a result of the efforts of Józef Razowski, Polish Academy of Sciences, Krakow and his co-authors, the number of described species from North America has not increased dramatically since Powell (1983).

Michael G. Pogue (pers. comm.) repeated anecdotal information provided by J. F. G. Clarke that approximately 2/3 of the species from North America are undescribed, suggesting that the North American fauna may include more than 300 species. Identifying specimens of Cochylina is problematic because of the number of undescribed species, lack of diagnostic illustrations, and a list of current names.

The frustration of not knowing the identity of an individual specimen of a "Cochylina" in the sea of named and unnamed species is an unresolved issue. Jason Dombroskie (pers. comm.), who is a consultant for Bug Guide (2013), finds that users are not satisfied if they do not receive a specific identification based on photographs of specimens that are neither spread nor dissected. Many species of Cochylina cannot be placed to genus without examination of the genitalia (Brown 2006). Identification is no less complicated because many species of Cochylina, even within a single genus, e.g., *Aethes* Billberg, 1820, often have forewing patterns that are incongruous. Many species' descriptions do not include illustrations of adults.

Photographs on Moth Photographers Group (2013) are useful for guidance on the habitus of many species. Genitalic illustrations of the types for many species are lacking. Information about descriptions, with references to literature, subsequent to Brown (2005), along with illustrations of type specimens is available at Gilligan et al. (2013). We caution that without examination aided by microscopy, many species simply cannot be identified.

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END NOTES

[1] *Aethes labeculana* was listed as a separate species by Pogue (1986); it was synonymized with *A. argentilimitana* by Sabourin et al. (2002).

[2] The synonymy of *Aethes ziscana* with *A. bomonana* is based on examination of photographs of the types and male genitalia of both species.

[3] These species were placed in "Recavicula" by Pogue (1986).

[4] These species were listed as "incertae sedis" by Pogue (1986).

[5] This name is supposedly based on a mislabeled specimen (Razowski, 2002).

[6] *Cochylis albidana* was listed as a synonym of *Cochylis dubitana* by Pogue (1986).

[7] The date was incorrectly listed as 1999 by Brown (2005).

[8] *Cochylis transversana* was placed in *Saphenista* by Pogue (1986).

[9] *Trachybyrsis* Meyrick, 1927 was listed as a separate genus by Brown (2005) and Aarvik (2010). It was listed as a synonym of *Eugnosta* by Razowski (2011). Because species of *Trachybyrsis* occur in Africa rather than in our faunal region, we make no further comments.

[10] *Carolella* was synonymized with *Eugnosta* by Razowski (2009).

[11] This species was placed in *Carolella* by Pogue (1986) and Brown (2005). The combination listed here was created by Razowski (2009).

[12] *Gynnidomorpha romonana* was listed in *Saphenista* by Pogue (1986).

[13] *Irazona* was treated as a separate genus by Pogue (1986) and synonymized with *Henricus* by Razowski (1997).

[14] *Henricus edwardsiana* is synonymized with *H. contrastana* based on examination of the types of both species.

[15] *Phalonidia felix* was placed in *Saphenista* by Pogue (1986), it was placed in *Platphalonidia* by Razowski (1985) and Brown (2005), and it was placed in *Phalonidia* by Razowski (2011).

[16] These species were listed in *Saphenista* by Pogue (1986).

[17] The relationship between *lepidana, plummeriana, schwarziana, straminoides*, and *zaracana* was variously presented (Pogue 1986, Razowski 1997, Brown 2005). We examined photographs of the types of *lepidana, plummeriana, schwarziana, straminoides*, and *zaracana*. We propose that *straminoides* is not conspecific with the others.

[18] Pogue (1986) listed *Phtheochroa pecosana* as a synonym of *P. cartwrightana*. Razowski (1997) did not include *pecosana* in the synonymy of *cartwightana*. Brown (2005) listed *cartwrightana* and *pecosana* as separate species. We validate the synonymy proposed by Pogue (1986).

[19] These species were listed in *Platphalonidia* by Brown (2005). When Razowski (2011) transferred *P. felix*, the type species of *Platphalonidia*, to *Phalonidia* the action resulted in the synonymy of *Platphalonidia* with *Phalonidia*. However, all other species of *Plaphalonidia* were left without a generic assignment. Metzler & Albu (2013) transferred some of the unplaced species to *Platphalonia*. More analysis is needed.

[20] *Rolandylis* was synonymized with *Cochylis* by Razowski (2009), and restated (2011). We consider *Rolandylis* to be a separate genus.

[21] These genera were proposed by Pogue (1986) in his unpublished Ph.D. thesis and used without descriptions or designation of type species in a phylogenetic analysis by Pogue & Mickevitch (1990). We retain the names here for the sake of continuity and clarity, but we do not publish the names here.

[22] These species were listed in *Rolandylis* by Brown (2005).

[23] *Saphenista parvimaculana* was listed in *Platphalonidia* by Brown (2005). When Razowski (2011) transferred *P. felix*, the type species of *Platphalonidia*, to *Phalonidia* the action resulted in the synonymy of *Platphalonidia* with *Phalonidia*. However, all other species of Plaphalonidia were left without a generic assignment. We follow Pogue (1986), and we place *P. parvimaculana* in *Saphenista*. More analysis is needed.

[24] *Thyraylia* was listed as a synonym of *Cochylis* by Razowski (1997, 2009, 2011). However, Pogue (1986) and Brown (2005) both listed *Thyraylia* as a separate genus. We follow the latter concept.

[25] *Clepsis listerana*, listed as "*incertae sedis*" in Pogue (1986), is in the tribe Archipini (Tortricidae).

[26] *Platphalonidia imitabilis* was listed in *Platphalonidia* by Brown (2005). When Razowski (2011) transferred *felix*, the type species of *Platphalonidia*, to *Phalonidia* the action resulted in the synonymy of *Platphalonidia* with *Phalonidia*. However, all other species of *Plaphalonidia* were left without a generic assignment. We propose that more study is needed before *P. imitabilis* can be placed in a genus.

[27] *Phalonia punctadiscana* was listed in "Recavicula" (unavailable name) in Pogue (1986). It was listed in "Cochylini Unplaced Species" by Brown (2005).

[28] *Phalonia voxcana* was listed as a synonym of *Thyraylia hollandana* by Pogue (1986), placed in *Cochylis* in Razowski (1997) and Brown (2005). The genitalia illustrated by Razowski (1997) are congeneric with *Thyraylia*. Our examination of the wings of the types of *hollandana* and *voxcana* indicate they are not conspecific.

[29] This species was listed in *Thyraylia* by Pogue (1986), and it was listed in *Cochylis* by Razowski (1997) and Brown (2005). Our examination of the male genitalia shows that it should be listed in *Thyraylia*.

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METABOLISM OF SAFROLE BY *HERACLIDES THOAS BRASILIENSIS* (PAPILIONIDAE)

Additional key words: Safrole, *Piper divaricatum*, *Heraclides thoas brasiliensis*, metabolism

As part of the systematic study of chemical interactions between plant-insect (Ramos et al. 2012) we have found the plant *Piper divaricatum* (Piperaceae) as a new source of safrole (Barbosa et al. 2012). Safrole is a natural insecticide useful in the management of insecticide-resistant insects and it also is an important raw material used in the synthesis of piperonyl butoxide, a crucial ingredient in pyrethroid insecticides (Bizzo et al. 2001). Despite the toxicity and insecticidal activity of safrole (Wen et al. 2001), *Heraclides thoas brasiliensis* (Rothschild & Jordan, 1906) caterpillars can be found feeding ravenously on *Piper* species including *P. divaricatum* leaves (Vanin et al. 2008). Thus, the present study aimed to describe mechanisms by which safrole is metabolized by *H. thoas brasiliensis* in order to understand the adaptation allowing the caterpillar to live on a diet rich in safrole.

For this study, fresh young leaves of *P. divaricatum* were collected in the city of Itabuna-BA, Brazil, at 3 a.m., 6 a.m., 9 a.m., noon, 3 p.m., 6 p.m., 9 p.m. and midnight for a previously planned circadian rhythm study. The samples were collected in triplicates. The leaves were stored in hermetically sealed plastic bag and kept under refrigeration at + 5 ºC until an extract of leaf chemicals could be obtained. Dried leaves (40 °C for 24 h) of *P. divaricatum* (8 g) were milled and extracted with dichloromethane (100 mL x 3), which after concentration in vacuum, yielded 0.9 g of crude extract. The botanical material was identified by Dr. Elsie F. Guimarães (Instituto de Pesquisas Jardim Botânico do Rio de Janeiro, Brazil) and a voucher specimen (Kato-1063). Heraclides thoas brasiliensis caterpillars were collected from *P. divaricatum* and identified by Dr. Sérgio Antônio Vanin of the Zoology (Department of the Biosciences Institute of the University of São Paulo). A voucher specimen (CSR 001) was deposited at the Zoology Museum of the University of São Paulo.

The caterpillars were reared separately in three cages (5 individuals in each cage at a temperature of 28 ± 2 ºC, relative humidity of 70 ± 10% and under a 15L:9D photoperiod) on an exclusive diet of *P. divaricatum* leaves in the laboratory. Insects were fed with the same plant material as used for the leaf analyses. Dried feces (40 °C for 24 h) were extracted with dichloromethane (100 mL x 3) and the extract obtained was concentrated under reduced pressure and subjected to chromatographic and spectrometric analysis. The GC/MS analyses of the extracts were carried out at a concentration of 2mg/mL dichloromethane. The fecal and leaf extracts were analyzed by GC-MS (60-240 ºC at 3 ºC min. rate) in a Varian 431-GC coupled to a Varian 220-MS instrument using a fused-silica capillary column (30 m × 0.25 mm i.d. × 0.25 µm.) coated with DB-5. MS spectra were obtained using electron impact at 70 eV with a scan interval of 0.5 s and fragments from 40 to 550 Da. The leaves were also analyzed by HPLC using a Shimadzu chromatograph model SCL-10A with UV–VIS detector (model SPD-M10A) with reversed phase column (Supelco, C18; 5 µm i.d., 4 x 250 mm). Elution was carried out in a gradient mode starting with methanol:water (3:7) for 10 min, rising to (9:1) in 30 min and maintained for to 35 min. The flow rate was 1 mL/min; injection volume 20 µL; UV scan, 200-400 nm, and all chromatograms were obtained at λ max = 254 nm. The content of safrole in plant material was calculated by comparison of HPLC data obtained for samples and standard solutions containing of safrole 0.1 – 2.0 mg/mL (R^2 = 0,985) in dichloromethane. The authentic standards of safrole as well as methyleugenol and eugenol were purchased from Sigma-Aldrich.

The chromatogram (GC-MS) of the dichloromethane extract from leaves of *P. divaricatum* showed the major compound as safrole. In addition, the circadian variation of safrole content in the dried leaves was investigated by HPLC. The results indicated maximum concentration at noon (34.5 ± 0.2 µg/mg) and minimum concentration at 6 a.m. (14.2 µg/mg ± 0.5), on a dry weight basis (Fig. 1).

The chromatogram (GC-MS) of the fecal extract showed one major peak at 23.6 min that was not detected in the chromatogram of the leaves (Fig. 2). The peak was identified as methyleugenol, a product of the biotransformation of safrole by the *H. thoas brasiliensis* caterpillars. The chromatogram of the fecal extract also revealed the presence of eugenol, indicating that the biotransformation of safrole to methyleugenol occurs via eugenol as an intermediate. Three compounds were identified by their mass spectra compared to the authentic standards. Methyleugenol as the main metabolite for cleavage of the methylenedioxy group of safrole has not been observed in studies with mammals. Cleavage of the methylenedioxy group of

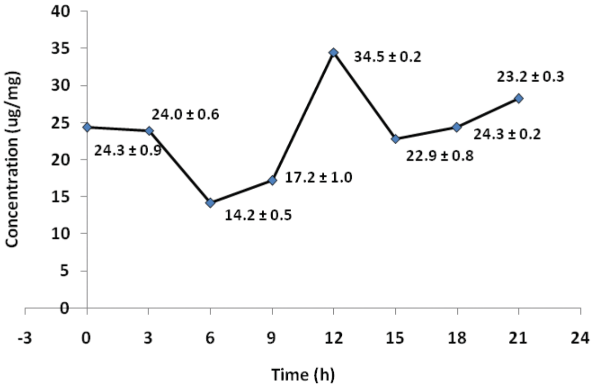

FIG. 1. The circadian variation in safrole content (μg/mg dry weight) in the leaves of *P. divaricatum*. The graphic was plotted using the values means of replicates.

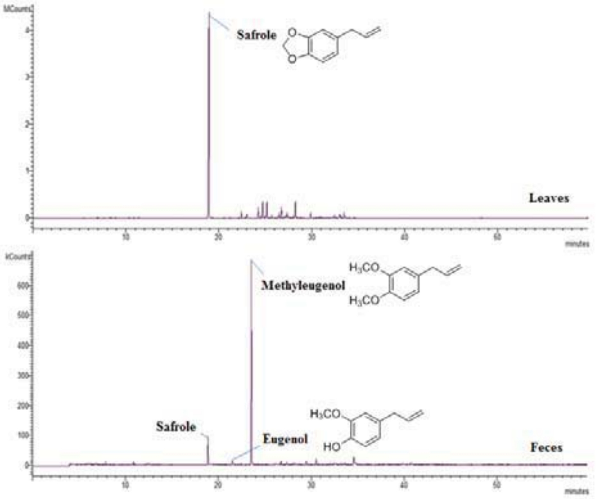

FIG. 2. GC-MS profiles of dichloromethane extracts from P. divaricatum (leaves) and *H. brasiliensis* caterpillar (feces).

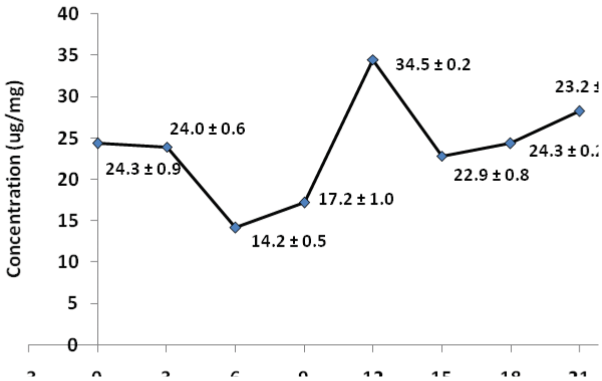

FIG. 3. The main metabolic pathways of safrole in mammals and caterpillar *H. brasiliensis* (Ioannides et al., 1985).

safrole has been observed in rats and humans as the main route of their metabolism, producing allylcatechol as the main compound and eugenol as a minor compound (Fig. 3). In insect in vitro metabolism of myristicin, an analog of safrole, indicated that this is metabolized to 1-(3`,4'-methylenedioxy-5'-methoxyphenyl)-2,3-epoxypropane, an epoxidation of the methylene group (Mao et al. 2008).

In summary, the in vivo metabolism study of safrole by *H. thoas brasiliensis* revealed that this is biotransformed to methyl eugenol (major metabolite) and eugenol (minor metabolite). The cleavage of the methylenedioxy group of safrole has also been identified as a major route of metabolism of piperonyl butoxide in mammals. Piperonyl butoxide is a semisynthetic derived from safrole and is a potent cytochrome P450 inhibitor in animals. This inhibitor is attributed to the methylenedioxy (Gokbulut et al. 2010; Ioannides et al. 1985) Thus, cleavage of the methylenedioxy group of safrole by caterpillars implies a probable mechanism of insect adaptation to a diet rich in safrole. This hypothesis is strengthened because the methylenedioxy group is an enzyme detoxification inhibitor (cytochrome P450).

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LABORATORY MATING OF MUTUALISTIC SEED-PARASITIC MOTH *EPICEPHALA BIPOLLENELLA* (LEPIDOPTERA: GRACILLARIIDAE)

Additional key words: *Glochidion*, obligate pollination mutualism, Phyllanthaceae, pollinator

The techniques of laboratory mating are vital for the successful rearing of model animals and are essential tools in various experiments, stable behavioral tests, and genetic research (Ohshima 2012). Breeding pollinating insects in the laboratory that are obligatorily associated with plants, such as yucca moths and fig wasps, under laboratory conditions has been especially unsuccessful. In such obligate pollination mutualisms, the floral volatiles are extremely important signals for attracting the species-specific pollinators (Svensson et al. 2005; Okamoto et al. 2007; Chen et al. 2009), and in behavioral tests using sufficient individuals it is critical to clarify the ecological and evolutionary roles of floral volatiles. Thus, the establishing of a method for successfully rearing insect pollinators will be a breakthrough for ecological and evolutionary studies of mutualistic interactions. This study presents a first step toward that goal.

Epicephala bipollenella Li, Wang & Hu, 2012 is a small moth species belonging to the family Gracillariidae, which has been recorded from southern Japan, Taiwan, and China (Okamoto et al. 2013; Zhang et al. 2012). Female adults actively pollinate the flowers of *Glochidion zeylanicum* and lay eggs in the ovaries. The emerging larvae feed only on a subset of the developing seeds (Kato et al. 2003; Okamoto et al. 2013). Just before pupation, the larvae emerge from the host fruit and immediately pupate on the ground. Adult moths, especially females, can be found on the host plants during the night. Adult males are found only occasionally, because only females visit the male and female flowers to pollinate them actively and oviposit, while males do not visit flowers to forage. Nonetheless, the mating behaviors of *E. bipollenella* have never been observed in the field, suggesting that they may be mating during a specific time of day. This makes it difficult to establish a method of successfully rearing in *Epicephala* moths. Here, I present a method for laboratory mating experiments with *E. bipollenella*.

To obtain last-instar larvae of *E. bipollenella*, I collected the mature fruit of *G. zeylanicum* on 13–17 June 2013 on Amami-Oshima Island, Japan. The fruit were kept in soft plastic bags until the larvae emerged from them and completed their pupation. The pupae were moved into plastic containers without plants to prevent any negative effect of plant degradation on moth survival. During the pupal stage, the insects were kept at 28 ± 2 °C or 15 ± 1 °C. At 28 °C, the length of the pupal stage was ca. 10–14 days. At 15 °C, the emergence was delayed by approximately 10–20 days relative to that at 28 °C. These results suggest that *E. bipollenella* is a multiple-brooded species. After adult emergence, I paired the moths in two ways: in one, each male and female adult moth was paired more than two days after their emergence; in the other; the moths were paired within 24 h of emergence. Each pair of moths was placed into a single plastic centrifuge tube (118 mm long, 28 mm in diameter) with tissue paper soaked with 1% sucrose solution for nourishment, because a previous study indicated that the gracillariid moths can be reared on 1% sucrose solution (Ohshima 2005). Each pair was first put under a photophase (16 h light), followed by a scotophase (8 h dark; i.e., L:D=16:8). I monitored them every 30 minutes to confirm mating, including during the scotophase (under a red light to avoid interrupting the night period). These observations showed that *E. bipollenella* was not active during the photophase and mated only during two hours at the end

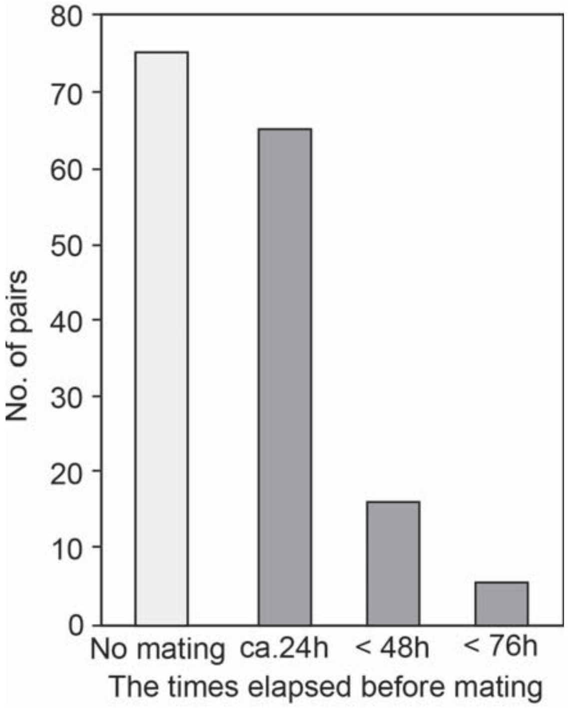

Fig. 1. The times elapsed before mating and the numbers of mated and unmated pairs.

of the scotophase. I confirmed the mating behavior of *E. bipollenella*, in which the male moth approaches the female and fans his wing, which is typical of various moth species (Parra-Pedrazzoli & Leal 2006). A total of 162 pairs of moths were used in the laboratory mating experiments: 65 mated at the end of their first scotophase; 16 pairs mated at the end of their second scotophase; five pairs mated at the end of a later scotophase, and the rest were not observed mating at all (Fig. 1). Thus, the copulation occurred in 53.1 % of all pairs and 1.3 ± 0.6 (SD) days after their emergence. These results strongly suggest that *E. bipollenella* mates during the first or second period of dusk after its emergence in the wild. Although multiple matings were observed in only one pair throughout the experiment, this indicates that these moths can mate multiple times at low frequencies. Further experiments are required using different combinations of moths to confirm whether multiple mating is a general phenomenon in *E. bipollenella.* The oviposition behavior of the female *E. bipollenella* on the host plant is frequently observed between evening and midnight in the wild (Kato et al. 2003), suggesting that the moths can be readily induced to oviposit on flowers. Therefore, cultivation of the host plant should permit the successive rearing of Epicephala moths under laboratory conditions.

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CORRECTION OF THE STATUS OF *SPEYERIA ATLANTIS* AND *S. HESPERIS*

Additional key words: DNA barcoding, mtDNA, Nymphalidae, species concepts

Hammond et al. (2013) incorrectly represented the writing of Grey (1951), a casual note in one of the original Lepidopterists' News, in an attempt to justify the hypothesis that eastern U.S. *Speyeria atlantis* are the same species as western U.S. *S. hesperis*. Grey actually wrote that ssp. *atlantis* & *canadensis* "are not sharply different races" and wrote that some Colorado specimens are "so exactly like Appalachian individuals that nobody…could tell them apart.", then on p. 34 he wrote "in the Riding Mts…we meet again with eastern *atlantis* in the dark phase *hollandi*." The intergradation that Grey noted and found in his decades of study, was within the ssp. of western butterflies that we now know as *S. hesperis*, as ssp. *hesperis* gradually changes into *irene* for instance in a roundabout journey hopping from one mountain range to another. Grey's major failure was his lumping of the two species *S. atlantis* and *S. hesperis*, which was corrected by Scott et al. (1998), who split them into the two species that are now generally recognized (including in the Pelham catalogue), based on numerous traits of adults and larvae and the intergradation of ssp. *atlantis* with ssp. *hollandi* (Klassen et al. 1989 also demonstrated that eastern *S. atlantis atlantis* is conspecific with western *S. atlantis hollandi* in Manitoba), and named three western ssp. *S. atlantis pahasapa* and *S. atlantis sorocko* and *S. hesperis brico* that were previously unrecognized in the area of sympatry of *S. atlantis* with western *S. hesperis*. The mature larvae of West Virginia ssp. *atlantis* and western ssp. *hollandi* and ssp. *sorocko* are identical with "crocodile skin" dorsal stripes and complex lateral white markings (Allen et al 2005, James & Nunnallee 2011, Scott et al. 1998), while *S. hesperis* and other *Speyeria* larvae differ. The mtDNA study of McHugh et al. (2013) found that *sorocko* and *hollandi* are a monophyletic sister group in the "mitochondrial, the nuclear and the full concatenated analyses (Fig. 2, 4)." The barcoding mtDNA phenogram made by two of us (Guppy and Kondla, unpublished) likewise found that *S. atlantis atlantis* specimens (4 from Virginia, 1 from Nova Scotia) were thoroughly mixed together with specimens of *hollandi* (6 from British Columbia, 4 from Manitoba) on that same monophyletic branch, while 20 specimens of *S. hesperis* (ssp. *lais, beani, brico, nausicaa*,) were clustered together on the other side of the phenogram as the sister group of 13 specimens of *S. aphrodite* from Virginia and British Columbia. There are no consistent diagnostic mtDNA differences between Virginia *S. a. atlantis* and BC and Manitoba *S. a. hollandi*, compared to 25 differences between those and *S. hesperis*. The minimum distance between *S. atlantis* and *S. hesperis* in this study was 4.25% (using standard genetic data analysis tools available on the BOLD systems workbench at http://www.boldsystems.org/), which is twice the distance commonly considered to indicate different species. In contrast, the genetic distance within specimens of each species was less than 1% and there was no consistent difference between Va./N.S. *atlantis* and *hollandi*. (Dunford [2007] found 4.5% gene difference between Vermont *S. atlantis* and Wyoming "*atlantis*" based on one male, but photos of it prove that the specimen is actually *S. hesperis hesperis*. McHugh et al. [2013] also misidentified some specimens, including a "*S. callippe elaine*" whose photo suggests it is *S. zerene picta*.) So *S. atlantis* and *S. hesperis* are not even closely-related species; *S. zerene* is closer to *S. hesperis* than is *S. atlantis*, while *S. aphrodite* is nearest to *S. hesperis* on the phenogram.

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TWO NEW COMBINATIONS IN NEOTROPICAL *ECCOPSIS* ZELLER, 1852 AND ONE IN *MEGALOTA* DIAKONOFF, 1966 (TORTRICIDAE: OLETHRUETINAE)

Additional key words: Afrotropical, Ecuador, Olethreutini, Peru

During continuing studies on the tortricid fauna of the New World tropics, two species described in *Polychrosis* by Meyrick (1917) and subsequently transferred to *Lobesia* Guenée, 1845 by Clarke (1958) were determined to be assigned more appropriately to *Eccopsis* Zeller, 1852, as it is currently defined. *Eccopsis eltundana* Razowski & Wojtusiak, 2008, described from a single female from Ecuador, belongs in *Megalota* Diakonoff, 1966. The purpose of this note is to formally propose these three new combinations.

Eccopsis arenacea (Meyrick), **new combination**
Polychrosis arenacea Meyrick, 1917: 23.
Lobesia arenacea: Clarke 1958: 464; Powell et al. 1995: 152; Brown 2005: 407.

Polychrosis arenacea was described from Durán [province of Guayas], Ecuador, based on 23 specimens collected in June [probably 1914]. Clarke (1958) designated a lectotype and indicated that 10 of Meyrick's original specimens were missing from the collection of the British Museum of Natural History (BMNH; now The Natural History Museum, London). Clarke transferred the species to *Lobesia*, indicating it was a new combination, but gave no justification for the transfer. Powell et al. (1995) and Brown (2005) followed that assignment.

The forewing pattern of the lectotype of *Polychrosis arenacea* (illustrated by Clarke 1858: 464) is extremely similar to that of *Eccopsis floreana* Razowski & Landry, 2008 (Razowski et al. 2008: figs. 13, 14), described from the Galapagos Islands, Ecuador. Meyrick (1917) indicated that *arenacea* "varies remarkably," and the same is true of other Neotropical species of *Eccopsis*, including *E. floreana*. The male genitalia of *arenacea* are extremely similar to those of *Eccopsis galapagana* Razowski & Landry, 2008 (Razowski et al. 2008: fig. 43), with a few long spines from the apex of the uncus, digitate socii, and asymmetric valvae, in each species with a dense patch of long setae and a long, slender, rod-like process from the terminal part of the sacculus on the right valva. On the basis of its superficial and morphological similarity to these species of *Eccopsis*, *arenacea* is transferred to *Eccopsis*.

Eccopsis oxynochla (Meyrick), **new combination**
Polychrosis oxymochla Meyrick, 1917: 24.
Lobesia arenacea: Clarke 1958: 472; Powell et al. 1995: 152; Brown 2005: 408.

Polychrosis oxymochla was described from Lima, Peru, based on 28 specimens collected "8-14" [probably August 1914]. Clarke (1958) designated a lectotype and indicated that 16 of the original specimens were missing from the BMNH collection. He transferred the species to *Lobesia*, identifying it as new combination, but gave no justification for the action. Powell et al. (1995) and Brown (2005) followed that treatment without further comment.

The forewing pattern of the lectotype of *Polychrosis oxymochla* (illustrated by Clarke 1858: 472) is not particularly similar to that of other Neotropical species of *Eccopsis*, but Meyrick (1917) indicated that the species "varies considerably in distinctness of markings," which is common among Neotropical *Eccopsis*, and some of the paratypes are similar in facies to other New World *Eccopsis*. The male genitalia of *oxymochla* are similar to those of *Eccopsis razowskii* Vargas, 2011 (Vargas 2011: fig. 2), with a patch of long spines from the apex of the uncus, digitate socii, and asymmetric valvae, each valva somewhat divided near the middle by an oblique line separating the baso-anterior portion of the valva from the cucullus. In *Eccopsis razowskii*, each valva bears a short rod-like process, much shorter than that of *E. galapagana* (the latter has the process only on the right valva); however, similar processes are not apparent in *oxymochla*. On the basis of the forewing variation and similarity in male genitalia to other species of *Eccopsis, oxymochla* is transferred to *Eccopsis*.

Megalota eltundana (Razowski & Wojtusiak),
new combination
Eccopsis eltundana Razowski & Wojtusiak, 2008: 23.

Eccopsis eltundana was described from a single female from Loja Province, Ecuador. In facies (Razowski & Wojtusiak 2008: fig. 85) it is dissimilar to other New World species of *Eccopsis* and extremely similar to New World species of *Megalota* (Brown 2009:

figs. 1–24). The forewing pattern of the holotype of *Eccopsis eltundana* is similar to that of the holotype of *Megalota macrosocia* Brown, 2009, described from Pichincha Province, Ecuador, but the latter specimen is considerably more worn and the pattern elements are not clear. The female genitalia of *Eccopsis eltundana* has a small lobe immediately posterad of the ostium and a small signum comprised of a small cluster of short, blunt spines, both features of which are typical of many species in the *submicans* species-group of *Megalota* as defined by Brown (2009). On the basis of the facies and female genitalia, *eltundana* is transferred to *Megalota*.

Discussion. *Eccopsis* was proposed by Zeller, 1852, with *E. wahlbergiana* Zeller, 1852 (Type locality: South Africa) as the type species. Brown (2005) included 14 species in the genus, all from the Afrotropical region. Razowski & Wojtusiak (2008) described the first species of *Eccopsis* from the Neotropics (i.e., *E. eltundana* from the mountains of Ecuador), but that species is transferred to *Megalota* above. Razowski et al. (2008) followed with descriptions of two species of *Eccopsis* from the Galapagos Islands, Ecuador, and Vargas (2011) added another from Chile. Vargas (2011) and Gallego et al. (2012) provided information on the early stages of the New World species, which appear to be restricted to Fabaceae. The two new combinations proposed herein expand the known geographic distribution of *Eccopsis* in the New World to include Colombia, Ecuador (including the Galapagos Islands), Peru, and Chile—much of the western portion of South America.

Although New World species of *Eccopsis* (i.e., *galapagana, floreana, razowskii, arenacea*, and *oxynochla*) share many features with Old World members, they differ from Old World species in several characters. Afrotropical species of *Eccopsis* exhibit limited variation in facies (e.g., Aarvik 2004) in contrast to the highly variable forewing pattern of most Neotropical species. Males of Afrotropical species have a conspicuous "subbasal process of the valva" (sensu Brown 2009) which is lacking in New World species; and in most Afrotropical species the male genitalia are considerably more symmetrical compared to Neotropical species. Hence, it possible that Neotropical species currently assigned to *Eccopsis* require a new genus.

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NEW GEOGRAPHICAL RECORDS FOR THE THREATENED BUTTERFLY *ACTINOTE QUADRA* (LEPIDOPTERA: NYMPHALIDAE: HELICONIINAE)

Additional key words: Acraeini, Atlantic Rain Forest, conservation, montane butterflies, Serra da Mantiqueira.

Most species in the genus *Actinote* (Nymphalidae: Heliconiinae: Acraeini) are associated with forest edges, clearings and secondary vegetation, commonly found in high densities in disturbed habitats all over the Neotropics, especially in altitudes from 600 to 1200 m (Francini 1989, 1992; Francini & Freitas 2010; Paluch 2006). Some species, however, are rare, presenting small restricted populations associated with pristine and undisturbed habitats (Francini et al. 2004, 2005, 2011; Freitas et al. 2009, 2010; Freitas 2010). Two of them, namely *Actinote zikani* D'Almeida, 1951 (critically endangered) and *Actinote quadra* (Schaus, 1902) (vulnerable) (Fig. 1) are included in the most recent Brazilian red list of endangered fauna (Machado et al. 2008; Freitas & Brown 2008a,b) and in the 'National action Plan for conservation of Brazilian Lepidoptera' (a recent document containing revised and updated information on Brazilian endangered species; Freitas & Marini-Filho 2011). In the last two decades, efforts to increase the knowledge about Brazilian threatened butterflies resulted in valuable new information of about 10 butterfly species (see above, Kerpel et al. 2014, Freitas et al. 2014 and references therein). One of them is a detailed study of *A. quadra* (Freitas et al. 2009) that listed the 12 sites where this species has been recorded, as well as data on natural history and immature stages.

Since then, four new sites for *A. quadra* have been recorded by different research groups in Southeastern Brazil, increasing the number of localities where it occurs to 16 (Figure 2). The new sites (with number of adults collected and/or observed) were the following (see also Fig. 2): 1) Santo Antônio do Pinhal (22º49'26"S 45º37'37"W, 1200 m), São Paulo state, 4 males, 20.xi.2013, T. S. Souza leg. (Museu de Zoologia da Universidade Estadual de Campinas (ZUEC), Campinas, São Paulo, Brazil); 2) Serra do Rola Moça (20º3'29.90"S 44º00'6.20"W, 1474 m), Brumadinho, Minas Gerais state, 1 male, 29.xi.2012. S.P.A. Franco leg. (UFMG taxonomic collection, Belo Horizonte, Minas Gerais, Brazil); 3) Mina de Capanema

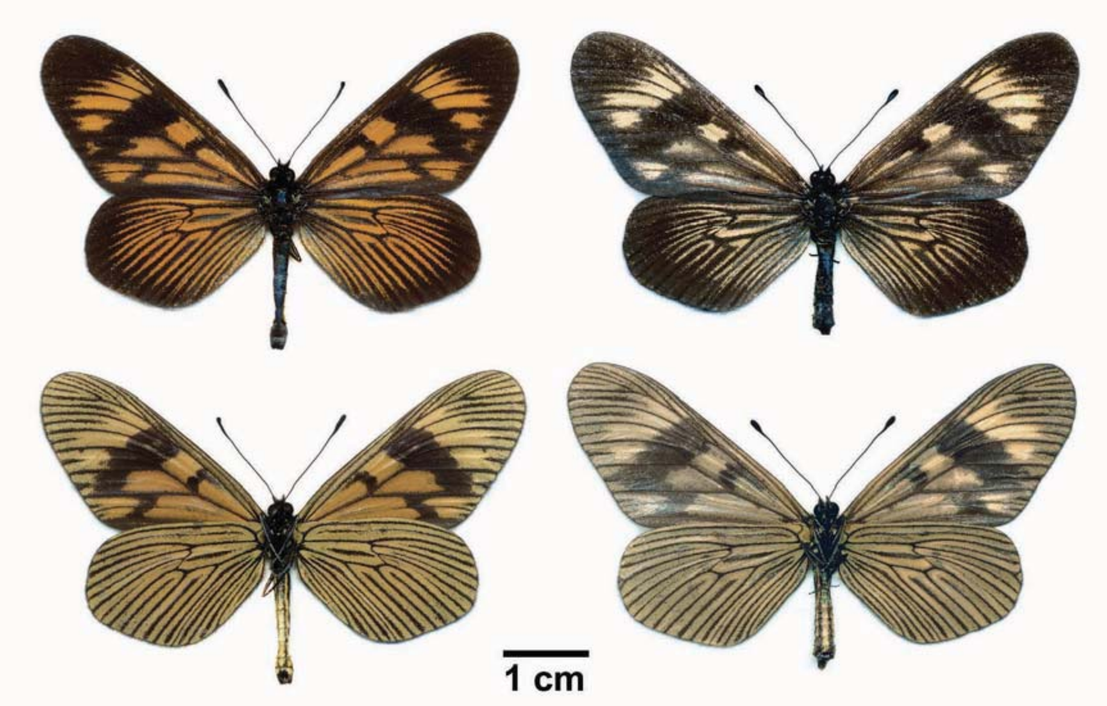

FIG. 1. Male (left) and female (right) of *Actinote quadra* from Parque Nacional do Caparaó, Minas Gerais, SE Brazil (dorsal above, ventral below). See text for additional information.

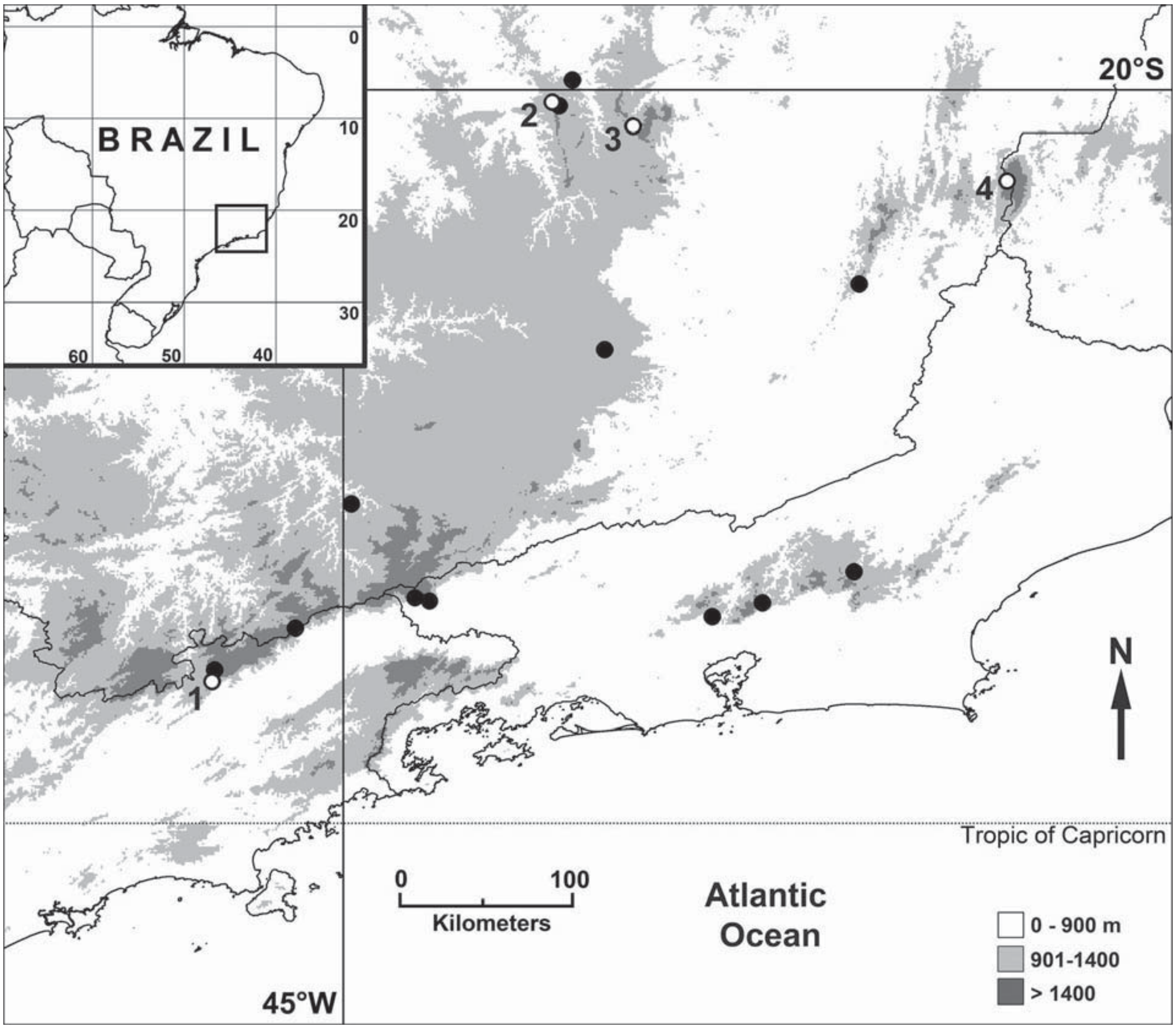

FIG. 2. Map showing the 14 known localities for *Actinote quadra* in Southeastern Brazil. The solid black circles represents the 12 previously known localities for *A. quadra* (see Freitas et al. 2009), and open circles represents the 4 new localities. **1.** Santo Antonio do Pinhal, São Paulo; **2.** Serra do Rola Moça, Brumadinho, Minas Gerais; **3.** Mina de Capanema, Santa Bárbara, Minas Gerais; **4.** Parque Nacional do Caparaó, Alto Caparaó, Minas Gerais.

(20º10'22.2"S 43º36'58.2"W, 1329 m), Santa Bárbara, Minas Gerais state, 6 males and 1 female, 3-5.iv.2011, V.A.A. Gomes & C.H.I. Costa leg, Mcn-inv 2094-2100 (Invertebrates Collection - Museu de Ciências Naturais, PUC-MG, Belo Horizonte, Minas Gerais, Brazil); additional males and females were observed flying around and perching on vegetation (ca. 2 m high); 4) Vale Verde (20º25'7"S 41º50'56"W, 1200–1300 m), Parque Nacional do Caparaó (Caparaó National Park), Alto Caparaó, Minas Gerais, 1 male and 1 female (Fig. 1), 9-15.xii.2011. A. V. L. Freitas, C. A. Iserhard & L. A. Kaminski, leg. (ZUEC); additional seven males and two females were observed flying high (ca. 3–5 meters above ground).

All four new sites for *A. quadra* are above 1200 m a.s.l., and agree with the previous altitudinal pattern recorded for this species (above 800 m, Freitas et al. 2009). Two of these new sites (sites 1 and 2) are very close to previously known sites. They were considered new sites, however, because in both cases the new site is in a different slope of the mountain range, being isolated from the neighbor site by low valleys where the species didn't occur (distribution is not continuous). The other two sites (sites 3 and 4), however, characterize new distributional data for this species, with Caparaó (site 4) representing an expansion in *A. quadra* distribution of about 100 km northeast from its previously known limit (the region of Rosário de

Limeira, Minas Gerais, see Freitas et al. 2009), and also one additional conservation unity where this species occurs. The presence of this species in the Caparaó National Park also reinforces the importance of this place as the northernmost refuge for all montane species occurring in the Serra da Mantiqueira mountain range, as recently confirmed for other butterfly species (Freitas et al. 2004 and unpublished results). The improvement of distributional data is required for an adequate assessment of the real conservation status of a threatened species, and the detection of additional populations of threatened butterfly species, both inside and outside conservation unities, is a priority in Brazil (Freitas & Marini-Filho 2011). The present findings are very encouraging since this information suggests that additional populations of *A. quadra* might occur is several other localities with similar conditions, including the full region of Serra da Mantiqueira and montane forests of Minas Gerais. The use of modelling to predict the potential distribution of this species may corroborate this idea, configuring a much more optimistic scenario for the conservation of *A. quadra.*

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FIRST RECORD OF AN EXOTIC HOST PLANT FOR THE OLIGOPHAGOUS MOTH *MACARIA MIRTHAE* (GEOMETRIDAE) IN THE COASTAL VALLEYS OF THE NORTHERN CHILEAN ATACAMA DESERT

Additional key words: *Acacia macracantha*, folivorous, host shift, *Leucaena leucocephala*

Although many Lepidoptera species are highly specialized in the use of their hosts, some species are able to colonize exotic plants (Graves & Shapiro 2003, Bowers & Richardson 2013). In butterflies, this capacity may be predicted by the geographic range and the native diet breadth (Jahner et al. 2011). Native host range has also been mentioned as an important factor correlating with the use of exotic plants by geometrid moths (Fraser & Lawton 1994).

Host shifts have been acknowledged as extremely important for the survival of the populations of native butterflies in some human-modified environments (Shapiro 2002, Graves & Shapiro 2003, Bowers & Schmitt 2013). Furthermore, host shifts may have a number of effects on phytophagous populations (Bowers & Richardson 2013). The establishment of these new associations could be interesting from an evolutionary perspective, as they open an unexpected window for the understanding of the ecology and evolution of phytophagous insects (Tuda et al. 2014). Additionally, host shifts may have unexpected consequences at higher trophic levels, affecting, for instance, the behavior and physiology of parasitoids (Collatz & Dorn 2013).

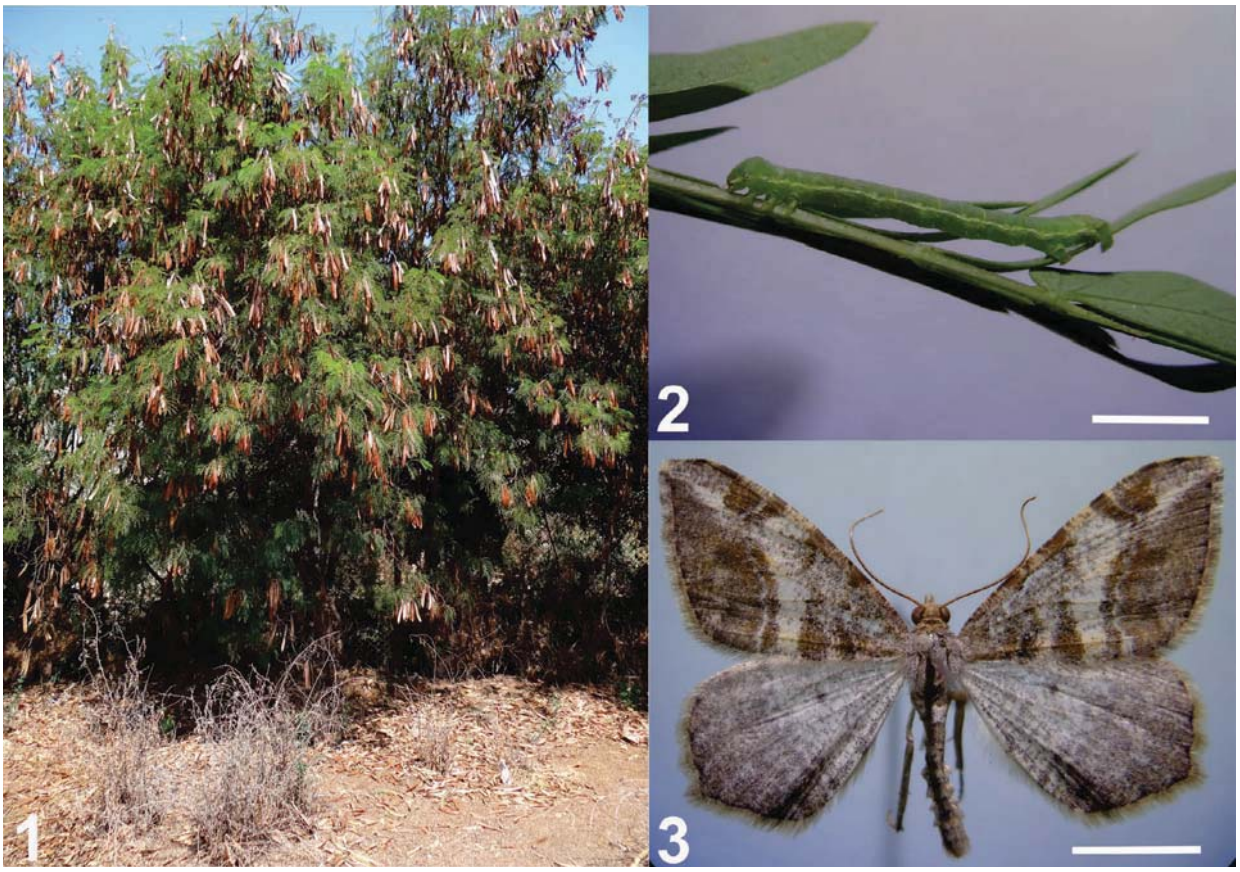
Leucaena leucocephala (Fabaceae) (Fig. 1) is a tree species native in Central America the distributional range of which has been greatly expanded around the world mostly due to its cultivation (Rengsirikul et al. 2011, GISD 2014). This plant has become an invader in many localities where it has been introduced as a cultivar, and its presence may have severe effects on the native plant communities (Yoshida & Oka 2004). As a result, *L. leucocephala* has been listed among the world's 100 worst invasive species (Lowe et al. 2000). In some places, however, *L. leucocephala* has been classified only as a ruderal plant, not reaching the status of invasive (Costa & Durigan 2010).

The coastal valleys of the northern Chilean Atacama desert are characterized by a high level of human disturbance, mostly due to agricultural activities that have resulted in habitat loss. As a consequence, the original habitat has been turned into farmland and native vegetation has been widely replaced by exotic cultivars and introduced plants (Luebert & Pliscoff 2006). Within this context, some native lepidopteran species have been found to colonize adventive plants, with a few examples reported for butterflies (Vargas 2013) and moths (Vargas 2010, Vargas et al. 2013).

The Geometridae (Lepidoptera) is one of the most diverse moth families (Scoble 1995). Their larvae are generally phytophagous, and may be very important components of folivorous assemblages (Scoble 1995, Marconato et al. 2008, Bodner et al. 2010). *Macaria mirthae* Vargas, Parra & Hausmann, 2005 (Fig. 2-3) is a geometrid moth native to the northern Chilean Atacama Desert, where its oligophagous folivorous larvae have been found to be associated to three native Fabaceae species: *Acacia macracantha*, *Geoffroea decorticans* and *Prosopis tamarugo*. These were the only host plants recorded for this moth until now (Vargas et al. 2005).

In January 2013 six geometrid larvae were collected from the exotic *L. leucocephala* in the Azapa valley (18° 31' S, 70° 10' W), northern Chilean Atacama Desert. The larvae were brought to the laboratory in plastic containers. Additional leaves of this tree were provided each day until the last instar larvae completed their feeding activity, about seven days after collection. Pupae were periodically observed in order to verify the emergence of adults. Three males and three females were obtained about fourteen days after pupation. Based on the original description provided by Vargas et al. (2005), we identified the specimens as *M. mirthae*. Subsequently, five males and six females were obtained between March and September 2013 following the same procedure.

This is the first mention of *L. leucocephala* as a host plant for *M. mirthae*, which coincides with the previously mentioned association of this moth with host plants of the family Fabaceae. In the same way, this report represents the first record of an exotic host plant for *M. mirthae*, adding one more record of an association of a native moth species with an exotic host plant in the coastal valleys of the northern Chilean Atacama Desert (Vargas 2010, 2013, Vargas et al. 2013). Our finding is coincident with observations made for some other Neotropical species of Geometridae. Host shifts to exotic plants have already been reported for



Figs. 1–3. Components of the new plant-phytophagous association in the northern Chilean Atacama Desert. **1.** The exotic host plant *Leucaena leucocephala* in a human-modified habitat in the Azapa Valley. **2.** Last instar larva of *Macaria mirthae* feeding on *Leucaena leucocephala*. **3.** Male adult of *Macaria mirthae* reared from a larva on *Leucaena leucocephala*. Scale bars = 5.0 mm.

Iridopsis herse (Schaus, 1912) and *Macaria abydata* (Guenée, 1858), whose larvae have been associated with *Glycine max* in Honduras and Brazil, respectively (Lourenção et al. 1980, Passoa 1983). Furthermore, *Thyrinteina arnobia* (Stoll, 1782) has been described as a defoliator of Eucalyptus in Brazil (Oliveira et al. 2005).

From an ecological perspective, an adequate knowledge of the larval host plant range of *M. mirthae* is extremely important in the study site, as the use of additional exotic hosts by *M. mirthae* could be an underlying factor shaping other ecological interactions in which this geometrid moth is involved (Collatz & Dorn 2013). Interestingly, besides the obvious ecological importance of *M. mirthae* due to the larval folivory on its host plants, its larvae have also been reported as an important prey item for the potter wasp *Hypodynerus andeus* (Packard, 1869) (Hymenoptera: Vespidae: Eumeninae) in the coastal valleys of the Atacama Desert (Méndez-Abarca et al. 2012). Additional studies should be performed to determine the importance of the association between *M. mirthae* and *L. leucocephala* in terms of the interaction between *M. mirthae* larvae and the potter wasp.

On the other hand, consequences of this new association could not be solely restricted to ecological interactions, but they should also involve a number of other life history traits of *M. mirthae* (Vanbergen et al. 2003, Oliveira et al. 2005). For instance, Jorge et al. (2011) and Mozzafarian et al. (2007) have shown wing phenotypic variation to be host-dependent for butterflies and moths, respectively. It should be interesting, then, to study the effects of the host shift here reported on the biology and evolution of this oligophagous phytophagous moth in the arid landscapes of northern Chile.

Voucher specimens will be deposited in the "Museo Nacional de Historia Natural" (MNNC), Santiago, Chile, and in the "Colección Entomológica de la Universidad de Tarapacá" (IDEA), Arica, Chile.

Material examined. CHILE, Arica. Three males and three females: Azapa, Arica, Chile, February 2013, H. A. Vargas coll., reared from larvae collected on

Leucaena leucocephala, January 2013 (MNNC); four males and five females: Azapa, Arica, Chile, March 2013, H. A. Vargas coll., reared from larvae collected on *Leucaena leucocephala*, February 2013 (IDEA); one male and one female: Azapa, Arica, Chile, September 2013, H. A. Vargas coll., reared from larvae collected on *Leucaena leucocephala*, August 2013 (MNNC).

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GENERAL NOTES

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NEW HOST AND DISTRIBUTIONAL RECORD FOR *DICHRORAMPHA INCANANA* (CLEMENS, 1860) (TORTRICIDAE: OLETHREUTINAE)

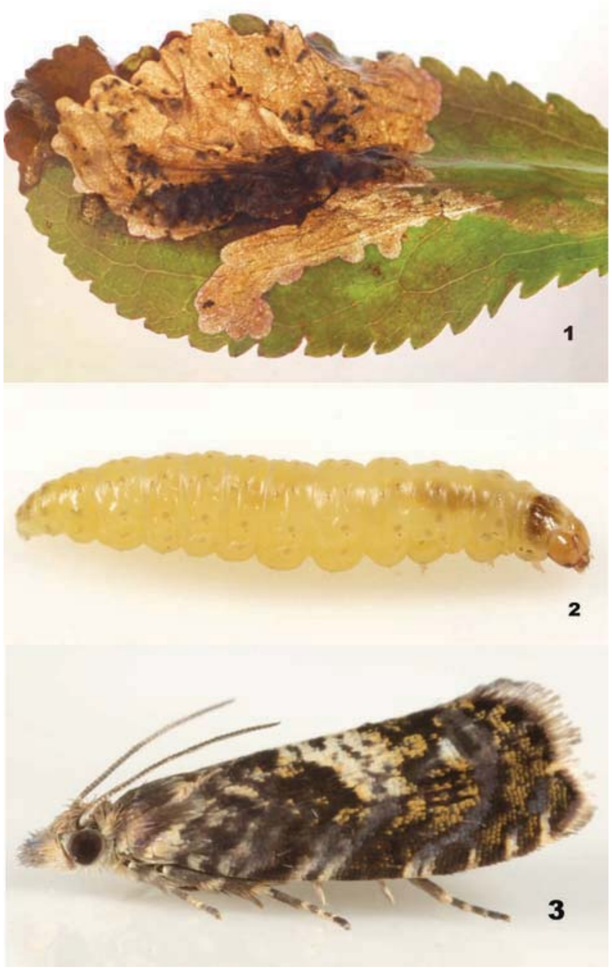
Additional key words: leaf mining, *Packera obovata*, Asteraceae, Senecioneae

The known larvae of moths in the genus *Dichrorampha* Guenée (Tortricidae) are mostly root borers in Asteraceae (Heinrich 1926; Brown et al. 2008). Two Florida species are clear exceptions among the North American fauna, feeding instead on flowers of *Manilkara* Adans. (Sapotaceae) (Heppner 1981). In addition, *D. radicicolana* Walsingham feeds in roots of a plant questionably identified as *Scrophularia* L. (Scrophulariaceae), and *D. leopardana* (Busck) is said to pupate within the rolled leaf of *Verbesina* L. (Asteraceae) but its feeding habits are unclear (Heinrich 1926).

Dichrorampha incanana (Clemens) is the only known leafminer in this genus, and its larval habits were only recently discovered. Priest (2008) found larvae mining leaves of *Arnoglossum atriplicifolium* (L.) H. Rob. (Asteraceae) in Michigan from late August to late September. His larval collections yielded an adult female in early October and a male the following spring. Because *D. incanana* adults had previously been collected in mid-July in Michigan and Wisconsin (Miller 1987), he suspected that this species is bivoltine in the northern US.

On 5 April 2012 in Canaan, Connecticut, I found full-depth blotch mines in two basal leaves of round-leaved ragwort (Asteraceae: *Packera obovata* (Muhl. ex Willd.) W.A. Weber & Á. Löve) (Fig. 1). I placed the leaves in a sealed plastic bag. On 8 April, one 7 mm-long larva had emerged and spun a flat, thin, oval cocoon of white silk on one side of the bag. On 10 April, it abandoned the cocoon and was found wandering in the bag (Fig. 2). I transferred it, along with the still-occupied leaf, to a small jar containing a damp, crumpled paper towel resting on a layer of soil. The second, somewhat smaller larva soon emerged and spun its cocoon in the paper. The first larva likewise showed no interest in burrowing and entered the crumpled paper within a few hours. Close examination of photographs revealed parasitoid oviposition scars in this larva's thorax.

On 3 June, a female adult moth appeared in the jar (Fig. 3), leaving its pupal exuviae protruding from the cocoon. No parasitoids were recovered from the first larva. J. W. Brown dissected the moth and reported that it was identical with *D. incanana* specimens in the National Collection, where it is now deposited. This Connecticut record, along with those from Michigan and Wisconsin noted above, expands the range for this species reported by Gilligan et al. (2008). They stated that it occurs from Pennsylvania to Ohio, south to North Carolina and Kentucky, noting that little is known about its distribution because it is poorly represented in collections.



FIGS. 1–3. *Dichrorampha incanana*. **1**) Completed mine of in a *Packera obovata* leaf; **2**) Mature larva; **3**) Reared adult.

This rearing would seem to confirm that *D. incanana* has at least two generations per year in northern states. It also indicates that this moth is oligophagous, suggesting that additional hosts might be sought among other genera of the tribe Senecioneae. *Phyllocnistis* *insignis* Frey & Boll (Gracillariidae), the other moth Priest (2008) found mining leaves of *Arnoglossum atriplicifolium*, was also found mining *Packera obovata* leaves when I collected the *D. incanana* larvae. I have also reared *P. insignis* from *Erechtites hieraciifolia* (L.) Raf. ex DC., *Petasites japonicus* (Siebold & Zucc.) Maxim., and *Tussilago farfara* L., so it is conceivable that some of these plants are likewise suitable hosts for this little-known tortricid.

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