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Cover illustration: Decoupled mating pair of a new species of *Atrytonopsis* (Hesperiidae) collected on Bear Island, Onslow County, North Carolina, 25 April 1985, by John M. Burns. Forewing apex more pointed in the male than in the female; hindwing facies more striking ventrally than dorsally in both sexes. Photos by Karie Darrow. See paper on page 275.

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EDITOR'S NOTE

The Lepidopterists' Society occasionally publishes longer, topical manuscripts in the serial publication ***Memoirs of the Lepidopterists' Society***. Beginning in January 2016, I will be assuming editorial responsibilities for ***Memoirs*** that involve detailed treatment of ecology, evolution, or systematics of lepidopteran taxa. Kelly Richers will continue to serve as the lead editor for ***Memoirs*** that involve historical treatment of the Society, the study of Lepidoptera, techniques for studying Lepidoptera. Manuscripts for any submission for the ***Memoirs*** series should follow the standard instructions for authors used by the ***Journal of the Lepidopterists' Society.*** Those instructions may be found at http://www.lepsoc.org/journal.php. If you are considering preparing a manuscript for the ***Memoirs*** series, please contact me for additional information (keith.summerville@drake.edu).

Keith S. Summerville, Editor
Journal of the Lepidopterists' Society

Detail from a wall painting in the tomb of Nebamun (British Museum). Photo by Monica Bowen (albertis-window.com), reproduced with permission. See article in this issue.

BUTTERFLIES OF ANCIENT EGYPT

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ABSTRACT. A review of butterflies depicted in ancient Egyptian tomb scenes and other artifacts dating from the predynastic period (c. 3000 BCE) until the end of the pharaonic era (c. 100 BCE) reveals a wide spectrum of stylistic changes over time. A cladistic analysis shows relative consistency of style during the Old Kingdom period, copying of old styles during the Middle Kingdom period, and a deviation from tradition during the New Kingdom period. The utility of a cladistic approach in assigning dates and localities to ancient Egyptian artifacts with unknown origins is demonstrated. We discuss lepidopteran symbolism in ancient Egypt, and investigate how some of these depictions may highlight historical shifts in species ranges since pharaonic times.

Additional key words: Egyptology, Lepidoptera, Iconography, Cladistic, Egyptian art

Butterflies have been represented in art since the Neolithic period (c. 5000 BC) (Schimitscheck 1978). Although their presence in antiquity is also significant in Minoan and Mycenaean art (Evans 1928, Brentjes 1964, Parent 1987), the use of butterflies, alongside other insects, by ancient Egyptian artists as a standard decorative element in tomb imagery over three millennia gave them a unique prominence that is unparalleled in art history. Several insects were revered by the Egyptians, represented deities, or otherwise had deep symbolic meaning (e.g. scarab beetles, locusts, honey bees, mosquitoes, mantids, fleas, etc.) (Ward 1994). However, the role of butterflies in Egyptian funerary contexts, if any, remains disputed (Fleuren 2010).

Ancient Egyptian culture, which developed over three thousand years, is usually divided into several major periods: the Predynastic era (Neolithic–3100 BCE), Early Dynastic period (3100–2686 BCE, Dynasties I–II), Old Kingdom period (2686–2181 BCE, Dynasties III–VI), Middle Kingdom period (2055–1650 BCE, Dynasties XI–XIII), and the New Kingdom period (1550–1069 BCE, Dynasties XVIII–XX). These were separated by intermediate periods marked by unrest. The Late Period (664–332 BCE, Dynasties XXV-XXXI) followed by Greek and Roman conquests marked the end of the pharaonic era (van de Mieroop 2011).

The significance of the afterlife for the ancient Egyptians is well documented (Kanawati 2002). The poor were interred in simple graves, but the country's elite, such as the king, noblemen, and high government officials, invested in elaborate tombs in which to spend eternity. Despite the development of different construction methods over time, every tomb (whether a free-standing structure or cut into the rock face) comprised three essential elements: an offering chapel or mortuary temple, a tomb shaft, and a subterranean burial chamber (Arnold 2003). The walls of the chapel, and occasionally those of the burial chamber, were usually decorated. During the Old Kingdom, the decoration was rendered in painted bas-relief in which the background around intricately carved figures was removed to create an embossed effect; sunken relief, in which figures were chiseled into the wall surface, was also used throughout the pharaonic era. In later periods, however, tomb scenes were painted directly on to prepared plaster walls. Only six colors were used commonly: red, green, blue, yellow, white and black, each with its own symbolic meaning. These pigments were prepared from natural substances such as red and yellow ochre, powdered malachite, carbon black, and gypsum (Robins 1997).

The stability of Egyptian life and culture resulted in a form of art that was characterized by a highly conservative adherence to rules favoring order and form over creativity and artistic expression. Strict representational guidelines determined how human figures could be depicted: sizes, poses and colors were all dictated by prescribed formulae that were followed for generations. Hence ancient Egyptian sculptors and painters were not artists in the modern sense, but rather paid and trained labor, working anonymously as part of a team of skilled craftsmen who were commissioned by the elite to build and decorate their tombs. These teams normally included stonemasons, plasterers, draftsmen, sculptors, carpenters, painters and scribes. In the case of rock-cut tombs, for example, stonemasons would first
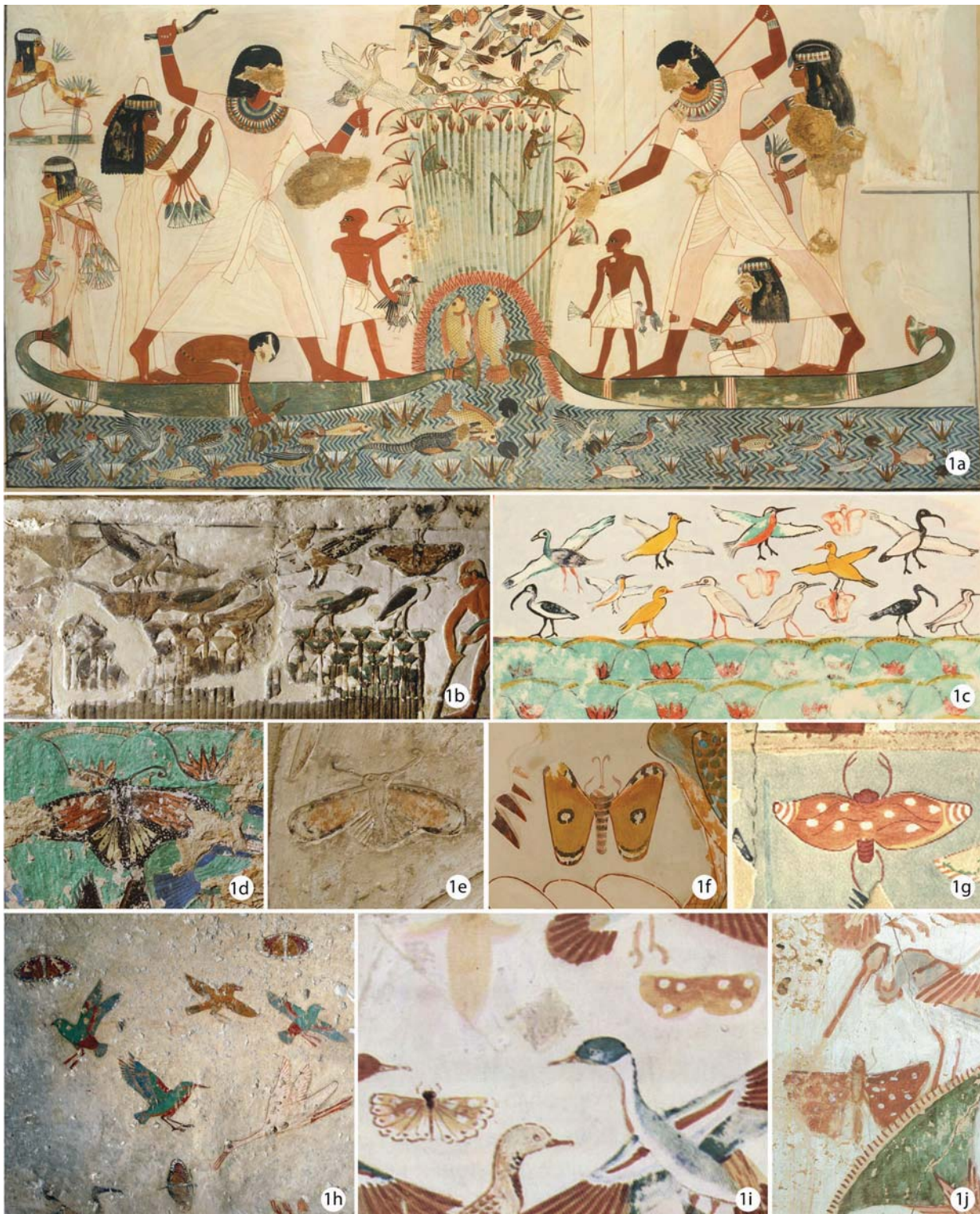
Fig. 1. Examples of marsh scenes and butterflies from the walls of Egyptian tombs. (**a**) Menna [70], (**b**) Nefer/Kahay [7]; (**c**) Kaemankh [34]; (**d**) Merefnebef [36]; (**e**) Nikauisesi [42]; (**f**) Puyemre [66]; (**g**) Amenemhat (excluded); (**h**) Khnumhotep II [63]; (**i**) Nakht [71]; (**j**) Horemheb [68]. See Table 1 for publication details. Photo credits: Figs. **1a**: Davies 1936: plate 54; **1b**: Lashien 2013; **1c**: Junker 1940: plate 11; **1d**: Karol Mysliwiec, © Polish-Egyptian Archaeological Mission in Saqqara, reproduced with permission; **1e**: kairoinfo4u on Flickr, CC license; **1f**: Metropolitan Museum of Art Gallery Images, in public domain; **1g**: Davies 1936: plate 19; **1h**: Australian Centre for Egyptology, reproduced with permission; **1i**: Mekhitarian 1978: 71; **1j**: Brack & Brack 1980: plate 22.

excavate the chapel rooms and tomb shaft. Plasterers then covered the uneven walls with a layer of gypsum and whitewash. Once the walls were smoothed and polished, they were turned over to the draftsmen who sketched out proposed designs in red. The master draftsman would then go over these designs in black ink, to ensure accuracy. Finally, the painters would add color with brushes made of a twig or reed with the fibers teased out.

Although religious imagery was introduced during the New Kingdom period, so-called "scenes of daily life" dominated the decoration throughout the pharaonic era. These images, arranged in horizontal panels (or registers), appear to show various activities on the tomb-owners' estates, such as men and women baking and brewing, plowing, harvesting and threshing grain, herdsmen at work in pastures caring for cattle, carpenters, potters and jewelers, social activities such as games, music and banqueting, and offering bearers bringing produce to the deceased owner at his funerary table. In "marsh scenes", the tomb-owner was shown hunting waterfowl and spearing fish on the Nile River (Fig. 1). These images reliably depict dense thickets of papyrus amongst which many bird species nest and small carnivores lurk, such as common genets (*Genetta genetta*) and Egyptian mongooses (*Herpestes ichneumon*). In the waters below swim fish, hippopotami, and crocodiles, while in the skies above fly waterfowl and insects. Butterflies are frequently found in such scenes, both at rest and flying above and within the papyrus thicket.

The purpose of these scenes, which conform to specific themes that are repeated from tomb to tomb, has been much debated. The images are believed by many to have had a magical function, to help sustain the spirit of the deceased in the afterlife (e.g. Smith 1978), but other theories view the scenes as indicators of social status (e.g. Moreno-Garcia 2006) or having a mythological meaning that allowed the deceased to partake in a broader cosmic drama (e.g. Altenmüller 1999). Whatever their function, the detailed wall paintings provide valuable insights into many aspects of ancient Egyptian life, including the natural environment.

Despite the strict rules governing representation in ancient Egypt, significant diversity and variation in style of lepidopteran imagery over time is evident (Keimer 1934, Verhoeven 1975, Evans 2010, Fleuren 2010). Here we attempt to shed light on the process and direction of this art form with a cladistic analysis, using the most comprehensive compilation to date of butterfly depictions in ancient Egyptian art. We also examine the possibility of inferring dates for artifacts of unknown origin through this approach, and investigate potential shifts in historical ranges of butterflies that no longer occur in Egypt today.

Materials and Methods

A list of Old Kingdom tombs containing scenes with butterflies (Harpur 1987) was used as a starting point, and structures from earlier or later time periods with similar scenes or recent discoveries were added following examination of published tomb reports. Artifacts such as amulets, pendants, jewelry, statuettes, etc. with butterfly themes or imagery were also included (Fig. 2). The final list (Table 1) contains 82 exemplars derived from a total of 194 depictions of butterflies from 20 different locations throughout the country (Fig. 3). It is likely, however, that further investigation will bring additional examples to light.

High quality images or drawings were sought for every entry in the list, mainly from tomb excavation reports and museum catalogues, but also from other publications, books, websites, Egyptological databases, and occasionally amateur photography (e.g. Flickr). In many cases the only available images were original line drawings made by the Egyptologists who first documented the tombs. We cannot exclude inaccuracies that may have been introduced in these works due to lack of attention to entomological detail; for example, the line drawings by Mohr (1943) from the mastaba of Hetepherakhti[11] (now in Leiden) were found to be highly inaccurate (Prof. Dr. Maarten Raven, pers. comm.).

Composite plates of obtained butterfly images were compiled in Adobe Photoshop CS.5 and subsequently re-drawn using India ink and a Rapidograph pen with 0.25 and 0.5 mm thickness on Mylar drafting sheets (Fig. 4). Shading was accomplished using Letraset Letratone sheets in three different intensities (LT15, LT25 and LT29). Where more than one butterfly was present in a tomb scene, or multiple objects of the same kind were stored in a museum, the best preserved types (a total of 82 exemplars) were selected for illustration and inclusion in the cladistic analysis.

Each image was also assigned a date. The dating of Egyptian tombs is based largely on inscriptions, the type of architecture, and stylistic elements in the decoration. Nevertheless, the dates for many structures, especially for the Old Kingdom period, are highly contentious. For this project, tomb dates were obtained from Yvonne Harpur's (1987, 2006) careful analysis and supplemented by re-assessments by later scholars (e.g. Swinton 2014 for Old Kingdom tombs). Standard dating terminology also follows Harpur (1987), with dynasties given in Roman numerals followed by the order of reigning king within the dynasty, and if known, approximate period

FIG. 2. Examples of butterfly artifacts: (**a**) Hetepheres bracelets [2], (**b**) a hippopotamus statuette [57f], (**c**) blue faience amulets [60], (**d**) Senworset amulet [62]; (**e**) Cleveland Museum inlay [76]. See Table 1 for publication details. **Photo Credits: 2a**: Egyptian museum in Cairo, in public domain; **2b**: © Rhode Island School of Design, photo by Linda Evans; **2c**: Arnold 1995; **2d**: Metropolitan Museum of Art Gallery Images, in public domain; **2e**: © Cleveland Museum of Art, reproduced with permission.

(Early, Middle or Late) during his reign (e.g. "XVIII.6L" indicates the later years of the reign of the 6th king of Dynasty XVIII). For tombs or artifacts where the dating is still disputed, a wider time period was considered.

During this study the first author examined a butterfly relief in the Los Angeles County Museum of Arts (LACMA #M.80.199.137) for which the provenance is unknown (Fig. 5). The artifact is part of a collection acquired by the museum from a private collector. To infer an approximate date or locality for this relief, it was also included in our analysis.

A set of 32 characters was selected for cladistic analysis, of which 16 were binary and 16 were multistate (Appendix 1). The final dataset included one outgroup and 81 ingroup taxa. Characters were scored using observed character states (Appendix 2). Dates were excluded from the analysis and subsequently plotted on the cladogram. The data matrix was then subjected to a cladistic analysis using the heuristic (add and re-arrange) modules implemented in Mesquite 2.75 (Maddison & Maddison 2011), with the NNI re-arranger (maxtrees=500) and under the Parsimony criterion with the "minimize Tree Value Using Character Matrix" option selected. A majority-rule consensus tree of 500 equally parsimonious trees with a total length of 407 steps was obtained (Fig. 10). Percent consensus frequencies for each node were calculated and plotted on the tree. An ostensible butterfly incised on a predynastic clay bowl [1] (see Table 1) was used to root the tree. Each branch was then colorized based on the main historical period.

Items excluded from the analysis. Several examples considered by past researchers to be possible lepidopterans were excluded from our analysis due to their dubious identity. These were (Fig. 6; Table 2):

a)   variants of an ideogram used in the word for "open" (s3š) (as found in surviving funerary inscriptions known as the Pyramid Texts), suggested by Keimer (1934) to have been modeled after a butterfly with open wings (Fig. 6A). However, the stylized nature of their representation and their visual conflation with bovine symbolism does not support such a notion;

b)   butterfly-like images on predynastic vases (von Bissing 1913) that have been dismissed as vegetation (Keimer 1934) (Fig. 6B);

c)   a kite-like object in the tomb of Ankhmahor: Seshi (Saqqara) (Fig. 6C);

d)   a Middle Kingdom faience plaque found at Lisht (Cairo Museum), resembling a rudimentary insect and suggested by Keimer (1934) to be a butterfly (Fig. 6D);

e)   a Dynasty XII butterfly pendant found in the tomb of Princess Khnumet at Dahshur, believed by many scholars to be of foreign origin due to the granulation method used in its construction (Lilyquist 1993) (Fig. 6E);

f)   a highly stylized insect with spiral wings on a Dynasty XVII–XVIII steatite amulet from Luxor, now in Cairo Agriculture Museum (Fig. 6F);

g)   two insects from the tomb of Amenemhat (TT82) with bifurcated forelegs, no antennae, and oddly shaped heads and abdomens that do not support their

identification as moths or butterflies (Davies 1936; Fleuren 2010), but most likely cicadas (Hemiptera) or ladybugs (Coleoptera: Coccinellidae) (Fig. 6G);

h)   an unfinished image from the tomb of Menkheperraseneb (TT79) (Fig. 6H);

i)   a flying insect from an anonymous Dynasty XVIII tomb in Thebes (Raven 2000) (Fig. 6I);

j)   an insect from the tomb of Djehutymes (TT32), with narrow forewings and wide hind wings that suggest it is most likely a locust (Fig. 6J).

Results

Location and frequency. The earliest unambiguous examples of butterflies appear on jewelry dating to Dynasty IV from the site of Giza (Fig. 2a), however most of the surviving images examined in our study were located in the Old Kingdom necropolis at Saqqara and the Theban burial grounds of the New Kingdom period (Table 1). Provincial sites overall contained fewer examples.

Butterfly imagery was found predominantly in painted or carved wall decorations in royal mortuary complexes (e.g. Userkaf [3] and Niuserre [6]) and private tombs, and among these the most common context was in or near marsh scenes. A small number were depicted in other locations however (e.g. in bird-catching (Neferherenptah [21]), clapnet (Ankhmahor: Seshi [41]), and hippopotamus hunt scenes (Hemre: Isi [55]). In the tomb of Ankhmahor: Seshi [41], a butterfly is perched on a bundle of reeds among a group of men pulling the rope of a clapnet (Kanawati & Hassan 1997), while in another rare instance, one of the butterflies in the tomb of Mehu[46] is hunted by an ibis (Fig. 7). The number of butterflies per tomb varied greatly, with most tombs having one or two instances, but some displaying as many as 11 (Hesi [40]) or 13 (Mehu [46]).

In the Middle Kingdom period, butterflies began to appear on a new element of funerary furniture: hippopotamus statuettes [57], which were produced in blue faience and decorated with marshland motifs. Butterflies also occurred in non-funerary decoration for the first time during the New Kingdom period, painted on a ceiling in the palace of Amenhotep III [73] at Malqata, as well as on a floor at Tell el-Amarna [74].

Representations. Butterflies were generally depicted in their most conventional form and showing their most characteristic features. They are thus often pictured with their wings open, although from late Dynasty V (i.e. Ptahhotep II: Thefi [26] and Nebet [28]) they also began to appear in a lateral pose and with their wings closed. Among the images examined, 11 butterflies were represented laterally, and in a few cases (e.g. Senbi [61], Khnumhotep II [63] and Ukhhotep [64]), they
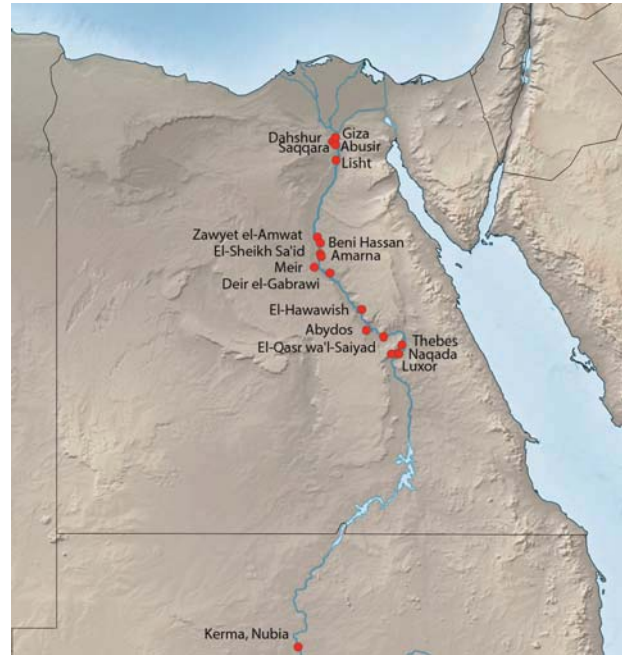
Fig. 3. Location of tombs and artifacts examined in this study.

were clearly drawn ventrally. Apart from once exception (that of Neferseshemptah/Sekhentiu [15]; see below), all butterflies prior to late Dynasty V were represented with just two wings, while thereafter anatomically correct details were added to indicate four wings, confirming an earlier observation made by Evans (2010: 51) and Fleuren (2010: 62-63) that a stylistic change occurred during the Dynasty V.9 reign of king Unas. In later periods (especially during the New Kingdom), butterflies were again often represented with two wings.

Identification. The present butterfly fauna of Egypt is well studied and to date 61 species of butterflies are known to occur (Larsen 1990, Gilbert & Zalat 2007). The vast majority of lepidopteran depictions examined in our study, however, were too stylized to be scientifically identifiable. Many images showed exaggerated morphology or unusual wing coloration, suggesting that zoological accuracy was not always of primary concern for some artists. Furthermore, often no trace of the original paint remained and the mere outline did not always provide helpful clues to identify the insects.

Among the images studied only a handful could be attributed with any certainty to modern-day butterflies (Table 1). These are spread across the Old, Middle and New Kingdom periods and were from different locations. The oldest identifiable depiction was found in the tomb of Nefer/Kahay [7] (Fig. 1b). Three butterflies appear in this wall scene, carved in bas-relief and painted, only one of which is well preserved. Both its
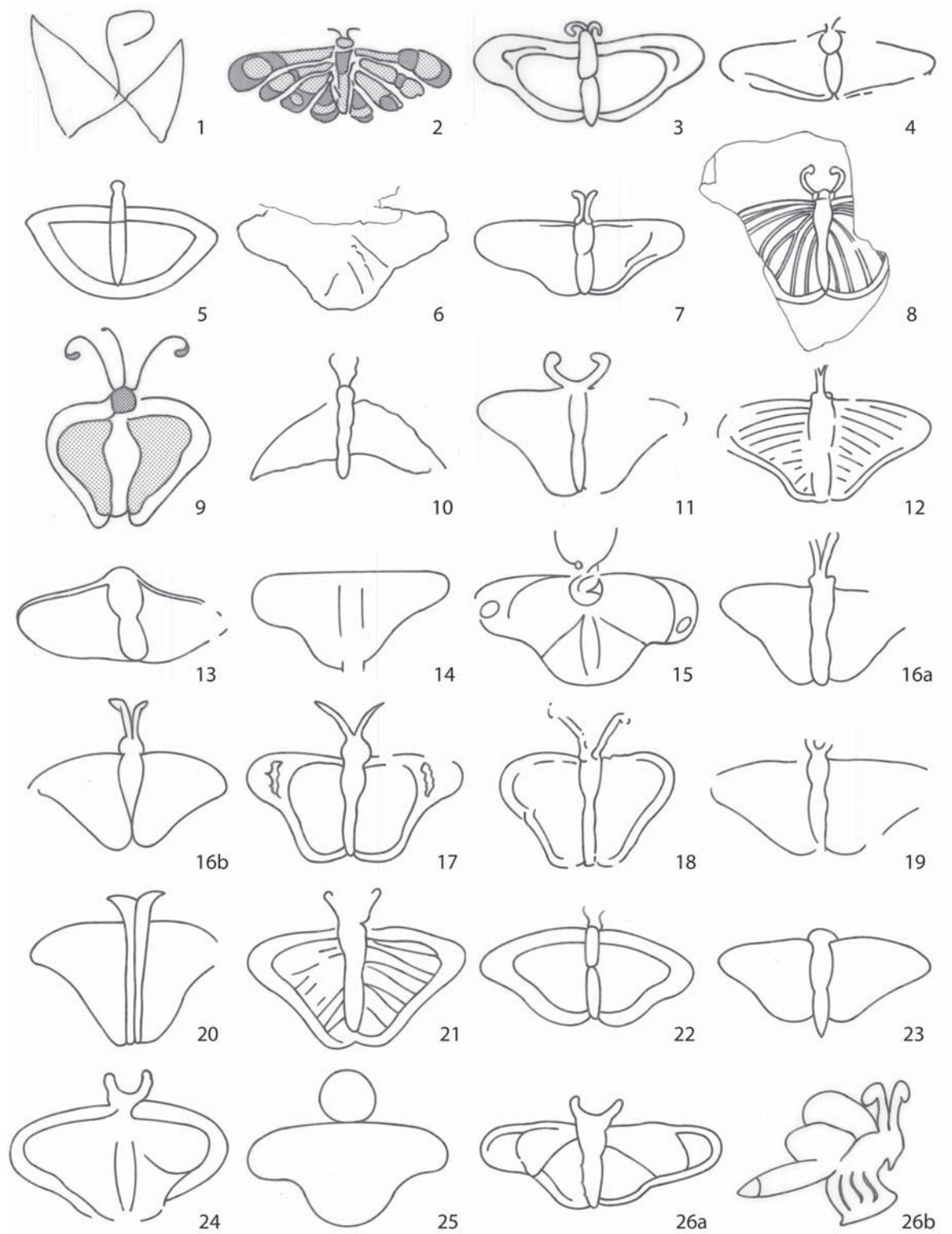
FIG. 4. Line drawings of selected butterflies from ancient Egyptian artifacts and wall scenes examined in this study. For corresponding information, see Table 1.

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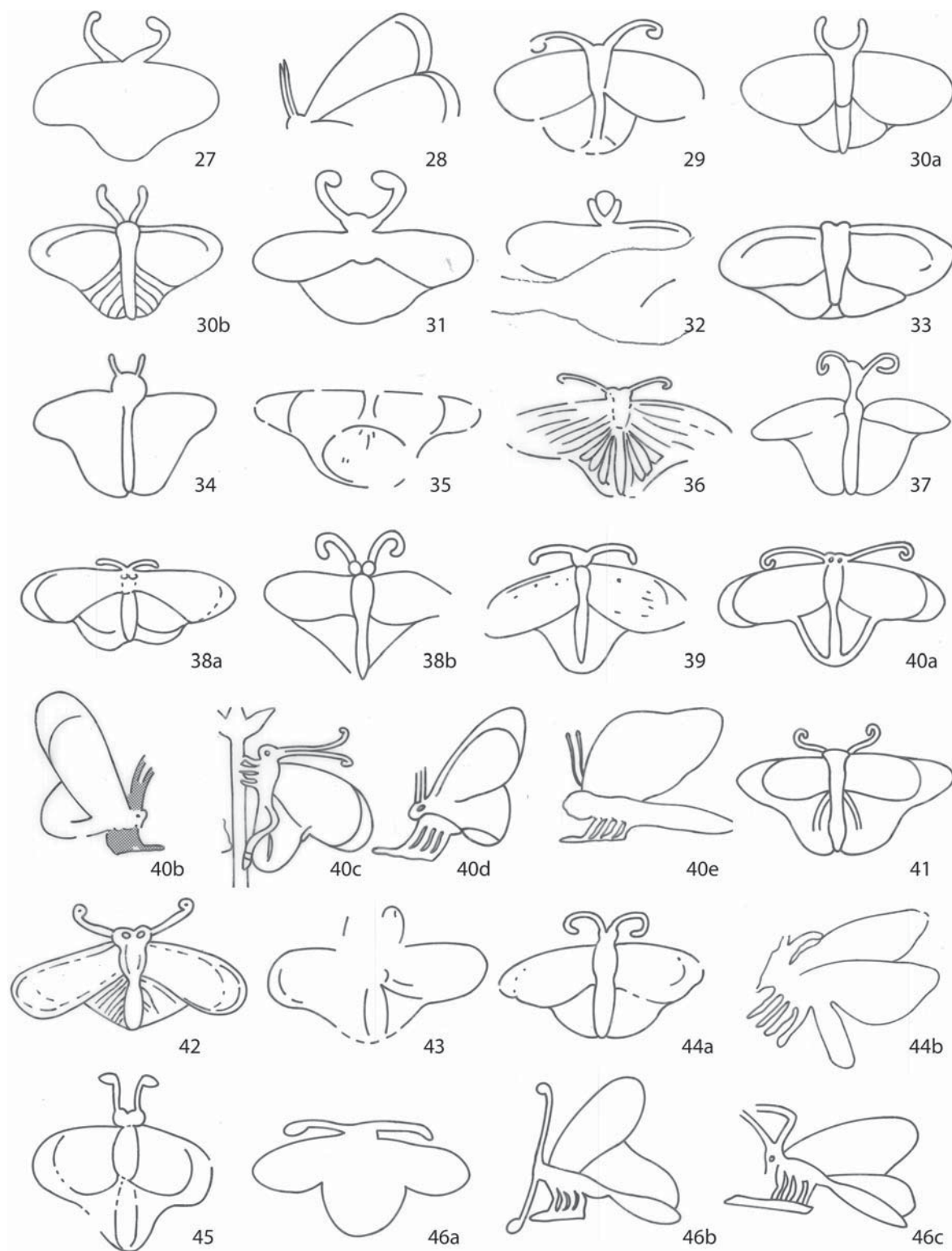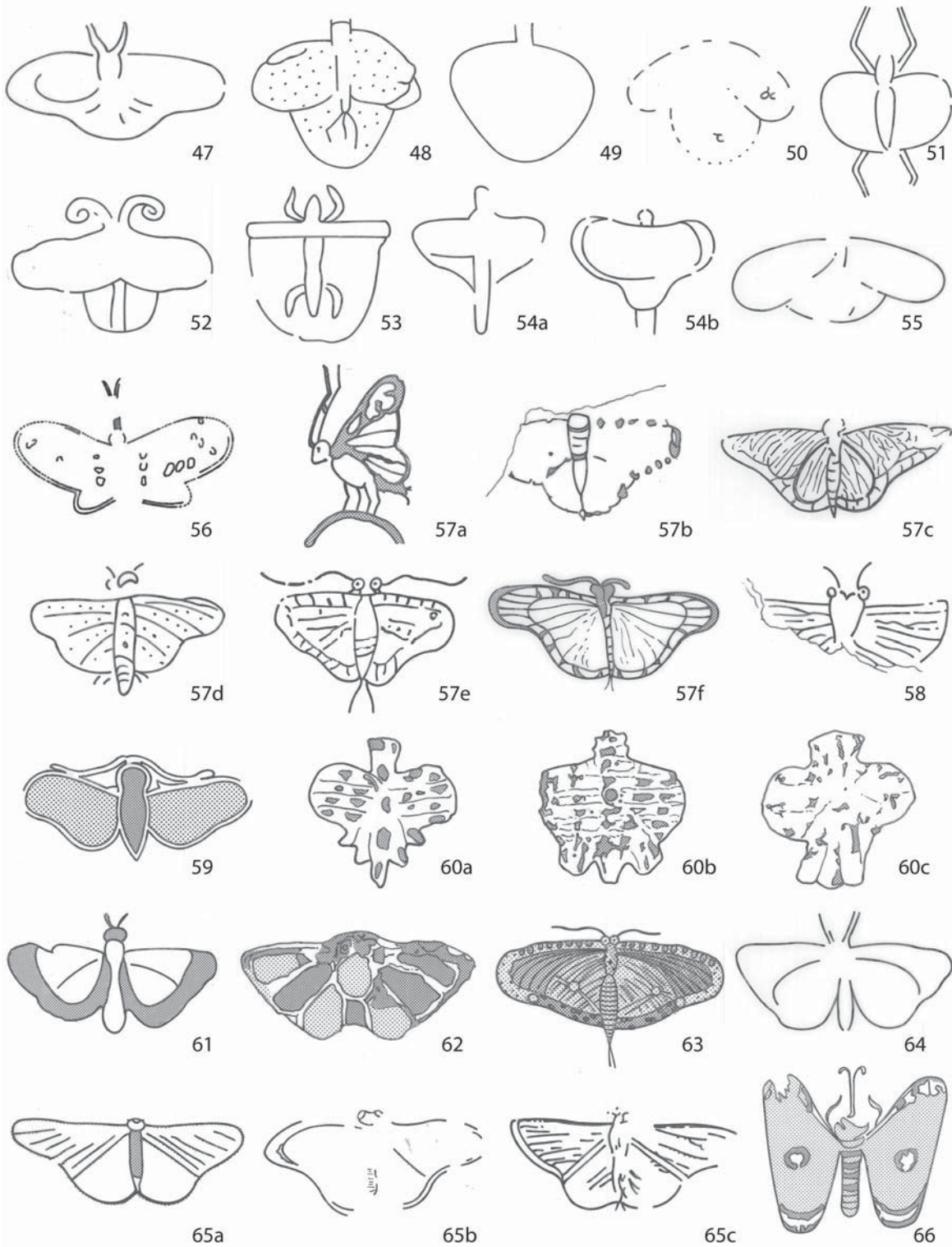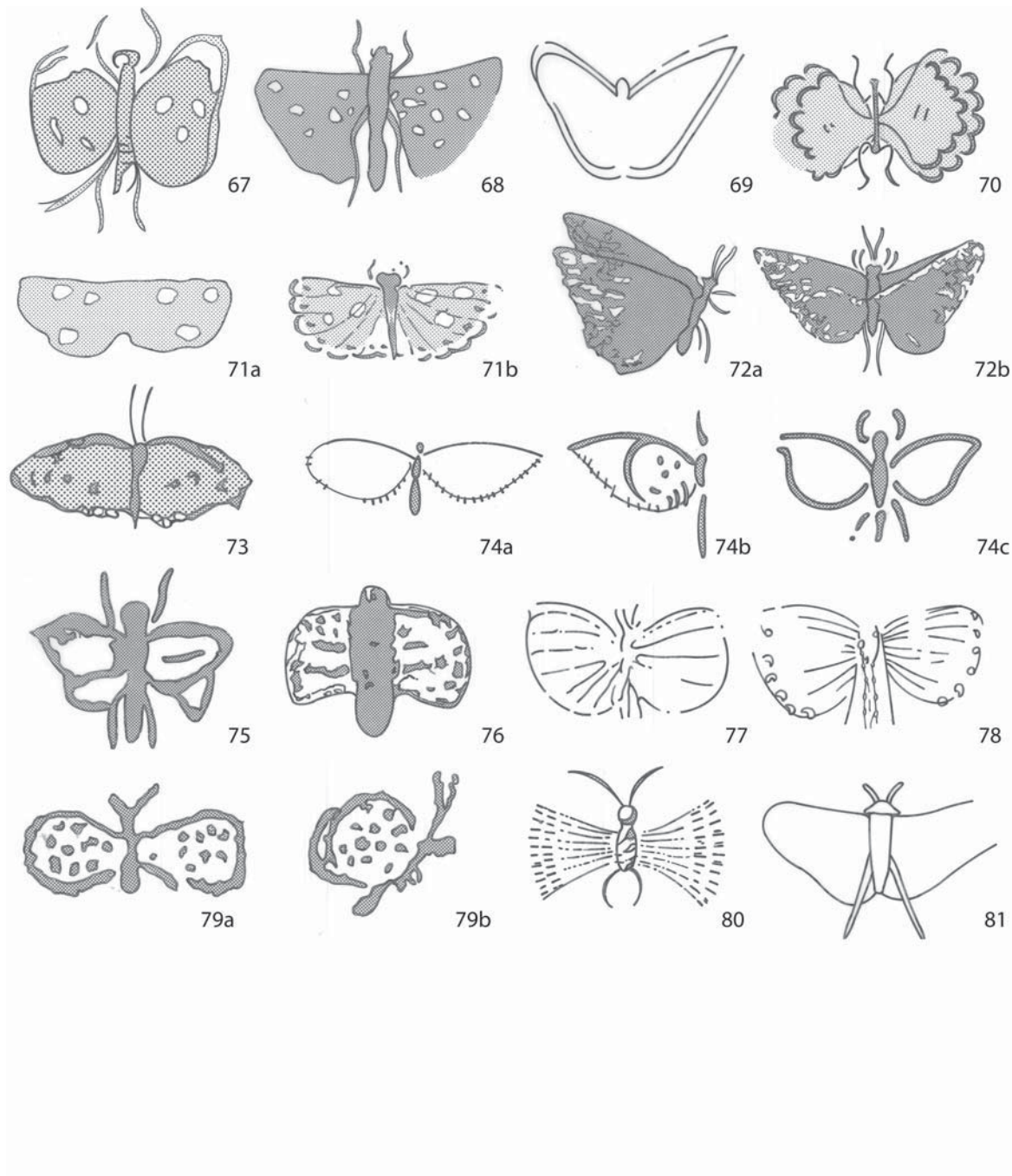TABLE 1. Material examined. NBT=Number of butterflies in the tomb; NBI= Number of butterflies illustrated in this study; LV=butterfly in lateral view; DR=dragonfly-like insects present in tomb scene. NTN = no tomb number. Periods from Harpur (1987); those revised by Swinton (2014) are marked with °. Dates are presented as dynasties in Roman numerals followed by the period of the reigning pharaoh; e.g. VI.4 indicates the sixth dynasty during the reign of the fourth king, Pepi I (E=early, M=middle, L=late). Identification sources: 1) This study, 2) Fleuren 2010, 3) Lopez-Moncet & Aufrere 1999, 4) Myśliwiec 2004, 5) Klebs 1934, 6) Keimer 1934, 7) Davies 1922, 8) Larsen 1979, 9) Keller 1913, and 10) Leith Adams 1870.

#	Period	Tomb owner / object type	Provenance	Tomb #	Image from	NBT	NBI	LV	DR	Identification
1	Naqada I-III	Clay bowl (3850–2960 BCE)	Mesaid	764	Museum of Fine Arts Boston (13.5448)	1	1			
2	IV.2	Hetepheres I Bracelet inlay (Ḥtp-ḥr-s I)	Giza	G7000X	O'Neill 1999: cat. no. 31 (JE 53271)	2	1			
3	V.1	Userkaf (Wsr-k3=f)	Saqqara	ntn	Keimer 1934: fig. 92 (Cairo Museum, JE56601)	1	1			
4	V.1-5	Hetepet (ḥtpt)	Giza	ntn	Keimer 1934: fig. 95 (Berlin Museum, 15420)	1	1			
5	V.2	Sekhemkare (sḫm-k3-rˁ)	Giza	LG89	Hassan 1943: fig. 59	1	1			
6	V.6	Niuserre (N(y)-wsr-Rˁ)	Abu Ghurab	-	Edel & Wenig 1974: pl.15	1	1			
7	V.6	Nefer/Kahay (nfr/k3-ḥ3.j)	Saqqara	ntn	Lashien 2013: pls. 10 and 81	3	1			D. chrysippus or H. misippus (1,2)
8	V.6L*	Ptahshepses (Ptḥ-špss)	Abusir	ntn	Vachala 2004: 160-161 (no. 1259)	1	1			D. chrysippus or H. misippus (2)
9	V.6-8	Fetekta (ftktj)	Abusir	LS1	Lepsius 1842-45 Band IV: pl. 96	1	1			D. chrysippus or H. misippus (2)
10	V.6-8?	Itisen (jtj-sn)	Giza	ntn	Hassan 1944: fig. 123	1	1			
11	V.6-8E	Hetepherakhti (ḥtp-ḥr-3ḫtj)	Saqqara	D60	Mohr 1943: fig. 34 (in Leiden)	1	1			
12	V.6-8E	Akhethetep (3ḫtj-ḥtp)	Saqqara	ntn	Ziegler 1993: 130-131 (in Louvre)	3	1			
13	V.6-9	Rudj-ka (Rwd-ka)	Giza	ntn	Unpublished internet news source (2010)	1	1			Noctuidae? (1)
14	V.6E-8L*	Irenkaptah (jrj-n-k3-ptḥ)	Saqqara	ntn	Moussa & Junge 1975: pl. 12	4	1			
15	V.6-8E*	Neferseshemptah/Sekhentiu (nfr-sšm-ptḥ/sḫntjw)	Saqqara	ntn	Moussa & Junge 1975: pl. 6	1	1			
16	V.6L-8E*	Niankhkhnum/Khnumhotep (nj-ˁnḫ-ḫnmw/ḫnmw-ḥtp)	Saqqara	ntn	Moussa & Altenmüller 1977, fig. 5	2	2			
17	V.7-8E	Ty (tjj)	Saqqara	D22	Wild 1953, pl. 115	1	1			D. chrysippus (1)
18	V.7-9E	Kaemnefert (k3.j-m-nfrt)	Saqqara	D23	Simpson 1992: pl. A	1	1			
19	V.8E	Werirni (Wr-jr-n.j)	El Sheikh Said	no. 25	Davies 1901a: pl. 11	2	1			
20	V.8-9	Sekhemankhptah (sḫm-ˁnḫ-ptḥ)	Saqqara	D41	Simpson 1976: pl. C (in Boston Museum of Arts)	3	1			
21	V.8-9	Neferherenptah(Nfr-ḥr.n-Ptḥ)	Saqqara	ntn	Smith 1981: fig. 121	1	1			
22	V.8-9?	Khunes (ḫw-ns)	Zawyet el-Amwat	no. 2	Lepsius 1842-45 Band IV: pl. 106a	2	1			
23	V.8L-9*	Iasen (j3zn)	Giza	G2196	Simpson 1980: fig. 30	1	1	1		
24	V.8L-9E	Akhethotep (3ḫtj-ḥtp)	Saqqara	D64	Davies 1901b: pls. 8 and 14	3	1			
25	V.9E*	Senezemib: Inti (snḏm-jb: jntj)	Giza	G2370	Brovarski 1999: fig. 42	2	1			
26	V.9*	Ptahhotep II: Thefi (ptḥ-ḥtp II: tfj)	Saqqara	D64	Paget & Pirie 1896: pl. 32	2	2	1		
27	V.9	Khenut (ḫnwt)	Saqqara	ntn	Munro 1993: pl. 33	2	1			
28	V.9	Nebet (nbt)	Saqqara	ntn	Munro 1993: pl. 10	1	1	1		
29	V.9	Iynefret (jj-nfrt: š3.n.f)	Saqqara	ntn	Kanawati & Abder-Raziq 2003: pl. 37	1	1			
30	V.9	Unas (Wnjs)	Saqqara	ntn	Labrousse & Moussa 2002: fig. 42	2	2	1		
31	V.9-VI.1*	Seshseshet: Idut (zšzšt: jdwt)	Saqqara	ntn	Kanawati & Abder-Raziq 2003: pl. 54	1	1			
32	V.9-VI.1	Nimaetre (nj-m3ˁt-rˁ [jzzj-mr-nṯr])	Giza	G2097	Roth 1995: pl. 185	1	1			
33	V.9-VI.2	Akhethotep (3ḫtj-ḥtp)	Saqqara	E17	Petrie & Murray 1952: pl. 6	1	1			
34	VI.1	Kaemankh (k3.j-m-ˁnḫ)	Giza	G4561	Junker 1940: abb. 8 and pl. 11	6	1			
35	VI.1	Hem-min (ḥm-mnw)	El-Hawawish	M43	Kanawati 1985: figs. 6 and 7	2	1			
36	VI.1-2L	Merefnebef (mrrw-n-nbw.f)	Saqqara	ntn	Mysliwiec 2004: pls. XXI and LXVI (j)	2	1			D. chrysippus (3,4); ibid. or H. misippus (2)
37	VI.1?	unknown owner (fragments inside tomb of In-sneferu-ishtef)	Dahshur	-	de Morgan 1896: fig. 516 (under "Mera"); Porter & Moss 1981: 891-2.	2	1			
38	VI.1E-M	Kagemni: Memi (k3.j-m-nj: mmj)	Saqqara	LS10	Firth and Gunn 1926: pl. 52	3	2			
39	VI.1*	Seankhuiptah: Hetepniptah (sˁnḫ-w(j)-ptḥ)	Saqqara	ntn	Kanawati & Abder-Raziq 1998: pls. 69 and 76	7	1		1	
40	VI.1L*	Hesi (ḥzj)	Saqqara	ntn	Kanawati & Abder-Raziq 1999: pls. 53-55	11	5	3	1	
41	VI.1M-2E*	Ankhmahor: Seshi (ˁnḫ-m-ˁ-ḥr: zzj)	Saqqara	ntn	Kanawati & Hassan 1997: pl. 42	1	1			
42	VI.1M*	Nikauisesi (nj-k3w-jzzj)	Saqqara	ntn	Kanawati & Abder-Raziq 2000: pl. 50	5	1		1	D. chrysippus (1)
43	VI.1L*	Mereruka: Meri (mrrw-k3j: mrj)	Saqqara	ntn	Kanawati et al 2010: pl. 67	2	1			
44	VI.1M-L	Niankhnesut (nj-ˁnḫ-nswt)	Saqqara	ntn	Leahy & Mathieson 2001: pl. 4	2	2			
45	VI.2	Meryre-meryptahankh: Nekhebu (mrjj-rˁ-mrj-ptḥ-ˁnḫ: nḫbw)	Giza	G2381	Smith 1958, fig. 2	1	1		1	
46	VI.2M-3?	Mehu (mḥw)	Saqqara	ntn	Altenmüller 1998: pl. 34b	13	3	2		
47	VI.2L-4E*	Wernu (wr-nw)	Saqqara	ntn	Davies et al. 1984: pl. 25	1	1			

Table 1. Continued.

#	Period	Tomb owner / object type	Provenance	Tomb #	Image from	NBT	NBI	LV	DR Identification
48	VI.3-4E*	Ibi (*jbj*)	Deir el-Gebrawi	no. 8	Davies 1902: pl. 5	1	1		Lycaenidae? (1)
49	VI.4-5	Pepyankh: Heni-kem (*ppjj-ˁnḫ-ḥnj-km*)	Meir	A2	Kanawati & Evans 2014a: pl. 84	2	1		
50	VI.4L	Zau (*dˁw*)	Deir el-Gebrawi	no. 12	Davies 1902: pl. 3	2	1		
51	VI.5-6	Kahep: Thei-iker (*k3.j-ḥp/Ttj-jqr*)	El-Hawawish	H26	Kanawati 1980: fig. 8	1	1		
52	VI.5-6?	Pepiankh-heri-ib: Neferka/Heny (*ppjj-ˁnḫ-ḥrj-jb*)	Meir	D2	Kanawati 2012: pl. 80	2	1		
53	VI.6	Idu: Seneni (*jdw: snnj*)	El-Qasr wa'l-Saiyad	T66	Keimer 1934: fig. 102; Wreszinski 1927: pl. 30A	1	1		
54	VI.6	Shepsipumin: Kheni (*špsj-pw-mnw: ḫnj*)	El-Hawawish	H24	Kanawati 1981: figs. 18 and 22	2	2		locust or dragonfly? (2)
55	VI.7	Hemre: Isi (*ḥm-rˁ:Izj*)	Deir el-Gebrawi	N72	Davies 1902: pl. 20	1	1		
56	XI.5	Intef (*Jnj-jtj.f*)	El-Assasif	TT386	Jaros-Deckert 1984: pl.16.	1	1		
57	XI-XII	Hippopotamus statuette a	Dra Abu el-Naga	-	Keimer 1934: fig. 106 (Cairo Antiquities Museum, 877 *bis*)	1	1		
57	XI-XII	Hippopotamus statuette b	Abydos	-	Keimer 1934: fig. 104 (Musées Royaux d'Art et d'Histoire de Bruxelles, E.02676)	1	1		
57	XI-XII	Hippopotamus statuette c	unknown	-	Page-Gasser & Wiese 1997: fig. 56 (private collection, Switzerland)	1	1		
57	XI-XII	Hippopotamus statuette d	Dra Abu el-Naga	-	Keimer 1934: fig. 105 (Cairo Antiquities Museum, 877)	1	1	1	
57	XI-XII	Hippopotamus statuette e	unknown	-	Musées Royaux d'Art et d'Histoire de Bruxelles (E.07055)	1	1		
57	XI-XII	Hippopotamus statuette f	unknown	-	Rhode Island School of Design (29.119)	1	1		
58	XII	Vase fragment	Kerma en Nubie	-	Keimer 1934: fig. 107; Reisner 1923: pl. 45	1	1		
59	XII	Gold pendant	unknown	-	Müller 1972: abb. 45 (State Museum of Egyptian Art, AS5381)	1	1		
60	XII-XIII	Faience amulets	Lisht	-	Arnold 1995: cat. 31 (22.1.1394, 15.3.512 and 15.3.513)	5	3		
61	XII.1	Senbi (*Snbj*)	Meir	B1	Keimer 1937: fig. 211a; Blackman 1915a, pl. 2	2	1		
62	XII.2	Faience amulet (Senworset) (*S-n(y)-Wsr.t*)	Lisht	-	Metropolitan Museum of Art (15.3.307)	1	1		
63	XII.3	Khnumhotep II (*Hnmw-ḥtp*)	Beni Hassan	no. 3	Rosellini 1834: pl.14; Kanawati & Evans 2014b	3	1		*D. chrysippus* f. *chrysippus* and *D. chrysippus* f. *alcippus* (2,3,6) ; moths (5);
64	XII.3	Ukhhotep (*wḫ-ḥtp*) (son of Ukhhotep and Mersi)	Meir	B4	Blackman 1915b: pl. 6	1	1		*D. chrysippus* f. *alcippus* (2); *D. chrysippus* (3)
65	XII.4	Ukhhotep (*wḫ-ḥtp*) (son of Ukhhotep and Henyheryib)	Meir	C1	Blackman & Apted 1953: pl. 13	3	1		*D. chrysippus* (2)
66	XVIII.5	Puyemre (*Pwj-m-Rˁ*)	El-Khokha	TT39	Metropolitan Museum of Art (30.4.12: watercolour copy by H.R. Hopgood)	2	1		*Aglia tau*? (Saturniidae)(1); *D. chrysippus* (1, 2,7); moths (5); unidentifiable (6)
67	XVIII.5-7	Neferhotep (*Nfr-ḥtp*)	Thebes	A5	Louvre (E 13101)	5	1		*H. misippus* (1); unidentifiable (2)
68	XVIII.5-9	Horemheb (*Ḥr-m-ḥb*)	Sheikh Abd el-Qurna	TT78	Brack & Brack 1980: pl.22	1	1		*Limenitis reducta* (1); unidentifiable (2)
69	XVIII.6	Amenhotep(?)	Sheikh Abd el-Qurna	TT73	Säve-Söderbergh 1957: pl. 7	6	1		
70	XVIII.8	Menna (*Mnn3*)	Sheikh Abd el-Qurna	TT69	Davies 1936: pl. 54	2	1		*Colotis fausta* (1); *D. chrysippus* or *H. misippus* (2)
71	XVIII.8	Nakht (*Nḫt*)	Sheikh Abd el-Qurna	TT52	Davies 1917: pl. 24; Mekhitarian 1978: 71	4	2	?	*H. misippus* or *D. chrysippus* (2); butterflies and moths (5)
72	XVIII.8-9	Nebamun (*Nb(=jj-Jmn*)	Luxor	ntn	Davies 1936: pls. 65 and 66	7	2	1	*Issoria* (2); *D. chrysippus* (2,8); *Vanessa* (9); *Euploea* (10)
73	XVIII.9	Amenhotep III (*Jmn-ḥtp III*)	Malqata	-	Curtius 1913: fig. 47.	3	1		*D. chrysippus* f. *dorippus* or *Precis octavia* (1); *D. chrysippus* (2, 3); "*Pyrameis cardui*" (6)
74	XVIII.10	Pavement (Amenhotep IV / Akhenaton) (*3ḫ-n-Jtn*)	Amarna	-	Keimer 1934: fig. 111; Petrie 1894: pls. 2 and 3	3	3	1	*D. chrysippus* or *H. misippus* (2)
75	XVIII.10	Ceramic tile	probably Amarna	-	Keimer 1934: fig. 112; Wallis 1900: fig. 10	1	1		
76	XVIII.10-15	Inlay	unknown	-	Cleveland Museum of Art (1914.789)	1	1		
77	XVIII.13	Neferhotep (*Nfr-ḥtp*)	El-Khokha	TT49	Germond 2008: fig. 11; Keimer 1934: fig.113; Davies 1933: p. 79/82	6	1		
78	XVIII.14-XIX.3	Neferhotep (*Nfr-ḥtp*)	Deir el-Medina	TT6	Wild 1979: fig.1	1	1	1	
79	XIX.3	Simut (*S3-mw.t, Kjkj, Z3-mwt*)	El-Assasif	TT409	Wilkinson 1837: no. 336; Malek 1993: fig. 41	3	2	1	Lycaenidae? (1)
80	XIX.3	Nebwenenef (*Nb-wnn.f*)	Dra Abu el-Naga	TT157	Wilkinson 1837: no. 341	1	1		Alucitidae? (1)
81	XXV.3-XXVI.1	Montuemhat (*mnt-m-ḥ3t*)	El-Assasif	TT34	Malek 1993: fig. 21 (Museo Gregoriano Ergizio, 22765)	1	1		
82	unknown	Relief fragment	unknown	-	Los Angeles County Museum of Art (M.80.199.137)	1	1		

FIG. 5. Butterfly relief from Los Angeles County Museum of Art (LACMA #M.80.199.137). Photo Credit: Los Angeles County Museum of Art, reproduced with permission

coloration and patterning suggest that the latter is a Plain Tiger, *Danaus chrysippus* (Fig. 8a). This common species (or its close mimic, the female of *Hypolimnas misippus*) also appears in many other tombs, from the Old Kingdom period through to the New Kingdom, including Ty [17], Merefnebef [36], Nikauisesi [42], Khnumhotep II [63], Ukhhotep [64], Nebamun [72], and others (Keimer 1934, Larsen 1979, Lopez-Moncet & Aufrère 1999, Fleuren 2010). Some of these (e.g. Merefnebef [36]) were evidently drawn from specimens of the form *f. alcippus*, which display whitish hindwings (Fig. 8b). The butterflies on the ceiling of the New Kingdom palace of Amenhotep III [73] seem to belong to *D. chrysippus f. dorippus*, a form that lacks the black area on the tip of the forewings (Fig. 8c). Other possibilities in this case are *Vanessa cardui* (Keimer 1934: 210) as well as the summer form of *Precis octavia* Cramer, 1777 (Nymphalidae) (Fig. 8d), although this savannah butterfly today occurs only south of Somalia to South Africa (Larsen 1991).

If the salmon color of the two butterflies in the tomb of Menna [70] reflects their original coloration and is not a product of their age, it may suggest that *Colotis fausta* was the model and not *D. chrysippus* as posited by Fleuren (2010), although the painting is otherwise highly stylized (Fig. 8e). Round-winged, light-colored butterflies with black dots speckled on the upper- or undersides of the wings are found in the tombs of Ibi [48] and Simut [79]; these may have been inspired by polyommatine blue butterflies (Lycaenidae).

Some of the butterflies depicted on the hippopotamus figurines [57] could also be interpreted as *D. chrysippus*; Germond (2008) suggested that *Polyommatus icarus* may have been another model, although this species is very rare in Egypt today. He also proposed that the butterflies in the Middle Kingdom

tombs of Senbi [61] and Ukhhotep [64] are probably *D. chrysippus*, but in our opinion these insects are too stylized to be certain.

Dark butterflies with white dots first appear in tomb paintings from Dynasty XVIII onwards (Neferhotep [67], Horemheb [68], Nakht [71]). The only butterfly matching this profile in Egypt today is the male of *Hypolimnas misippus*, with dark wings marked by six conspicuous white spots (Fig. 8f–g). This morphology closely matches butterflies in the tombs of Neferhotep [67] and Nakht [71], where (in the latter case) the *Danaus*-mimicking female is also depicted (Fig. 1i). A dark butterfly in the tomb of Horemheb [68] has numerous white dots, and its pointed wings also suggest that it may have been drawn from a specimen of *Limenitis reducta*, a butterfly that is absent from Egypt but is found today in southern Europe to northern Israel, Jordan, Lebanon, Syria and Iran in the Mediterranean zone (Higgins & Riley 1970)(Fig. 8h).

In some cases, a thicker body and triangular shape of the wings suggest that the image was perhaps drawn from a moth model rather than a butterfly (e.g. Hetepet [4]; Rudj-Ka [13]). The two insects in the tomb of Puyemre [66] with stout bodies and large eye-spots on each wing (Fig. 1f) have been suggested to be a stylized ventral view of *D. chrysippus* (Davies 1922), although they also resemble Saturniid moths, namely the Eurasian *Aglia tau* (Fig. 1f). The "butterfly" in the tomb of Nebwenenef [80] may have been derived from an Alucitid moth. The insect depicted in the tomb of Hesi [40] with three pairs of wings and long antennae resembles a pterophorid moth (Fig. 9a) (Evans 2010). Pterophorids favor humid habitats and are common in marshes. Similar insects with only two pairs of identical narrow wings (e.g. Itisen [10], Iasen [23], Iynefret [29], Nakht [71], etc.) have been thought to represent dragonflies or locusts (Keimer 1932). We suggest that some of these may be Neuropterans, namely antlions (Myrmeleontidae) and owlflies (Ascalaphidae) (Fig. 9b–c). These are dragonfly-like insects with visible, often long antennae that are also common in marshes and along riverbanks. At least 70 species of antlions and six species of owlflies have been recorded in Egypt (El-Hamouly & Fadl 2011).

Cladistic analysis. In our inferred tree (Fig. 10), the examined images from the three main historical time periods were not monophyletic. Although Old Kingdom butterflies mostly stayed together, odd butterflies from the provincial tombs of Kahep/Theti-iker [51] and Idu: Seneni [53] were outliers. Most of the Middle Kingdom butterflies also clustered closely and emerged near to or within examples from the Old Kingdom, although a few (especially jewelry and faience amulets) diverged. Butterflies painted on hippopotamus statuettes from
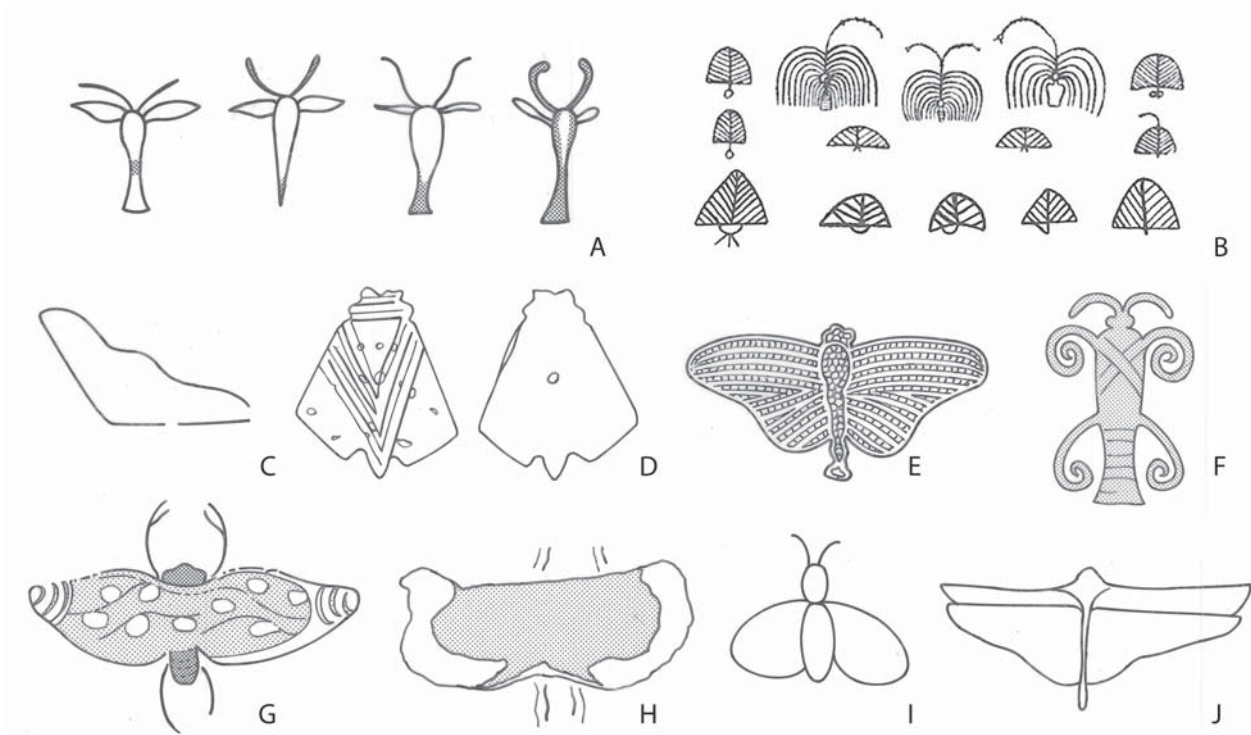
Fig. 6. Items excluded from this study. For corresponding information, see Table 2.

Discussion

this period were also dissimilar and did not cluster together. Similar diversity was evident among the New Kingdom butterflies: The majority of examples from this period appeared in two monophyletic clusters, while a few from mid-Dynasty XVIII onwards (i.e. Amenhotep III[73], Amenhotep IV/Akhenaton[74] and Montuemhat[81]) diverged from the rest.

The relief without provenance in the LACMA (Fig. 5) emerged as most similar to a butterfly from the Dynasty V tomb of Iynefret [29] and in a large cluster with several other late Dynasty V-early Dynasty VI butterflies, mostly from Saqqara.

Evolution of an art form. Ancient Egyptian art conformed to very strict graphic principles, but it seems that butterflies were to some extent exempt from these rules as evident by variations in their representation, even within the same time period. The unique range of artistic manifestations expressed by the Egyptian artists in painting butterflies in tomb scenes extends throughout the Old and New Kingdom periods (2686-1069 BC): Some are abstract and stylized, while others show such great attention to detail that they can be easily identified to species today.

Table 2: Items excluded from this study. For identification Sources, see Table 1.

| #	Period	Tomb owner / object type	Provenance	Tomb #	Image from	Identification
a	Predynastic	Letter T			Keimer 1934:205	bovine symbolism? (1)
b	Predynastic	Vase ornaments (von Bissing 1913)			Keimer 1934:188-191; in Cairo Museum	trees (6)
c	VI.1M-2E*	Ankhmahor: Seshi (ʿnḫ-m-ʿ-ḥr: zzj)	Saqqara	ntn	Kanawati and Hassan 1997: pl. 72; fragment TNE95:147 (found inside the tomb)	not a butterfly (1)
d	XI-XII	faience plaque	Lisht	-	Keimer 1934; in Cairo Museum	stylized insect (1,6)
e	XII.1	Khnumet (Khenemet) Jewelry	Dahshur	-	Lilyquist 1993: 36-37.	not of Egyptian origin (Lilyquist 1993)
f	XVII-XVIII	insect with spiral wings on steatite amulet	Luxor	-	Keimer 1934; in Cairo Museum	stylized insect (1,6)
g	XVIII.6	Amenemhat	Sheikh Abd el-Qurna	TT82	Davies 1936:Pl.19	probably a Cicada (1)
h	XVIII.6-7	Menkheperraseneb	Sheikh Abd el-Qurna	TT79	Fleuren 2010	unfinished, butterfly? (1,2)
i	XVIII	unknown	Thebes		Raven 2000:68	probably Diptera (1)
j	XIX	Thutmoses (Djehutymose, Djehutymes)	El-Assasif	TT32	Kákosy et al 2004:p.267	locust (1)
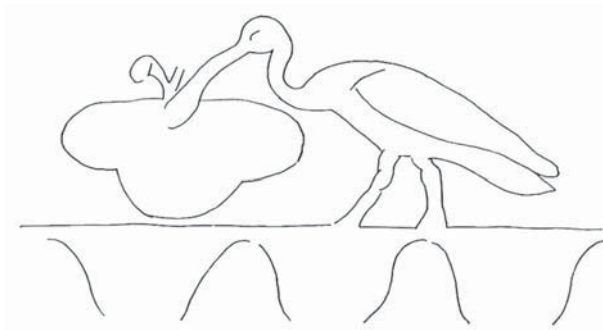
Fig. 7. Butterfly being hunted by an ibis, tomb of Mehu [46] (from Evans 2010).

Our results show that the artistic styles with which butterflies were represented in tombs reflects to a large extent the temporal divide in ancient Egyptian history. With a few exceptions, the butterflies of the Old Kingdom period clustered together, reflecting the relative consistency of the art during this period. While the Old Kingdom butterflies of Giza and Saqqara were relatively similar in style, those in the provincial cemeteries of El-Hawaish (Kahep/Theti-iker [51]) and El-Qasr wa'l-Saiyad (Idu: Seneni [53]) were drastically different, suggesting that their location, far away from the country's capital, may have contributed to a more unique type of representation. During the Middle Kingdom period, although some unique new forms appeared (e.g. faience amulets from Lisht [60]), representations of butterflies remained similar to the Old Kingdom styles popular in Saqqara and Giza. This finding accords well with other evidence indicating that Middle Kingdom artists actively copied earlier images in order to re-establish traditional decorative themes and styles that had been abandoned following the collapse of the Old Kingdom period in late Dynasty VI (Kanawati 2011).

By the beginning of the New Kingdom, very little was left of the designs of the Old or Middle Kingdom periods. Butterfly imagery flourished in form and began to appear outside of tombs, in palaces and temples. Most of the butterflies in this period were drawn with meticulous attention to detail (e.g. Nebamun [72]), although apparently realism was not always of concern. This freer approach to butterfly morphology possibly reflects radical changes to the traditional arts that took place briefly in the Dynasty XVIII reign of king Akhenaton (c. 1352–1336 BC), during which a more naturalistic style was encouraged. The greater diversity in butterfly shapes in the New Kingdom period may also indicate a growing interest in, and awareness of, the natural world, as does the increased number of identifiable species from this period (Table 1).

Dating of unknown artifacts. The close association between the LACMA relief (Fig. 5) and a butterfly from the Dynasty V tomb of Iynefret 29 in Saqqara strongly suggests an Old Kingdom date for the former, as well as a possible place of origin. Also, a polychrome faience inlay with painted decoration from the Cleveland Museum of Art [76], currently dated to 1350–1296 BC (Dynasty XVIII.10-15), appeared among a number of New Kingdom butterflies from Dynasty XVIII.6–8, all from Thebes, hinting at a specific locality and a slightly earlier date for this artifact.

The predominance of two-winged butterflies prior to late Dynasty V in all but one tomb (Neferseshemptah/Sekhentiu [15]) suggests that the latter may have been dated incorrectly, and perhaps belongs to a later period. Indeed, our working date of Dynasty V.6-8E for the tomb is based on Swinton's (2014) recent re-assessment of the structure. Earlier studies (Moussa & Junge 1975; Harpur 1987, 2006), however, dated Neferseshemptah/Sekhentiu to Dynasty V.9, the reign of Unas (during which the proposed style change occurred). Our cladistic analysis suggests strongly that a later date is preferable and indeed, the butterfly in this tomb appears most similar to one from the tomb of Ankhmahor: Seshi [41], recently re-dated by Swinton (2014) to early Dynasty VI. In addition, it would appear that the two-winged butterfly from the tomb of Kaemankh [34], which has frequently been dated to early Dynasty VI (e.g. Junker 1940: 4; Smith 1978: 206, etc) and upon which our analysis was performed, more likely dates to late Dynasty V or earlier, agreeing with Kanawati (2001: 15–18) and Woods (2009: 172), who believe that architectural and artistic details support a date in the reign of Djedkare/Isesi (Dynasty V.8).

Historical biogeography. Past studies attempting to identify ancient Egyptian butterflies have tried to corroborate them with the present fauna of the region (Keimer 1934, Larsen 1979, Lopez-Moncet & Aufrère 1999, Fleuren 2010; etc.). Of the 61 butterfly species known to occur in Egypt today, it seems only a few were used as models by ancient Egyptian artists. Among the identifiable butterflies in Egyptian tombs, various forms of *D. chrysippus* and the dark male of *H. misippus* are unmistakable (Table 1). In general, *D. chrysippus* was the most commonly depicted butterfly throughout the pharaonic period (Fleuren 2010). All other identifications however should be considered doubtful and tentative. Here we propose that in at least two instances, both from the New Kingdom period (Dynasty XVIII), the depicted butterflies may have been modeled after species that no longer occur in Egypt: *Limenitis reducta* (tomb of Horemheb [68], Sheikh Abd el-Qurna), and *P. octavia* (palace of Amenhotep III [73], Malqata).

Fig. 8. Potential model butterflies for ancient Egyptian painters. (**a**) *Danaus chrysippus*; (**b**) *D. chrysippus* f. *alcippus*; (**c**) *D. chrysippus* f. *dorippus*; (**d**) *Precis octavia*; (**e**) *Colotis fausta*; (**f**) *Hypolimnas misippus* male; (**e**) *H. misippus* female; (**f**) *Limenitis reducta*. Photo Credits: **8a**: Wikimedia Commons, CC license; **8b**: Liyana Zolpakar, reproduced with permission; **8c**: Elena Stefanova, reproduced with permission; **8d**: Bart Wursten, reproduced with permission; **8e**: Wikimedia Commons, CC license; **8f**: Oleg E. Kosterin, reproduced with permission; **8g**: Milind Bhakare, reproduced with permission; **8h**: Bernard Fransen, reproduced with permission.

While these butterflies are common throughout their present range in Eurasia (*L. reducta*) and Africa (*P. octavia*) (Williams 1969; Higgins & Riley 1970) and their larval host plants still occur in Egypt (*L. reducta*: *Lonicera caprifolium*; *P. octavia*: *Plectranthus* spp.)(Muschler 1912), both species prefer humid habitats. If our identifications are correct therefore, it would suggest that the climate during the New Kingdom period was not as hot and dry as currently believed. Although both identifications are speculative, it is plausible to think that the species may have occurred in Egypt in the past but have since disappeared from the area, an argument that can also be made for many other animals depicted in ancient Egyptian art. For example, hippopotamus (*Hippopoatums amphibius*) and addax

(*Addax nasomaculatus*) are no longer found in the country, having succumbed to hunting and habitat pressure in the late 1800s, while other species (e.g. African elephants (*Elephas maximus*), Cape hunting dogs (*Lycaon pictus*) etc) may have became locally extinct during the pharaonic period (Osborn & Osbornová 1998). It is nevertheless unwise to infer either species occurrences or extinctions from Egyptian visual data as this was heavily constrained by tradition, such that animals might be illustrated for cultural reasons, irrespective of their natural occurrence. Artists frequently copied motifs from earlier tombs, which could potentially include animals that no longer survived in the region. It is interesting to note, therefore, the divergent butterflies found in the Dynasty XXV–XXVI
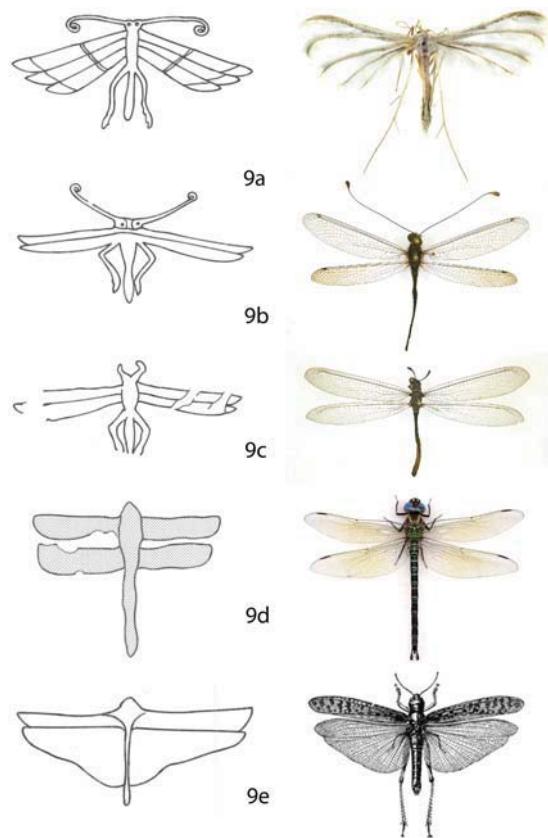
Fig. 9. Pterophorids and other insects in tombs. (**a**) Hesi [40]; (**b**) Nikauisesi [42]; (**c**) Seankhuiptah: Hetepniptah [39]; (**d**) Nakht [71]; (**e**) Kaemnefert [18].

tomb of Montuemhat [80] (see above), as this structure dates from a period when both the content and style of Dynasty V and VI tombs were copied frequently; indeed, Montuemhat is one of the most extreme examples of this archaistic practice.

Symbolism. The symbolic meaning of butterflies in art and history in later periods is well documented (Gagliardi 1976, Nazari 2014). The best examples come from the Roman era and the story of Psyche and Cupid, where the death and rebirth of the former is symbolized by the fragile wings of a butterfly going through the stages of metamorphosis ([Blatchford] 1889). Although some insects, such as scarab beetles, had clear religious or cultural connotations (e.g. Ward 1994), the symbolic significance of butterflies for the ancient Egyptians is yet to be determined. Several authors have argued that because the butterflies found in Egyptian tombs were part of the funerary goods of the deceased, they must also have possessed a symbolic or magical meaning related to the afterlife (e.g. Lopez-Monet & Aufrère

1999, Germond 2008, Espinel 2015). The marsh scene, where butterflies appear most often, has been variously interpreted to have a symbolic meaning, either as the re-establishment of order and defeat of chaos, as an identification of the tomb owner with the king who could perform fishing and fowling on sacred lakes as a royal ritual, or as a sexual unification between the tomb owner and his wife with aspects of rebirth (Dodson & Ikram 2008). Many of the elements in marsh scenes are considered to have symbolic meanings, e.g. the Nile tilapia (*Tilapia niloticus*) is described as a symbol of sexuality, rebirth and renewal, and the lotus flower, usually held by figures accompanying the deceased, is interpreted as an icon of fertility (Desroches-Noblecourt 1954). Similarly, butterflies have been interpreted as symbols of transformation and regeneration (Keimer 1934, Servajean 1999, Germond 2008). Lopez-Moncet & Aufrère (1999) have argued that because *Calotropis*, a host plant of *D. chrysippus*, was associated with the goddess Hathor and was known to have magical properties, the butterfly itself must also have had a great symbolic meaning for the ancient Egyptians.

Such speculations remain controversial however due to lack of concrete evidence. Considering the very large number of surviving Egyptian tombs, butterfly iconography must be considered quite rare. Among tombs with a marsh scene, only about 20% contain butterflies (Fleuren 2010). There is no evidence that the ancient Egyptians knew anything about metamorphosis, and in fact even the Egyptian word for butterflies is not yet known (Hannig & Vomberg 1998). Butterflies, together with birds and bats, were considered "beasts of the sky" (Levinson & Levinson 2009). These facts undermine the significance of butterflies as essential symbolic icons. Based on several ancient Egyptian texts, Feucht (1992) has argued that the meaning behind fishing and fowling scenes was simply that the tomb owners wished to continue the pleasure of these activities in the afterlife, and so butterflies were sometimes added as naturalistic elements of the marsh (Fleuren 2010). Today butterflies are commonly found in the Egyptian swamps, and the most common butterfly species in the country, *D. chrysippus*, is also the most frequently depicted in tomb scenes. It may be, therefore, that this species simply represented a faunal "type" by which to indicate the presence of butterflies in general in such environments (Evans, in press).

CONCLUSION

This study has demonstrated the utility of cladistic analysis in estimating dating patterns for archaeological artifacts of unknown origin when examined in the larger context of similar objects. It has also shown the ways in
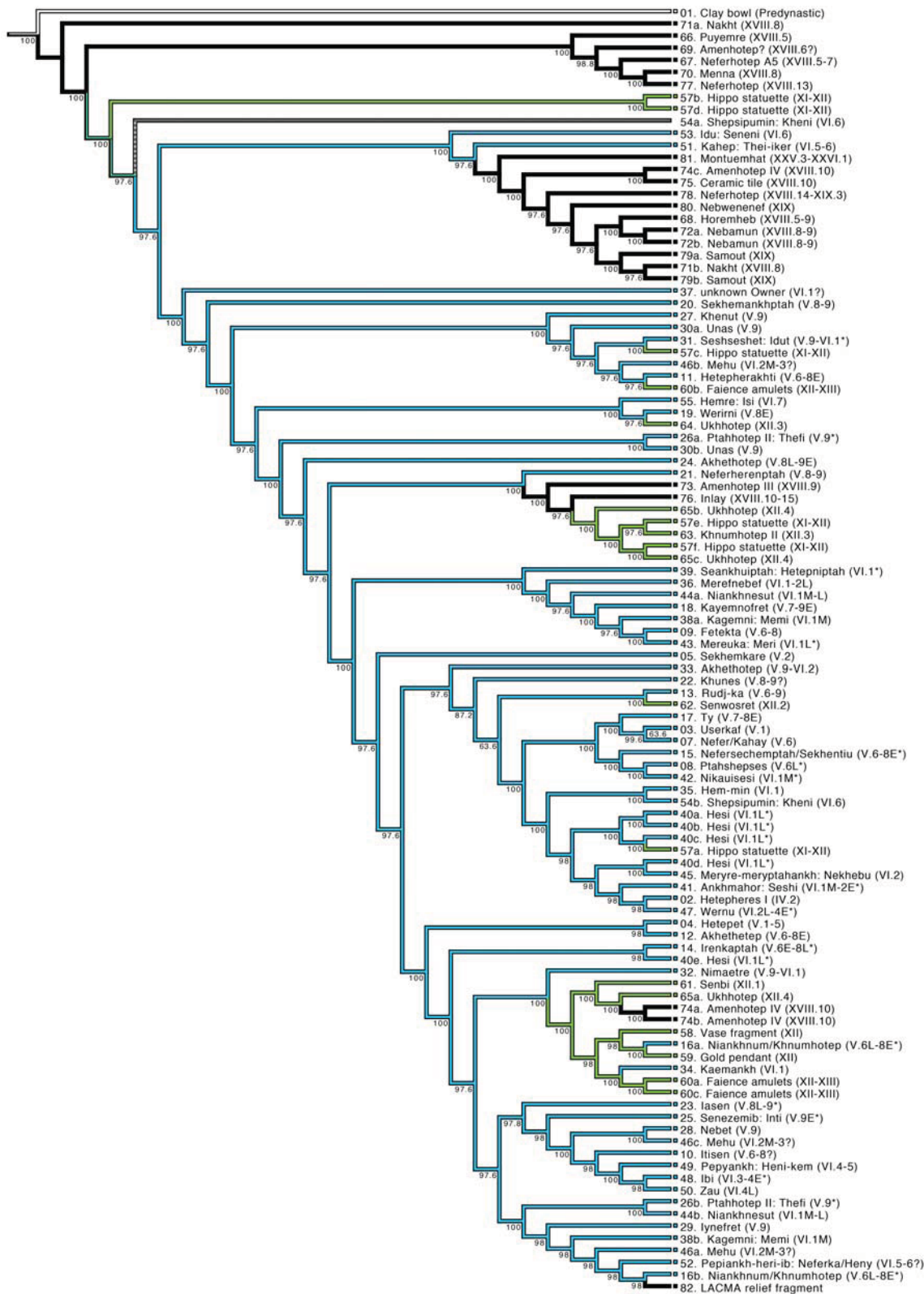
FIG. 10. Majority-Rule consensus tree of 500 equally parsimonious trees (TL=407). Percent consensus frequencies are plotted below each node. Branch colors were plotted post-tree reconstruction based on time periods (blue=Old Kingdom, green=Middle Kingdom, black=New Kingdom).

which butterflies featured in ancient Egyptian cultural materials throughout the pharaonic era. Although it cannot yet be understood what function these insects may have filled—perhaps as symbols of regeneration (Germond 2008) or a wish by the tomb owner to defeat death (Espinel 2015)—their representation may well have been thought to impart a beneficial effect of some kind. Indeed, the repeated occurrence of specific animal species, such as butterflies, within the tomb environment certainly hints at an underlying rationale for their inclusion (Evans, in press). Ultimately, however, as butterflies are inherently decorative, their greatest contribution to Egyptian culture will have been their brilliant colors and graceful forms, which made them a striking addition to artworks in any medium.

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Appendix 1. Characters and character state definitions

1. General shape: trapezoid (0), "><" (1), "<>" (2), triangulate Δ (3), round ¢ (4), "o|o" (5)

2. Discernible number of wings: 4 wings (0), 2 wings (1), >4 wings (2)

3. Forewing costa vs. body axis: 135-108° (4), 107-91° (3), 90° (2), 89-62° (1), 61-45° (0)

4. Head: absent (0), present (1)

5. Thorax: absent (0), present (1)

6. Abdomen: absent (0), present (1)

7. Eyes: absent (0), present (1)

8. Spots within eyes: absent (0), present (1)

9. Body ornamentation: none (0), dots (1), segmented thorax/abdomen (2), abdomen colored (3), body vertically divided (4), 1+2 (5), 2+3 (6), 1+3 (7)

10. General proportions: ~2:1 (0), ~1:1 (1), ~1:2 (2)

11. Groove between forewing and hindwing: absent (0), slight (1), normal (2), very deep (3), wavy or serrated edge (4)

12. Line dividing FW and HW: absent (0), present (1)

13. Fringes: absent (0), present (1)

14. Wings: open (0), closed (1)

15. Costal band: absent (0), present (1)

16. Forewing marginal band: absent (0), present (1)

17. Hindwing marginal band: absent (0), present (1)

18. Forewing apical area: absent (0), present (1)

19. Forewing apical patch: absent (0), present (1)

20. Dots on the wings: absent (0), present, positive (1), present, negative (2)

21. Wing venation: absent (0), present on both wings (1), present on HW only (2), present on FW only (3)

22. Antennae: absent (0), present (1)

23. Antennae length if unrolled: less than half length of FW (0), equal or more than half length of FW (1), longer than the length of FW (2)

24. Antennae filament: straight (0), curved inwards (1), curved outwards (2), wavy (3)

25. Antennae Club: absent (0), present, straight (1), present, curved inwards (2), present, curved outwards (3)

26. Antennae positioning compared to Forewing costa: 90° (0); 90°-45° (1), 45°-0° (2).

27. Number of front legs: 0 (0), 2 (1), 4 (2)

28. Number of thoracic legs: 0 (0), 2 (1), 4 (2)

29. Number of hind legs: 0 (0), 2 (1), 4 (2)

30. Hairpencils: absent (0), present (1)

31. Mouthparts: absent (0), present (1)

32. Location: Northern Egypt (0) (incl. Abusir, Abu Ghurab, Dahshur, Giza, Lisht and Saqqara); Middle Egypt (1) (incl. Amarna, Beni Hassan, Deir el-Gebrawi, El Sheikh Said, Meir, Zawyet el-Amwat); Lower Egypt (2) (incl. Abydos, El-Hawawish, El-Qasr wa'l-Saiyad, Luxor, Malqata, Naqada, and Thebes [Deir el-Medina, Dra Abu el-Naga, El-Assasif and El-Khokha and Sheikh Abd el-Qurna]); Nubia (Kerma, modern day Sudan) (3)

Appendix 2. Data matrix.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
01 Clay bowl Predynastic	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	?	?	–	0	0	0	0	0	0	0	2
02 Hetepheres I IV.2	0	2	2	1	1	1	0	0	3	0	4	1	0	0	0	1	1	1	0	0	0	1	0	1	0	1	0	0	0	0	1	0
03 Userkaf V.1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1	1	1	2	1	0	0	0	0	0	0
04 Hetepet V.15	2	0	3	?	1	1	0	0	0	0	0	?	0	0	1	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0
05 Sekhemkare V.2	0	1	3	1	1	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	?	?	–	–	0	0	0	0	0	0
06 Niuserre V.6	0	0	3	?	1	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	2	?	?	?	?	?	?	0	0	0	?	0
07 Nefer/Kahay V.6	0	0	1	?	1	0	0	0	2	0	1	0	0	0	1	1	1	1	0	0	0	0	0	1	2	0	0	0	0	0	0	0
08 Ptahshepses V.6L*	?	0	3	1	1	1	1	0	0	0	?	0	0	0	0	?	?	?	?	0	0	0	1	2	3	1	0	0	0	0	0	0
09 Fetekta V.6-8	0	0	1	1	1	1	0	0	0	1	1	0	0	0	1	1	0	0	0	0	0	1	2	1	2	1	0	0	0	0	0	0
10 Itisen V.6-8?	3	1	4	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	1	0	0	0	0	0	0
11 Hetepherakhti V.6-8E	0	0	3	?	1	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	2	3	1	0	0	0	0	0	0
12 Akhethetep V.6-8E	0	0	3	1	1	1	1	0	0	0	1	0	0	0	?	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
13 Rudj-ka V.6-9	2	0	3	1	1	1	0	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	–	0	0	0	0	0	0	0	0	0
14 Irenkaptah V.6E-8L*	0	0	3	?	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	–	–	–	–	0	0	0	0	0	0
15 Nefersechemptah/ Sekhentiu V.6-8E*	0	0	3	1	1	1	1	0	0	0	2	1	0	0	?	1	1	1	1	0	1	0	1	2	0	1	0	0	0	0	0	0
16a Niankhnum/ Khnumhotep V.6L-8E*	0	0	1	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0
16b Niankhnum/ Khnumhotep V.6L-8E*	0	0	3	1	1	1	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	1	1	1	2	0	0	0	0	0	0	0
17 Ty V.7-8E	0	0	1	1	1	1	0	0	0	0	1	0	0	0	1	1	1	1	1	0	0	1	1	1	0	1	0	0	0	0	0	0
18 Kayemnofret V.7-9E	0	0	1	1	1	1	1	0	0	0	1	0	0	0	1	1	0	0	0	0	0	1	0	1	2	1	0	0	0	0	0	0
19 Werini V.8E	0	0	3	1	1	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0	1	0	0	0	0	0	1
20 Sekhemankhptah V.8-9	0	0	3	1	1	1	0	0	4	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0
21 Neferherenptah V.8-9	0	0	3	?	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	2	1	1	0	0	0	0	0	1
22 Khunes V.8-9?	0	0	3	?	1	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	?	0	3	?	?	0	0	0	0	0	0
23 Iasen V.8L-9*	0	0	3	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	–	–	–	–	0	0	0	0	0	0
24 Akhethotep V.8L-9E	0	0	3	1	1	1	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	1	0	2	0	1	0	0	0	0	0	0
25 Senezemib: Inti V.9E*	0	0	3	1	?	?	0	0	0	0	2	0	0	0	1	1	0	0	0	0	0	?	?	?	0	1	0	0	0	0	0	0
26a Ptahhotep II: Thefi V.9*	0	0	3	1	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	2	3	1	0	0	0	0	0	0
26b Ptahhotep II: Thefi V.9*	0	0	–	1	1	1	0	0	–	0	2	1	1	0	0	0	0	0	0	0	0	1	1	1	2	2	1	0	0	0	0	0
27 Khenut V.9	0	0	3	?	1	?	0	0	0	0	2	0	0	0	0	1	0	0	0	0	0	1	1	2	3	1	0	0	0	0	0	0
28 Nebet V.9	0	0	4	1	1	?	0	0	0	0	2	1	1	1	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0
29 Iynefret V.9	0	0	3	1	1	1	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	1	1	1	2	2	1	0	0	0	0	0

Specimen																										
30a Unas V.9	0	0	3	1	1	1	0	0	1	0	0	0	1	0	0	0	1	1	0	1	3	2	1	0	0	0
30b Unas V.9	0	0	3	1	1	1	0	0	1	0	0	0	1	0	0	0	1	1	2	1	3	2	1	0	0	0
31 Seshseshet: Idut V.9-VI.1*	0	0	1	1	1	0	0	0	0	0	0	1	0	?	0	0	1	1	1	1	3	2	1	0	0	0
32 Nimaetre V.9-VI.1	0	0	1	1	?	0	0	0	0	0	0	2	0	0	0	0	1	1	1	1	1	1	1	1	0	0
33 Akhethotep V.9-VI.2	0	0	3	1	?	0	0	0	0	0	0	1	0	0	0	0	?	?	3	1	0	0	0	0	0	0
34 Kaemankh VI.1	0	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0	1	1	1	1	1	1	1	0	0	0
35 Hem-min VI.1	0	0	3	?	1	1	0	?	0	1	?	2	0	?	?	0	0	?	2	0	2	0	1	0	0	0
36 Merefnebef VI.1 2L	0	0	3	1	1	0	0	1	1	0	1	3	0	1	0	0	1	1	1	2	2	1	1	0	0	0
37 unknown Owner VI.1?	0	0	3	1	1	1	0	0	0	0	0	?	0	0	0	0	1	0	0	1	2	1	1	1	0	0
38a Kagemni: Memi VI.1M	0	0	1	?	1	0	0	0	0	0	?	1	0	?	0	0	0	1	0	1	2	0	1	0	0	0
38b Kagemni: Memi VI.1M	0	0	3	1	1	0	0	0	0	0	0	2	0	0	0	0	1	1	0	1	2	1	1	0	0	0
39 Seankhuiptah: Hetepniptah VI.1*	0	0	3	1	1	0	0	0	0	1	0	3	0	?	0	1	1	0	1	0	2	1	0	0	0	0
40a Hesi VI.1L*	0	0	3	1	1	0	1	0	1	0	0	3	0	1	0	0	?	0	?	1	2	1	?	1	1	0
40b Hesi VI.1L*	0	0	3	1	1	0	1	0	1	0	0	3	-	0	0	1	0	0	?	1	2	1	0	1	0	0
40c Hesi VI.1L*	0	0	3	1	1	0	1	0	1	0	0	3	-	0	0	1	0	0	?	1	0	?	1	1	0	0
40d Hesi VI.1L*	0	0	3	1	1	0	1	0	1	0	0	3	-	0	0	1	0	?	?	1	?	1	1	2	0	0
40e Hesi VI.1L*	0	0	3	1	1	0	0	0	0	0	0	1	-	0	0	0	0	0	0	0	0	1	1	1	1	0
41 Ankhmahor: Seshi VI.1M-2E*	0	0	3	1	1	0	0	0	0	0	0	1	0	1	0	1	1	0	1	1	2	1	1	2	0	0
42 Nikauisesi VI.1M*	0	0	3	1	1	1	0	0	1	0	1	3	0	1	0	1	1	0	2	0	3	2	1	2	0	0
43 Mereuka: Meri VI.1L*	0	0	1	1	?	0	0	0	0	?	?	1	0	0	0	0	0	0	0	0	3	2	?	0	0	0
44a Niankhnesut VI.1M L	0	0	3	1	1	0	0	0	0	0	0	2	0	0	0	1	1	1	1	1	2	1	1	1	0	0
44b Niankhnesut VI.1M L	2	1	3	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	2	1	?	1	1	0
45 Meryre-meryptahankh: Nekhebu VI.2	0	0	3	1	1	0	0	1	0	0	0	1	1	0	0	0	1	0	1	1	2	1	1	0	0	0
46a Mehu VI.2M-3?	0	0	3	?	?	0	0	0	0	0	0	3	0	0	0	0	0	0	0	1	2	1	1	2	0	0
46b Mehu VI.2M-3?	0	0	3	1	1	0	0	0	-	0	0	3	0	0	0	0	1	0	1	1	3	2	1	2	0	0
46c Mehu VI.2M-3?	0	0	4	1	1	1	0	0	-	0	0	3	0	0	0	0	1	0	1	1	0	2	?	0	0	0
47 Wernu VI.2L-4E*	0	0	3	1	1	?	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	1	0	1	0
48 Ibi VI.3-4E*	4	0	4	1	?	2	1	0	0	0	0	2	0	0	0	0	0	1	-	-	0	0	-	0	0	1
49 Pepyankh: Heni-kem VI.4-5	4	?	3	?	?	0	1	0	?	0	0	0	?	0	?	0	?	?	0	1	0	0	?	0	0	1

Appendix 2. Data matrix. (continued)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
50 Zau VI.4L	4	0	4	?	?	?	0	0	?	1	3	0	0	0	0	0	0	0	?	0	0	?	?	?	–	–	0	0	0	0	0	1
51 Kahep: Thei-iker VI.5-6	4	1	1	?	1	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	?	?	?	–	–	1	0	1	0	0	2
52 Pepiankh-heri-ib: Neferka/Heny VI.5-6?	0	0	3	?	?	1	0	0	0	0	3	0	0	0	0	0	0	0	0	1	1	1	1	1	2	1	0	0	0	0	0	1
53 Idu Seneni VI.6	4	?	2	1	1	1	0	0	0	1	0	?	0	0	0	0	0	0	0	0	0	0	–	–	–	1	1	0	1	0	0	2
54a Shepsipumin Kheni VI.6	0	0	3	1	?	1	0	0	0	2	1	1	0	0	0	0	0	0	0	0	0	0	–	–	–	–	0	0	0	0	0	2
54b Shepsipumin Kheni VI.6	0	0	1	1	?	?	0	0	0	2	2	1	0	0	0	1	0	0	0	0	0	0	–	–	–	–	0	0	0	0	0	2
55 Hemre: Isi VI.7	0	0	3	?	1	?	0	0	0	0	2	1	0	0	0	0	0	0	0	0	?	?	0	–	–	–	0	0	0	?	0	1
56 Intef XI.4	0	4	1	1	?	?	0	0	?	0	3	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	?	0	2
57a Hippo statuette XI-XII	0	0	3	1	1	1	0	1	3	–	2	1	1	0	1	1	1	1	?	1	1	1	1	3	0	2	1	1	0	1	1	2
57b Hippo statuette XI-XII	0	0	3	1	1	1	0	0	2	0	2	1	0	0	1	0	0	0	0	0	0	0	0	–	–	?	0	0	0	0	0	?
57c Hippo statuette XI-XII	0	0	1	1	1	1	0	0	2	0	1	1	0	0	1	0	0	0	0	1	1	1	0	2	?	2	0	0	0	0	0	?
57d Hippo statuette XI-XII	0	0	3	1	1	1	0	0	2	0	2	?	0	0	0	0	0	0	0	1	1	0	1	0	0	1	1	0	2	0	0	2
57e Hippo statuette XI-XII	0	0	3	1	1	1	1	1	1	0	1	?	0	0	1	0	0	1	0	1	1	2	2	3	1	2	0	0	0	1	0	?
57f Hippo statuette XI-XII	0	0	1	1	1	1	1	0	2	0	2	0	0	1	1	1	1	1	0	0	1	1	1	3	1	2	0	0	1	1	0	?
58 Vase fragment XII	0	0	1	1	1	?	1	1	0	0	1	?	0	0	?	?	?	0	0	1	1	?	0	1	0	1	0	0	0	0	0	3
59 Gold pendant XII	0	0	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	3	1	2	0	0	0	0	0	?
60a Faience amulets XII-XIII	4	0	1	1	?	1	0	0	1	1	?	?	0	0	0	0	0	0	0	0	0	0	–	–	–	–	0	0	?	0	0	0
60b Faience amulets XII-XIII	4	?	3	1	?	1	0	0	1	1	?	0	0	0	0	0	0	0	0	1	0	0	–	–	–	–	0	0	?	0	0	0
60c Faience amulets XII-XIII	4	1	?	1	?	1	0	0	1	1	?	0	0	0	0	0	0	0	0	1	0	0	–	–	–	–	0	0	?	0	0	0
61 Senbi XII.1	0	0	1	1	1	1	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1
62 Senwosret XII.2	0	0	3	1	1	1	0	0	3	0	1	0	0	0	0	0	0	?	?	0	0	0	–	–	–	–	0	0	0	0	0	0
63 KhnumhotepII XII.3	0	0	3	0	1	1	1	1	5	0	1	0	0	0	1	1	1	1	1	1	1	0	–	3	1	2	1	1	1	1	1	1
64 Ukhhotep XII.3	0	0	3	?	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1
65a Ukhhotep XII.4	0	0	1	1	1	1	0	0	3	2	0	0	0	0	0	0	0	0	0	3	3	0	–	–	–	–	0	0	0	0	0	–
65b Ukhhotep XII.4	0	0	3	1	?	1	1	0	2	0	2	1	0	0	1	1	0	0	0	0	0	0	–	–	–	–	0	0	0	0	0	1
65c Ukhhotep XII.4	0	0	1	1	1	1	0	0	0	0	2	1	0	0	?	1	0	0	0	1	0	0	–	–	–	–	0	0	0	1	?	1

	66 Puyemre XVIII.5	67 Neferhotep XVIII.5-7	68 Horemheb XVIII.5-9	69 Amenhotep? XVIII.6?	70 Menna XVIII.8	71a Nakht XVIII.8	71b Nakht XVIII.8	72a Nebamun XVIII.8-9	72b Nebamun XVIII.8-9	73 Amenhotep III XVIII.9	74a Amenhotep IV XVIII.10	74b Amenhotep IV XVIII.10	74c Amenhotep IV XVIII.10	75 Ceramic tile XVIII.10	76 Inlay XVIII.10-15	77 Neferhotep XVIII.13	78 Neferhotep XVIII.14-XIX.3	79a Samout XIX	79b Samout XIX	80 Nebwenenef XIX	81 Montuemhat XXV.3-XXVI.1	82 LACMA Relief fragment
	2	2	2	2	2	2	2	2	2	2	1	1	1	1	?	2	2	2	2	2	2	?
	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	?	2	0	0	0	0	0
	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0
	0	1	1	0	1	0	0	1	1	0	0	0	1	1	0	?	1	0	0	1	1	0
	1	1	1	0	1	0	0	0	1	0	0	0	1	0	0	?	?	1	0	0	0	0
	2	0	-	0	0	0	-	0	1	1	-	0	0	-	-	0	-	0	0	1	0	0
	1	-	-	0	-	-	-	0	1	1	-	0	-	-	-	0	-	-	0	1	0	0
	1	0	-	?	-	-	-	0	0	1	-	0	-	0	-	-	-	-	0	1	1	2
	0	0	0	1	0	0	1	0	1	1	0	0	1	0	0	1	1	1	0	1	1	0
	1	0	0	0	0	0	1	?	?	1	0	0	1	0	0	0	1	?	?	1	0	0
	0	2	0	2	0	2	1	1	1	1	0	1	0	0	1	0	1	1	1	?	0	0
	1	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	?	0	0	?	0	0
	1	1	1	0	1	0	1	0	0	1	0	1	0	0	1	1	?	1	0	?	0	0
	1	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	?	0	0	0	0	0
	1	1	-	-	1	-	0	0	1	1	-	0	?	-	-	0	-	0	1	0	0	0
	2	-	-	0	-	-	0	0	1	1	-	0	0	-	-	0	-	0	1	0	1	2
	0	1	1	1	0	0	-	0	1	1	1	1	0	1	1	0	?	?	0	1	0	0
	0	1	1	0	0	0	0	0	1	1	0	0	0	1	0	?	?	1	0	1	1	0
	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	1	0	0
	1	0	1	0	1	4	1	4	1	1	1	0	0	1	1	0	1	0	0	1	1	2
	1	1	0	1	0	0	0	0	-	0	0	0	0	0	1	0	1	0	-	0	0	0
	6	6	3	0	3	?	3	7	7	3	3	3	3	3	3	?	1	3	3	?	0	0
	0	0	1	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0
	1	1	1	?	1	0	1	1	1	1	1	1	1	1	1	1	?	1	1	?	1	1
	1	1	1	?	1	0	1	1	1	?	1	1	1	1	1	1	1	1	1	1	1	1
	0	0	1	1	1	1	1	1	1	3	1	1	1	1	3	1	1	1	1	1	1	3
	1	1	0	0	1	1	1	0	0	0	1	1	1	1	1	0	1	1	1	1	0	1
	1	1	0	1	1	0	2	0	0	0	0	?	?	0	5	5	5	5	5	1	0	0

LIFE TABLE PARAMETERS AND DIGESTIVE ENZYMATIC ACTIVITY OF *PLODIA INTERPUNCTELLA* (HÜBNER) (PYRALIDAE) ON ARTIFICIAL DIET CONTAINING BRAN OF VARIOUS WHEAT CULTIVARS

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ABSTRACT. The eggs and larvae of the Indian meal moth, *Plodia interpunctella* (Hübner), are widely used for mass rearing of parasitoids and predators. Life table parameters and digestive enzymatic activity (protease and α-amylase) of *P. interpunctella* were studied on bran of different wheat cultivars ('Backcross Roshan', 'Khooshe Pishgam', 'Khoshki line 9', 'Arg', 'Alvand', 'Pishtaz', 'WS-89-2', 'Sepahan' and 'Bam') when incorporated into artificial diets under laboratory conditions (25 ± 1ºC, 65 ± 5% R.H., and a 16:8 h light-dark photoperiod). The net reproductive rate (R_0) of *P. interpunctella* was highest on 'Backcross Roshan' (78.05±4.80 female/female/generation) and lowest on 'Pishtaz' (21.82±0.96 female/female/generation). The intrinsic rate of increase (r_m) ranged from 0.0520±0.0006 to 0.0836±0.0008 (day^{-1}), which was lowest on 'Pishtaz' and highest on 'Backcross Roshan'. The highest and lowest levels of proteolytic activity were recorded in the fifth instar larvae fed with 'Backcross Roshan' (1.19 ± 0.16 U mg^{-1}) and 'Bam' (0.24 ± 0.08 U mg^{-1}). Also, the highest level of amylolytic activity was recorded on 'Alvand', 'Backcross Roshan', 'Arg' and 'Khoshki line 9' (0.85 ± 0.02, 0.83 ± 0.09, 0.78 ± 0.05, 0.77 ± 0.04 mU mg^{-1}, respectively) while the lowest activity was on 'Sepahan' and 'Bam' (0.36 ± 0.06 and 0.43 ± 0.06 mU mg^{-1}, respectively). The results show that, among the different wheat cultivars tested, 'Backcross Roshan' was the most suitable cultivar for rearing *P. interpunctella*, as an alternative host, in order to optimize the mass production of natural enemies.

Additional key words: Indian meal moth, population growth, digestive physiology, wheat bran

The Indian meal moth, *Plodia interpunctella* (Hübner) (Lepidoptera: Pyralidae), is a major cosmopolitan pest of granaries, food processing plants, warehouses, retail stores, and households. *Plodia interpunctella* larvae are able to feed on a wide range of dried vegetable and animal materials including grain, cereal products, oilseeds, dried fruits, dried vegetables, nuts, animal feed (Cox and Bell, 1991), walnut, almond, pistachio and dates in Iran (Sepasgozarian 1979) and other parts of the world (Azelmat et al. 2005). In addition, the eggs and larvae of *P. interpunctella* have been used as alternative hosts in the mass rearing of several natural enemies, such as *Orius albidipennis* (Reuter) (Hemiptera: Anthocoridae) (Ghadamyari et al. 2001), *Venturia canescens* (Gravenhorst) (Hymenoptera: Ichneumonidae) (Spanoudis and Andreadis 2012), *Habrobracon hebetor* (Say) (Hymenoptera: Braconidae) (Akinkurolere et al. 2009, Ghimire and Phillips 2010) and *Trichogramma brassicae* (Bezdenko) (Hymen optera: Trichogrammatidae) (Iranipour et al. 2009), under laboratory conditions.

Biological aspects such as the development and survivorship of the pre-imaginal stages, as well as physiological indices of insect pests, can be affected by temperature, moisture, photoperiod, host commodity and the quality of food eaten (Johnson et al. 1997, Na and Ryoo 2000, Musa and Ren 2005, Bouayad et al. 2008). The developmental time and adult progeny production of the Indian meal moth are significantly influenced by the type of diet consumed during the larval stage (Cline and Highland 1985). Life table parameters can provide a comprehensive description of the development, survivorship, and fecundity of a population, and is an appropriate tool to study the dynamics of animal populations, especially arthropods (Maia et al. 2000), and may be useful in constructing population models (Carey 1993) and understanding interactions with other insect pests and natural enemies (Omer et al. 1996). Southwood (1966) stated that the life table parameters, particularly the intrinsic rate of increase (r_m), are the most useful parameters to compare and estimate the population growth potential of different species under specific climatic and food conditions (Ricklefs and Miller 2000). Consequently, this research examined the life table parameters in order to compare the population growth of *P. interpunctella* on artificial diet containing bran of various wheat cultivars. Several researchers have previously studied the biology of *P. interpunctella* on various diets. For example, Arbogast (2007) evaluated the development of immature stages of *P. interpunctella* under different temperature, humidity and dietary conditions, and found that moisture content had a significant effect on the developmental period of this insect. Bouayad et al. (2008) examined the effect of the four commodities (wheat flour, dates, sorghum and barely) on the post-embryonic development of this insect pest, and reported that the shortest development time was on wheat flour and dates. Also, population growth parameters of the Indian meal moth on three date cultivars were studied by Pourbehi et al. (2013), who observed the highest value of intrinsic rate of increase on cultivar Zahedi.

However, since insects derive most of their nourishments from proteins and soluble carbohydrates, proteases and amylases, which are the key insect-gut digestive enzymes, are essential for their survival (Ishaaya et al. 1971). Bouayad et al. (2008) examined the effect of four commodities (wheat flour, dates, sorghum and barely) on the α-amylase activity of *P. interpunctella*, and reported that the lowest amylolytic activity was found in the larvae reared on wheat flour and dates. Farshbaf Pour Abad et al. (2010) examined some properties of α-amylase in the Indian meal moth larvae fed pistachio, and detected the highest amylolytic activity in the fifth instar larvae. Recently, Borzouei (2012) considered the effect of different diets on proteolytic and amylolytic activities of *P. interpunctella*, and stated that the highest enzymatic activity was in the larvae fed on artificial diet containing wheat bran, yeast, honey and glycerol. Also, Nasirian et al. (2014) examined the feeding performance of *P. interpunctella* on different artificial diets and detected the highest efficiency of conversion of ingested food (ECI) on bran of the wheat cultivar 'Backcross Roshan'.

To date, no published information exists concerning life table and digestive enzymatic activity (amylases and proteases) of *P. interpunctella* on artificial diet containing bran of various wheat cultivars. Therefore, this research was performed to elucidate the life table parameters and activity of two main digestive enzymes of *P. interpunctella* in response to feeding on artificial diet prepared by bran of nine wheat cultivars. The findings of this research will be useful in selecting the most suitable wheat cultivar for optimal feeding, rapid development, maximum survival and high fecundity of *P. interpunctella* in order to optimize the mass rearing of some natural enemies under laboratory conditions.

Materials and Methods

Artificial diet. Different wheat cultivars including 'Backcross Roshan', 'Khooshe Pishgam', 'Khoshki line 9', 'Arg', 'Alvand', 'Pishtaz', 'WS-89-2', 'Sepahan' and 'Bam' were acquired from the Agricultural and Natural Resources Research Center of Isfahan, Iran, and used to prepare artificial diets. To prepare the dry part of the artificial diet, 800 gr of bran of each wheat cultivars was mixed with 160 gr of brewer's yeast. For preparing the aqueous part, 200 ml of honey and 200 ml of glycerol were dissolved and mixed together. Thereafter, the dry and liquid components were mixed, and held at room temperature for one week in closed containers (Silhacek and Miller 1972).

Insect colony. Eggs of the Indian meal moth were obtained from a laboratory colony maintained on an artificial diet (Silhacek and Miller 1972) from Tarbiat

Modares University (Tehran, Iran). Test insects were maintained on their respective test diets under laboratory conditions (25 ± 1ºC, 65 ± 5% R.H., and a 16:8 h light-dark photoperiod) for two generations prior to the start of the life table analysis.

Life table parameters. Age-specific survival rate (l_x) and fecundity (m_x) on different artificial diets were calculated according to Carey (1993) as well as the intrinsic rate of increase (r_m), net reproductive rate (R_0), finite rate of increase (λ), mean generation time (T) and doubling time (DT) (Birch 1948, Southwood and Henderson 2000) were also estimated on different artificial diets.

Extraction of digestive (gut) enzymes. The fifth instar larvae of *P. interpunctella* fed with artificial diets prepared by bran of various wheat cultivars for 24 h were chilled and quickly dissected under a stereo-microscope. The guts were gathered into a known volume of distilled water and were homogenized using a handheld glass grinder on ice. The homogenates were centrifuged at 16000 × g for 10 min at 4 °C. The resulting supernatants were then collected into new micro tubes and stored at -20°C until further use.

Protein determination. Protein concentration in the gut of the fifth instar larvae of *P. interpunctella* was quantified by the method of Bradford (1976) using bovine serum albumin (BSA) (Roche Co., Munich, Germany) as standard.

Proteolytic activity. General proteolytic activity in the midgut of *P. interpunctella* fifth instar larvae was assayed using azocasein (Sigma chemical Co., St Louis, USA) as a substrate at the optimal pH. The method of Elpidina et al. (2001) was used with slight modifications in determining the optimal pH of proteolytic activity in the gut. To evaluate the proteolytic activity, the reaction mixture containing 80 μL of 1.5% azocasein solution in 50 mM universal buffer (pH 12) and 50 μL of crude enzyme was incubated at 37 °C for 50 min. The reaction was ended by adding 100 μL of 30% trichloroacetic acid (TCA). Precipitation was achieved by cooling at 4° C for 30 min, and the reaction mixture was centrifuged at 16000 × g for 10 min. The supernatant (100 μL) was added to 100 μL of 2 M NaOH and the absorbance was read at 440 nm. Appropriate blanks that TCA had been added before the substrate was prepared for each examine. One unit of protease activity was determined as an increase in optical density mg⁻¹ protein of the tissue min⁻¹ due to azocasein proteolysis. All experiments were done in triplicates with three different supernatants.

Amylolytic activity. Amylolytic activity in the midgut of *P. interpunctella* fifth instar larvae was assayed using 1% soluble starch (Sigma chemical Co., St Louis, USA)

as substrate at the optimal pH, according to the method of Bernfeld (1955). A quantity of 20 µL of the enzyme extract was incubated with 500 µL of universal buffer (pH 10) and 40 µL of soluble starch for 30 min at 37 °C. The reaction was stopped by adding 100 µL of DNSA (Sigma chemical Co., St Louis, USA) and heated in boiling water for 10 min. The absorbance was read at 540 nm after cooling on ice. Unit activity was characterized as the amount of enzyme required to produce 1 mg of maltose (Sigma chemical Co., St Louis, USA) in 30 min at 37 °C under the given assay conditions. All experiments were carried out in triplicates with three different supernatants.

Data analysis. Life table parameters and digestive enzymatic activity of *P. interpunctella* reared on different artificial diets were analyzed by one-way ANOVA, followed by the comparison of means with LSD test at α = 0.05, using statistical software Minitab 16.0. All data were tested for normality before analysis. Differences in each life table parameter on different artificial diets were tested for significance by estimating variances using the jackknife procedure (Meyer et al. 1986, Maia et al. 2000).

RESULTS

Survival and fecundity. Age-specific survival rate (l_x) and fecundity (m_x) of *P. interpunctella* on different artificial diets are shown in Figure 1. The survival rate of individuals to adulthood from the initial cohort stage was estimated to be 0.88, 0.81, 0.82, 0.77, 0.81 , 0.44, 0.73, 0.81 and 0.62 on 'Back cross Roshan', 'Khoshki line 9', Khooshe Pishgam, Arg', Alvand', 'Pishtaz', 'WS-89-2', 'Sepahan' and 'Bam, respectively. Our results showed

that the death of the last female on mentioned wheat cultivars artificial diets occurred in the age of 57, 57, 62, 58, 62, 63, 58, 60 and 63 days, respectively (Fig. 1).

First oviposition on the examined cultivars occurred in the age of 48, 50, 54, 52, 55, 57, 52, 53, and 58 days, 'Back cross Roshan', 'Khoshki line 9', Khooshe Pishgam, Arg', Alvand', 'Pishtaz', 'WS-89-2', 'Sepahan' and 'Bam, respectively. The highest daily fecundity (m_x) of *P. interpunctella* adult emerged from the larvae reared on these cultivars was 16.4, 16.3, 17.87, 13.4, 18.16, 11.8, 18.0, 13.9 and 16.2 females/female/day, respectively that occurred in the ages of 52, 52, 57, 55, 60, 60, 54, 56 and 60 days, 'Back cross Roshan', 'Khoshki line 9', 'Khooshe Pishgam', 'Arg', Alvand', 'Pishtaz', 'WS-89-2', 'Sepahan' and 'Bam', respectively (Fig. 1).

Life table parameters. The net reproductive rate (R_0) of *P. interpunctella* was the highest (78.05±4.80 female/female/generation) on 'Backcross Roshan' (F = 13.17; df = 8, 36; *P*<0.01). However, no significant differences were observed for the R_0 value of *P. interpunctella* fed with 'Backcross Roshan', 'Alvand' and 'Khooshe Pishgam' (Table 1). However, the intrinsic rate of increase (rm) ranged from 0.0520 ± 0.0006 to 0.0836 ± 0.0008 (day⁻¹), which was lowest on 'Pishtaz' and highest on 'Backcross Roshan' (F = 69.67; df = 8, 36; *P*<0.01). Furthermore, the finite rate of increase (λ) value of this insect showed significant differences based on rearing diet (F = 68.86; df = 8, 36; *P*<0.01), being lowest on 'Pishtaz' (1.053 ±0.001 day⁻¹) and highest on 'Backcross Roshan' (1.087 ± 0.001 day⁻¹). Among the different artificial diets, the mean generation time (*T*) was longest on 'Bam' (60.09±0.11 days) and 'Pishtaz' (59.36 ± 0.34 days) and shortest on 'Backcross Roshan'

TABLE 1. Mean (± SE) life table parameters of *Plodia interpunctella* on artificial diet containing bran of various wheat cultivars under laboratory conditions

	Parameter (mean ± SE)				
Wheat cultivars	**R_0** (female/female/generation)	**r_m** (day⁻¹)	**λ** (day⁻¹)	**T** (day)	**DT** (day)
'Backcross Roshan'	78.05±4.80a	0.0836±0.0008a	1.087±0.001a	52.12±0.40e	8.28±0.08f
'Khooshe Pishgam'	64.97±6.98ab	0.0739±0.0016bcd	1.076±0.002bcd	56.57±0.39c	9.37±0.20cde
'Khoshki line 9'	58.31±5.92bc	0.0772±0.0014b	1.080±0.002b	52.75±0.47e	8.97±0.17e
'Arg'	49.02±3.92bc	0.0715±0.0013cd	1.074±0.001cd	54.51±0.16d	9.69±0.18cd
'Alvand'	64.49±5.90ab	0.0719±0.0010cd	1.074±0.001cd	57.99±0.71b	9.63±0.13cd
'Pishtaz'	21.82±0.96d	0.0520±0.0006f	1.053±0.001f	59.36±0.34a	13.33±0.16a
'WS-89-2'	60.57±3.69b	0.0756±0.0007bc	1.078±0.001bc	54.28±0.35d	9.16±0.09de
'Sepahan'	50.26±1.91bc	0.0705±0.0007d	1.071±0.001d	55.59±0.32cd	9.83±0.10c
'Bam'	41.80±1.83c	0.0621±0.0007e	1.064±0.002e	60.09±0.11a	11.15±0.14b

The means followed by different letters in the same column are significantly different (LSD, P<0.01)

R_0= net reproductive rate, *rm* = intrinsic rate of increase, λ = finite rate of increase, *T* = mean generation time, *DT* = doubling time
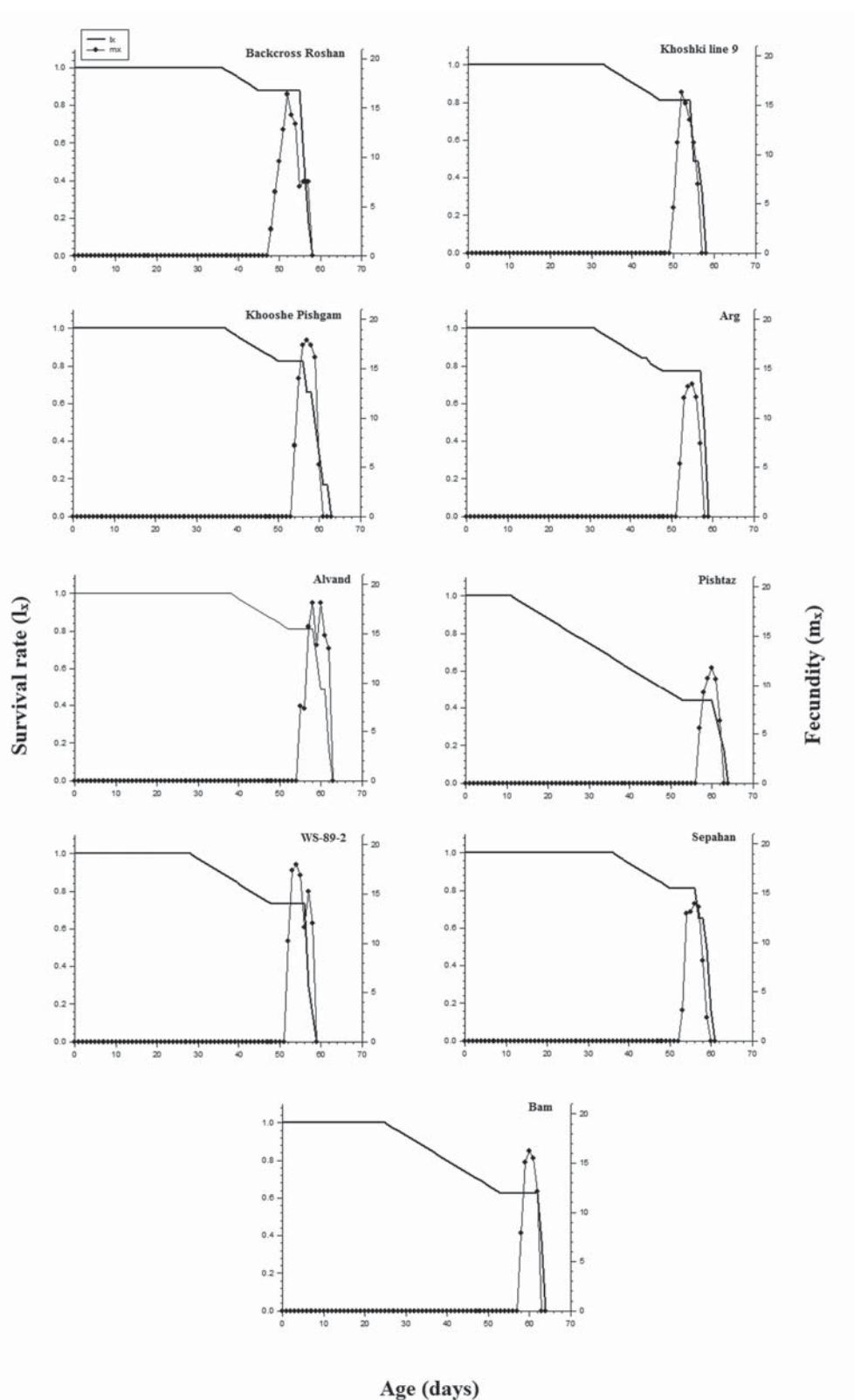
FIG. 1. Age-specific survival rate (l_x) and fecundity (m_x) of *Plodia interpunctella* fed on artificial diet containing bran of various wheat cultivars.

Table 2. Mean (± SE) proteolytic (U mg⁻¹) and amylolytic (mU mg⁻¹) activities of *Plodia interpunctella* fifth instar larvae fed on artificial diet containing bran of various wheat cultivars under laboratory conditions

Wheat cultivars	Index (mean ± SE)	
	Proteolytic activity (U mg⁻¹)	Amylolytic activity (mU mg⁻¹)
'Backcross Roshan'	1.19 ± 0.16a*	0.83 ± 0.09a
'Khooshe Pishgam'	0.53 ± 0.11bcd	0.68 ± 0.02ab
'Khoshki line 9'	0.83 ± 0.28abc	0.77 ± 0.04a
'Arg'	0.90 ± 0.03ab	0.78 ± 0.05a
'Alvand'	0.80 ± 0.30abc	0.85 ± 0.02a
'Pishtaz'	0.41 ± 0.04bcd	0.69 ± 0.15ab
'WS-89-2'	0.33 ± 0.10cd	0.54 ± 0.05bc
'Sepahan'	0.35 ± 0.03cd	0.36 ± 0.06c
'Bam'	0.24 ± 0.08d	0.43 ± 0.06c

The means followed by different letters in the same column are significantly different (LSD, $P < 0.01$; $P < 0.05$*)

and 'Khoshki line 9' (52.12 ± 0.40 and 52.75 ± 0.47 days, respectively) ($F = 49.30$; df = 8, 36; $P<0.01$). Moreover, the doubling time (DT) value of *P. interpunctella* on 'Pishtaz' was longer (13.33±0.16 days) than the other cultivars ($F = 98.67$; df = 8, 36; $P<0.01$).

Proteolytic activity. The highest value of proteolytic activity was found in larvae reared on 'Backcross Roshan' (1.19 ± 0.16 U mg⁻¹), and the lowest value was on 'Bam' (0.24 ± 0.08 U mg⁻¹). ($F = 12.50$; df = 8, 18; $P<0.05$)(Table 2).

Amylolytic activity. The highest amylolytic activity was found in the larvae fed with 'Alvand', 'Backcross Roshan', 'Arg' and 'Khoshki line 9' (0.85 ± 0.02, 0.83 ± 0.09, 0.78 ± 0.05 and 0.77 ± 0.04 mU mg⁻¹, respectively) and the lowest activity was in the larvae fed with 'Sepahan' and 'Bam' (0.36 ± 0.06 and 0.43 ± 0.06 mU mg⁻¹, respectively) ($F = 18.90$; df = 8, 18; $P<0.01$)(Table 2).

Discussion

Plodia interpunctella larvae are known for their ability to develop on a large variety of food hosts, and their development is largely influenced by the quality of food (LeCato 1976, Bouayad et al. 2008). In this study, it was shown that artificial diets containing bran of various wheat cultivars had significant effect not only on the life table parameters of *P. interpunctella*, but also on the two main digestive enzymes of this insect.

The higher rm value of *P. interpunctella* fed with an artificial diet containing bran of the wheat cultivar 'Backcross Roshan' was due to the greater fecundity, lower mortality and shorter development time of the immature stages on this cultivar. Nasirian et al (2014) showed that among different artificial diets, the efficiency of conversion of ingested food (ECI) value of

the fifth instar larvae of *P. interpunctella* was highest on cultivar 'Backcross Roshan', demonstrating that the fifth instar larvae fed with this cultivar, were more efficient at converting ingested food to body biomass. However, a lower rm value on cultivar 'Pishtaz' was mainly as a result of the lower fecundity and survivorship as well as longer development time of the immature stages of *P. interpunctella*. The r_m values of *P. interpunctella* in this study are different from the values reported by Pourbehi et al. (2008). Some probable reasons for these variations are due to physiological differences depending on the type of host and genetic differences in geographic populations of the insect. Although, a high value of r_m shows the suitability of a host to insect feeding, a low value shows that the host species is unsuitable to the insect. Since the cultivar 'Backcross Roshan' was a suitable host, *P. interpunctella* had the greatest chance of population increase. The net reproductive rate (R_0) indicates adult female production of *P. interpunctella* by a female during its lifetime. The highest net reproductive rate was on 'Backcross Roshan', which was 1.5 fold higher than that reported by Pourbehi et al. (2013), and this may be attributed to the difference in host-diet used for rearing *P. interpunctella*. However, the highest finite rate of increase (λ) and the shortest doubling time (DT) of *P. interpunctella* were on cultivar 'Backcross Roshan', and this is similar to that reported by Pourbehi et al. (2013) on date cultivar Zahedi (a suitable cultivar). The conformity between the results of the present study and the afore-mentioned study may be attributed to the polyphagous nature of the Indian meal moth. Moreover, the lowest net reproductive rate and longest doubling time of *P. interpunctella* was on cultivar 'Pishtaz', indicating that this cultivar is unsuitable for the mass rearing of this pest.

In the present research, the effects of various artificial diets on physiological responses were evaluated at the level of activity of two key digestive enzymes (i.e. protease and α-amylase) in *P. interpunctella* fifth instar larvae. In lepidopteran insects, differences in digestive enzymatic activity can influence feeding performance, especially ECI, in the ultimate instars (Slansky and Scriber 1985). Nasirian et al. (2014) showed that the highest value of ECI in *P. interpunctella* fifth instar larvae was on artificial diet containing bran of the wheat cultivar 'Backcross Roshan', demonstrating a positive correlation between feeding performance and digestive enzymatic activity. The gut enzymatic activity depends on the chemical composition of food sources and enzyme-inhibitors (Mendiola-Olaya et al. 2000). Borzouei (2012) reported that the highest proteolytic and amylolytic activity of *P. interpunctella* was on artificial diet (containing wheat bran, yeast, honey and glycerol) and the lowest activity was on raisin. Due to the fact that the lepidopteran larvae need a diet with high protein content, Borzouei (2012) found a positive correlation between the amounts of dietary protein and the level of proteolytic activity. The highest value of proteolytic activity was found in the fifth instar larvae fed with 'Backcross Roshan', which is probably related to the high protein content of the diet. The level of proteolytic activity on 'Backcross Roshan' was 5.5-fold higher than that detected for artificial diet-fed larvae of *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae) (Sarate et al. 2012), and was almost 2.5-fold lower than that reported by Mansouri et al. (2013) for *Phthorimaea operculella* (Zeller) (Lepidoptera: Gelechiidae) on potato germplasm Savalan (a suitable host). Farshbaf Pour Abad et al. (2010) reported that the amylolytic activity in the fifth instar larvae of *P. interpunctella* was higher than that observed in the fifth instar larvae of this research. The results of the present study indicate that the highest amylolytic activity of the fifth instar larvae on 'Alvand' is approximately 2.5 fold higher than that reported by Jafarlu et al. (2012), for the female fifth instar larvae of *Anagasta kuehnieklla* (Zeller) (Lepidoptera: Pyralidae) on wheat flour. The possible reasons for the afore-mentioned inconsistency could be attributed to differences in artificial diets, variations in experimental conditions and examined insect species. Silva et al. (2001) stated that the α-amylase gene is regulated according to the starch or glucose contents in the dietary substrate. In another study, Bouayad et al. (2008) showed that this regulation also existed in *P. interpunctella* larvae and the levels of α-amylase activity depended on both glucose repression and starch induction. Also, Borzouei (2012) showed that amylolytic activity decreased with increase in the amounts of dietary carbohydrates. As for the relationships between digestive enzymatic activity and protein/starch contents of various wheat cultivars, it seems that there is an insect mechanism that accurately assesses food contents and regulates the levels of these vital digestive enzymes (Kotkar et al. 2009). Typically, the variations in protease and amylase activities in *P. interpunctella* larvae fed with various artificial diets may be attributed to the differences in either the protein and starch contents of the diet or the response of the insect to dietary enzymes-inhibitors. To validate the findings of this study, additional studies should be considered in the future.

Since *P. interpunctella* is a suitable alternative host for the rearing of some predators and parasitoids (Ferkovich and Shapiro 2004, Ghimire and Phillips 2010, Spanoudis and Andreadis 2012), optimizing the mass rearing of this insect on artificial diets would be economically useful. By combining the results of the current study regarding life table parameters and the digestive physiology of the Indian meal moth on artificial diet based on bran of various wheat cultivars, it was found that the cultivar 'Backcross Roshan' is the most suitable host for preparing the artificial diet for *P. interpunctella* rearing. For a better confirmation and more application of the results of this study, supplementary researches need to focus on the study of the specific digestive enzymes properties of the Indian meal moth fed with various artificial diets containing bran of different wheat cultivars.

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SPECIATION IN AN INSULAR SAND DUNE HABITAT:
ATRYTONOPSIS (HESPERIIDAE: HESPERIINAE)—MAINLY FROM THE SOUTHWESTERN UNITED STATES AND MEXICO—OFF THE NORTH CAROLINA COAST

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ABSTRACT. Genus *Atrytonopsis* of the American Southwest and Mexico includes the distributionally anomalous species *Atrytonopsis hianna* of the eastern United States, which has given rise to a species that is, in addition, ecologically anomalous (not just for its genus but for US hesperiids generally): *Atrytonopsis quinteri* **new species** lives in sand dunes along a 50-km stretch of two North Carolina barrier islands (Bogue Banks and Bear Island) and on nearby man-made Radio Island. The oviposition site and larval foodplant of this skipper is the coastal grass *Schizachyrium littorale*, which thrives in the rigorous sand dune habitat. *Atrytonopsis quinteri* is bivoltine and locally abundant. Courtship can be cursory; larvae go through 6 instars; and adults have a notably distinctive facies but variable genitalia like those of *A. hianna* (except that some *A. quinteri* females more frequently express an extreme genitalic variant). Genitalia of this pair of species differ somewhat from those of their congeners, most of which are illustrated. Among these, female genitalia show that *A. margarita* **revised status** is a species separate from its current senior synonym, *A. python*. *Atrytonopsis quinteri* and *A. hianna* are geographically close to each other: at one point the intervening gap (mostly water and marsh) is no more than 5 km.

Additional key words: genitalia (male and female), life history, larval foodplant, *Schizachyrium littorale*, *Atrytonopsis quinteri* **new species**, *Atrytonopsis hianna*, *Atrytonopsis margarita* **revised status**

Breaking an ecologic mold may involve speciation. Of nearly 300 species of skipper butterflies (hesperiids) in the United States, a few are more or less coastal, frequenting salt to brackish marshes. But a notable differentiate of *Atrytonopsis* inhabits dry maritime sand dunes, primarily on Bogue Banks and Bear Island, North Carolina. This skipper's narrow, linear range is c. 50 km long (Fig. 1).

About 13 known congeners are mainland species occurring mostly in the southwestern United States and Mexico, with one of these species, *A. ovinia* (Hewitson), reaching Costa Rica, but also with an outlying species, *A. hianna* (Scudder), in most of the central and eastern United States and adjacent southern Canada. *Atrytonopsis hianna* includes geographic variants of debatable taxonomic rank, distribution, and designation (Hall 2004), i.e., *A. loammi* (Whitney) or *A. hianna loammi* or neither, in the Southeast; and *A. turneri* Freeman or *A. hianna turneri* or neither, in central and western Plains. Analysis of their mutual relationships is beyond the scope of this paper, in which use of the name *A. hianna* is inclusive.

The island skipper's limited range in a peculiar environment explains why it was overlooked for so long, despite its size, facies, abundance, bivoltinism, and presence on a populated strip of land (Bogue Banks). There, owing to natural phenomena and to human predilection for developing seasides, much of this skipper's requisite habitat has been modified or destroyed. But North Carolina's establishment of Fort Macon State Park (opened in 1936) and Hammocks Beach State Park (opened in 1961) chanced to preserve

significant areas of excellent habitat at opposite ends of the skipper's short range. The latter park, which occupies Bear Island, at the west end of the range, is especially beneficial because it is inaccessible by car or by other than a small boat and so is relatively unspoiled. At the east end of the range (Fort Macon), in 1978, Eric L. Quinter collected a pair of the ecologically restricted skipper, which he later passed on to me. Meanwhile, having been informed by Quinter of his odd catch, J. Bolling Sullivan verified it; and he and Richard A. Anderson brought several specimens to my attention in 1983.

MATERIALS AND METHODS

Armed with state permits, I went to Bogue Banks, Carteret County, North Carolina, and Bear Island, Onslow County, North Carolina, as well as to more or less adjacent islands and mainland, in late July 1983, late April/early May 1984, and late April 1985, collecting as much without as within the state parks. With special permission to collect, under supervision, at points along Onslow Beach in Camp Lejeune Marine Corps Base, Onslow County, North Carolina, I visited this locality on 26 April 1985. Using a Voigtländer Bessamatic 35mm camera, I photographed various prime areas harboring the dune skipper. I spread all specimens dorsal side up and, to document their size, measured the length of the right forewing (FW), from base of costa to apex, with a Helios vernier caliper calibrated to tenths of a millimeter. I defined each measured sample by locality, year of collection, generation, and sex of its specimens. To free genitalia, a separated abdomen was soaked for

FIG. 1. Islands along the North Carolina coast on four of which *A. quinteri* occurs, plus adjacent mainland harboring *A. hianna*.

5–10 minutes in a hot 10% solution of KOH, or overnight in that solution at room temperature; and the genitalia were dissected and cleaned with jeweler's forceps and a small paint brush. Using a Leitz Wetzlar stereomicroscope, I studied and compared, at all angles, a total of 285 dissected genitalia of the known species of *Atrytonopsis*, either in ethanol or in glycerol in 12-depression porcelain spotplates. In 1984 and 1985, starting with eggs seen laid in the field and, especially, with eggs obtained from caged females, I reared 18 adults from larvae that were individually housed in vials. Since reared adults average smaller than wild-caught ones, I discounted their measurements.

RESULTS

Atrytonopsis quinteri, new species

Description.—Size (Table 1): In both generations, FW length averages c. 17 mm in males and 18+ mm in females. As expected, females average a little larger than males; but, unexpectedly, at Fort Macon State Park, where sample sizes are biggest, males and females of the second generation average no larger than those of the first.

Facies (Figs. 2–14, 17–29): As is usual in hesperiids, wings of the female are broader and more rounded than those of the male. Pale spots of the FW are slightly yellowish cream both dorsally and ventrally, where they contrast with truly white spots of the ventral HW. Maximum expression of FW spots is (a) an irregular subapical to submarginal band of 8 spots, in which the 3 (usually elongate) subapical spots are offset inward and (unlike the 5 submarginal ones) tight together; and (b) a pair of spots, one above the other in the middle of the discal cell. The 8-spot band runs from cell R_3–R_4 to cell CuA_2–$1A+2A$. Spots are larger (a) in females than in males; and (b) ventrally than dorsally. Ventral HW spots form a nested pair of wide Vs lying on their side and pointing outward, with (a) one V submarginal and comprising 7 spots that run from cell $Sc+R_1$–Rs to cell CuA_2–$1A+2A$, with the point of the V in cell M_1–M_2; and (b) the other V basal and comprising only 3 spots, with the upper one in cell $Sc+R_1$–Rs, the middle one (which is the point of the V) in the discal cell, and the lower one in cell CuA_2–$1A+2A$. Part of the submarginal V (especially its lower arm) often appears, more or less faintly, and especially in females, on the dorsal HW. Dorsal ground color of both wings is a medium brown with a touch of gray. Ventral ground color is more complex: a narrow marginal zone of pale lavender-gray shingle-like scales distad of the major bands gives the outer edge of the wings a hoary look; and the pale bands themselves disrupt a ground color that ranges through light to medium browns, overscaled with scales and hairs of dull yellow to beige.

Large samples of adults reveal lots of individual variation in wing spotting, not just between, but also within, the sexes. For example, the characteristic submarginal FW spots in cells M_1–M_2 and M_2–M_3 diminish in size and vanish in the series of four males in Figs. 2–5, 17–20; and in the same four males (which are all from one population), ventral HW spots vary greatly in size and shape (as the spots generally

Table 1. Length (mm) of right forewing of *Atrytonopsis quinteri* and *A. hianna* at six localities in Carteret and Onslow counties, North Carolina. (The *A. hianna* populations are univoltine.)

Species	Locality	Year	Brood	Sex	N	Range	Mean	SD
A. quinteri	Bear Island	1985	1	M	18	15.6–18.2	16.78	0.65
	Bear Island	1985	1	F	24	16.0–19.4	18.14	0.86
	Bear Island	1983	2	M	8	16.2–17.5	17.15	0.40
	Bear Island	1983	2	F	5	18.3–19.6	18.62	0.55
	Bogue Banks, Emerald Isle	1984, 1985	1	M	30	16.2–18.4	17.34	0.57
	Bogue Banks, Emerald Isle	1984, 1985	1	F	10	16.9–20.4	18.66	1.16
	Bogue Banks, Ft. Macon	1984	1	M	70	15.8–17.8	17.00	0.47
	Bogue Banks, Ft. Macon	1984	1	F	35	16.8–19.5	18.20	0.58
	Bogue Banks, Ft. Macon	1983	2	M	64	15.5–17.7	16.58	0.44
	Bogue Banks, Ft. Macon	1983	2	F	35	16.2–19.1	18.00	0.71
	Radio Island	1984, 1985	1	M	30	15.9–17.7	17.02	0.50
	Radio Island	1984, 1985	1	F	33	17.2–20.0	18.29	0.74
A. hianna	Swansboro	1984, 1985	1	M	24	14.8–18.0	16.25	0.66
	Holly Ridge	1984, 1985	1	M	40	15.0–17.7	16.70	0.63
	Holly Ridge	1984, 1985	1	F	8	16.6–19.5	18.20	1.18

do). The FW spot in cell CuA_2–$1A+2A$ (which, unlike other spots, is diffuse) rarely shows dorsally in males but frequently does, to a variable extent, in females; present in both sexes ventrally, it is much better (although variably) expressed in females. The two FW discal cell spots may be missing or reduced to one, chiefly in males; both are usually present in females and, in either sex, may be joined in various ways (Figs. 2, 6, 7, 9–14, 17, 21, 22, 24–29).

The dorsal FW of the male bears an inconspicuous, slender, 3-part stigma (best seen in Figs. 5, 6, 11) that slants from a point at, or slightly proximad of, the union of veins M_3 and CuA_1 downward and inward to the middle of vein $1A+2A$. One part of the stigma spans cell CuA_1–CuA_2 and the other two parts span cell CuA_2–$1A+2A$.

Genitalia (Figs. 32, 43): Both sexes of *Atrytonopsis* closely reflect the genitalic template characterizing this genus. Interspecific expression is conservative (Figs. 33–42, 44–54). For species whose genitalia differ little from one another, isolated description is of little use. For appropriate treatment of *A. quinteri*, see "Genitalic context" in the Discussion.

Larval foodplant: *Schizachyrium littorale* (Nash) Bicknell; Poaceae.

Number of larval instars: 6.

Generations per year: 2: midspring (mostly late April to early May) and midsummer (mostly late July to early August).

Range and habitat (Figs. 1, 56–61): Coastal North Carolina: primarily Bogue Banks in Carteret County and Bear Island in Onslow County; secondarily Radio Island and two or three other dredge spoil islands in Carteret County. In insular sand dunes that support the endemic larval foodplant; these dunes lie behind barrier dunes (a.k.a. primary dunes or foredunes), except on dredge spoil islands, which lack them. See "Distributional detail" and "Natural history" in the Discussion.

Type material.—Holotype: ♂ (Figs. 11, 26) Hammocks Beach State Park, Bear Island, Onslow County, North Carolina, 28-VII-1983, John M. Burns, collector. Deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM).

Paratypes: Fort Macon State Park, Bogue Banks, Carteret Co., North Carolina: 26-VII-1978, 1♂, 1♀ (E. L. Quinter); 31-VII-1982, 2♂, 2♀ (R. A. Anderson); 10-V-1983, 3♂, 1♀ (J. B. Sullivan); 25-VII-1983, 5♂, 6♀; 26-VII-1983, 56♂, 28♀; 27-VII-1983, 4♂, 1♀; 25-IV-1984, 74♂, 36♀. Emerald Isle, Bogue Banks, Carteret Co., North Carolina: 1-V-1984, 21♂, 1♀; 24-IV-1985, 9♂, 9♀. Hammocks Beach State Park, Bear Island,
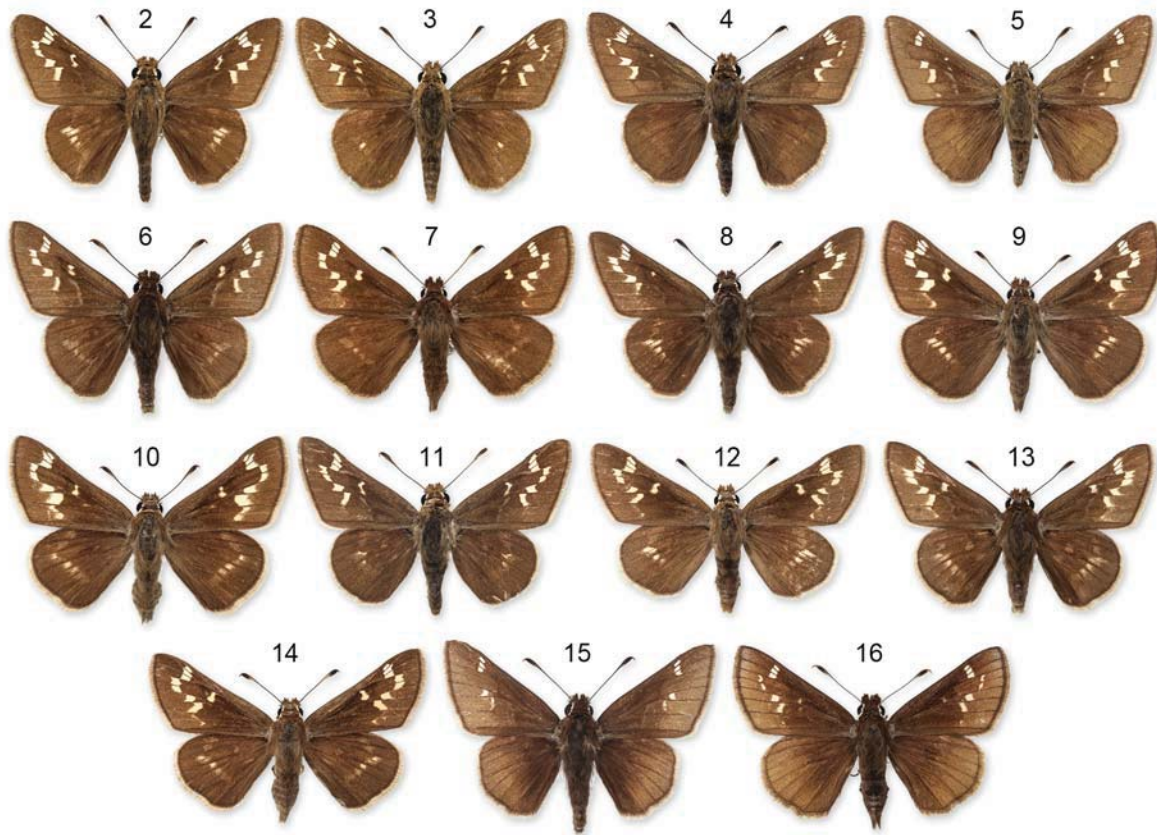
Figs. 2–16. *Atrytonopsis* adults from Carteret and Onslow counties, North Carolina. Dorsal views. **2–14,** *A. quinteri*; **15, 16,** *A. hianna*. **2–6, 8, 11, 13, 15,** Males; **7, 9, 10, 12, 14, 16,** Females. **2–5,** Ft. Macon State Park, Bogue Banks, 26 and 27-VII-1983. **6, 7,** Radio Island, 2-V-1984. **8–10,** Emerald Isle, Bogue Banks, 1-V-1984 and 24-IV-1985. **11–14,** Hammocks Beach State Park, Bear Island, 27 and 28-VII-1983, 25-IV-1985. **15,** 2 mi. N of Mill Creek, 5.5 mi. N of Morehead City, 3-V-1984. **16,** 1 mi. W of Swansboro, 26-IV-1985. All specimens collected by J. M. Burns.

Onslow County, North Carolina: 27-VII-1983, 3♂, 3♀; 28-VII-1983, 4♂, 2♀; 25-IV-1985, 18♂, 24♀. Radio Island, Carteret Co., North Carolina: 2-V-1984, 19♂, 20♀; 29-IV-1985, 3♂, 4♀; 30-IV-1985, 10♂, 12♀. Except as noted at the beginning of this list, specimens collected by John M. Burns. Paratypes deposited in USNM (some to be distributed).

Etymology.—Named in honor of Eric L. Quinter, who discovered and first collected this skipper, perceived its significance, and generously provided his specimens.

Diagnosis.—All females of *A. quinteri* have FW spots in cells M_1–M_2 and M_2–M_3 and most males express both of them (though sometimes they are small). These spots also appear in well-sampled neighboring populations of *A. hianna*, but are far less frequent (present in only ¼ of 64 males examined, where they are rudimentary and, with three exceptions, only in cell M_2–M_3; and present in 5 of 8 females, where they are small but in both cells [Figs. 16, 31]). However, other species of *Atrytonopsis* lack FW spots in cells M_1–M_2 and M_2–M_3, except for two species from central Mexico—*A. llorentei* Warren 2009

and some females of the large species *A. frappenda* (Dyar)—and, just barely, for *A. pittacus* (W. H. Edwards) of west Texas, southwestern New Mexico, southeastern Arizona, and Mexico, in which 5 of 80 specimens examined show traces of a spot in one or both cells. Although the dorsal ground color of the wings is a medium brown in both *A. quinteri* and eastern populations of *A. hianna*, the brown usually looks grayer and colder in *A. quinteri*. This subtle difference is clearest when directly comparing large samples of each species. In *A. hianna*, far more than in *A. quinteri*, the dorsal brown is lighter distally than proximally so that the wing veins (which are darker) often stand out where they cross the light area; and, ventrally, the distal hoariness of the wings extends much more proximad than it does in *A. quinteri*. The ventral HW does not exhibit *A. quinteri*'s usually bold spotting. FW length in neighboring populations of *A. hianna* is like that of *A.*
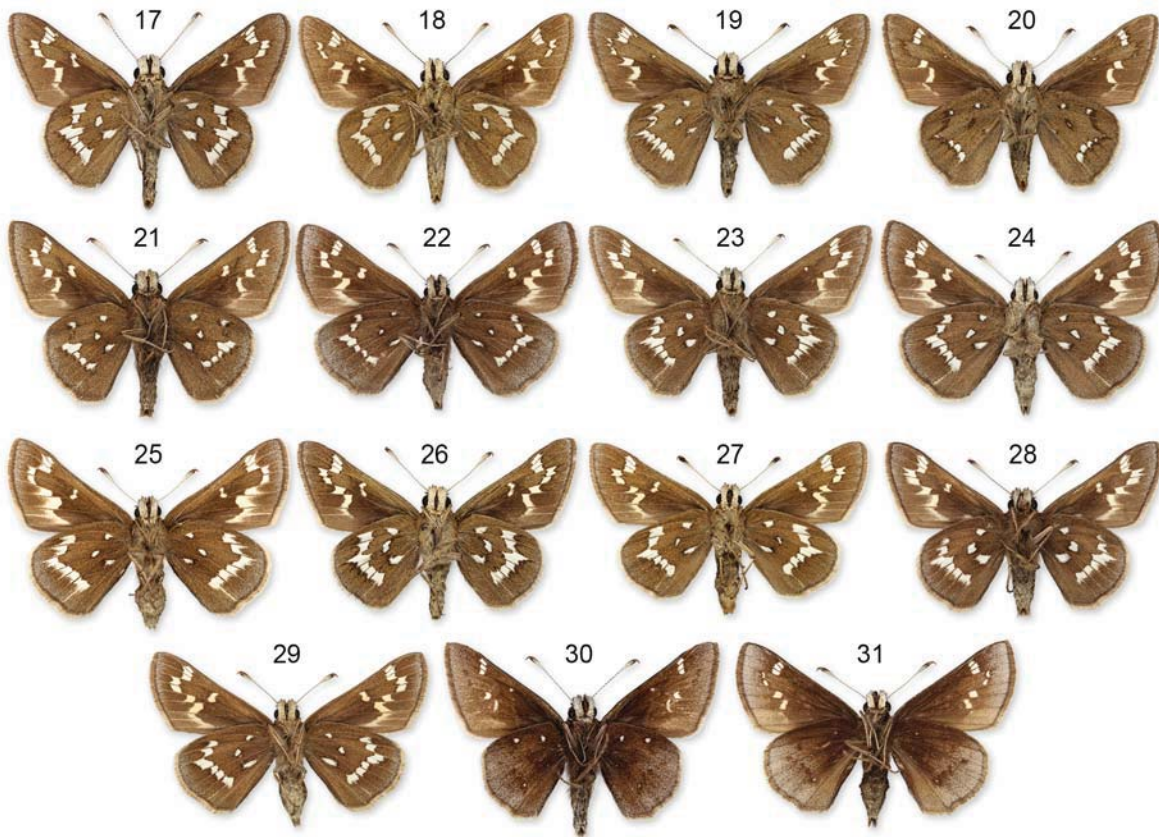
Figs. 17–31. *Atrytonopsis* adults from Carteret and Onslow counties, North Carolina. Ventral views of the same specimens as in Figs. 2–16 in the same sequence. **17–29,** *A. quinteri*; **30, 31,** *A. hianna.* **17–21, 23, 26, 28, 30,** Males; **22, 24, 25, 27, 29, 31,** Females. **17–20,** Ft. Macon State Park, Bogue Banks, 26 and 27-VII-1983. **21, 22,** Radio Island, 2-V-1984. **23–25,** Emerald Isle, Bogue Banks, 1-V-1984 and 24-IV-1985. **26–29,** Hammocks Beach State Park, Bear Island, 27 and 28-VII-1983, 25-IV-1985. **30,** 2 mi. N of Mill Creek, 5.5 mi. N of Morehead City, 3-V-1984. **31,** 1 mi. W of Swansboro, 26-IV-1985. All specimens collected by J. M. Burns.

quinteri (Table 1). For consideration of an interspecific difference in the frequency of an odd variation in female genitalia, see "Genitalic context" in the Discussion. For differences in eggs and larvae of these two species, see "Natural history" in the Discussion. *Atrytonopsis quinteri* is extremely limited in distribution and habitat, abundant where it occurs, and not sympatric with any of its congeners.

Discussion

Distributional detail (Fig. 1). *Atrytonopsis quinteri* can cross water. I discovered a thriving population of the skipper, along with ample foodplant, when I drove onto Radio Island on 2 May 1984. This sandy island, aptly dubbed a "dredge spoil island," surfaced in 1911 and mushroomed in the 1940s and 1950s, when material from deepening the channel between Morehead City and Beaufort was dumped on what had been no more

than a salt marsh island. As a result, Radio Island differs from Bogue Banks and Bear Island: it is lower, flatter, and devoid of barrier dunes and maritime forest. Because it lies between the two cities, with its south edge c. ¾ km north of the east end of Bogue Banks, it may be more protected from the elements—but not from human exploitation (some of which was already evident [Fig. 60] and is ongoing).

Although potentially accessible natural habitat extends beyond the documented range of *A. quinteri*, unnatural conditions may hamper the skipper. Having arranged passage to and from the west end of Shackleford Banks (a long-uninhabited island c. 1 km east of Fort Macon [a distance of this kind varies with storms, which constantly move and reshape the barrier islands—see below]), I spent a few hours on 2 May 1984 exploring that area: the physical habitat looked promising, but the larval foodplant was scarce and severely grazed by wild horses,
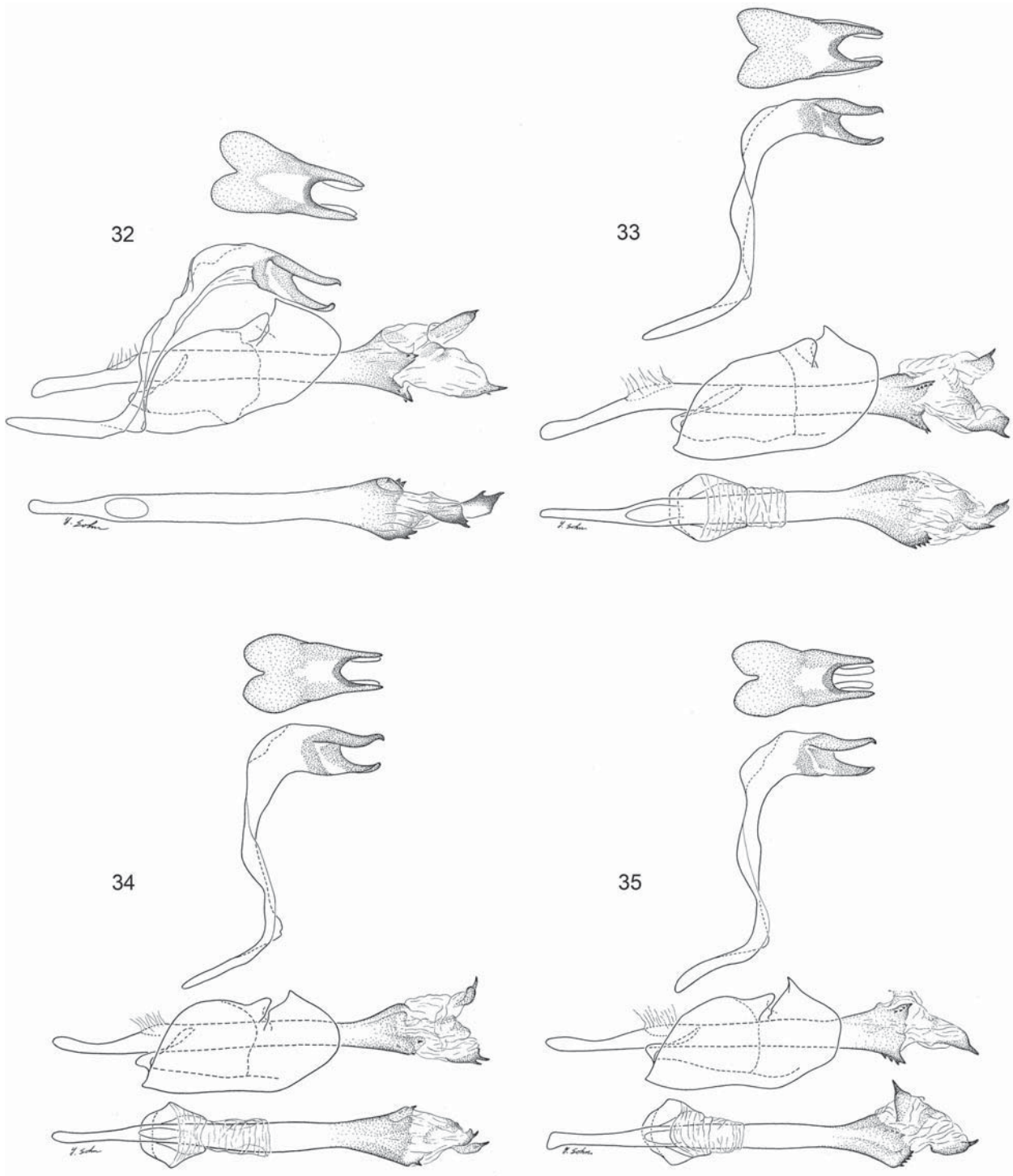
FIGS. 32–35. Male genitalia of *Atrytonopsis*. **32,** *A. quinteri*, Hammocks Beach State Park, Bear Island, Onslow Co., NC, 25-IV-1985, X-3554 (JMB). **33,** *A. hianna*, St. Petersburg, Pinellas Co., FL, 24-VI-1930, X-1196. **34,** *A. hianna*, Lexington (Grant St.), Middlesex Co., MA, 15-VI-1972, X-1199 (JMB). **35,** *A. hianna*, Bare Hills (area of serpentine outcrop just N of Baltimore city), Baltimore Co., MD, 29-V-1972, X-1096 (JMB). (X-codes designate genitalia dissections; JMB = John M. Burns, collector.)
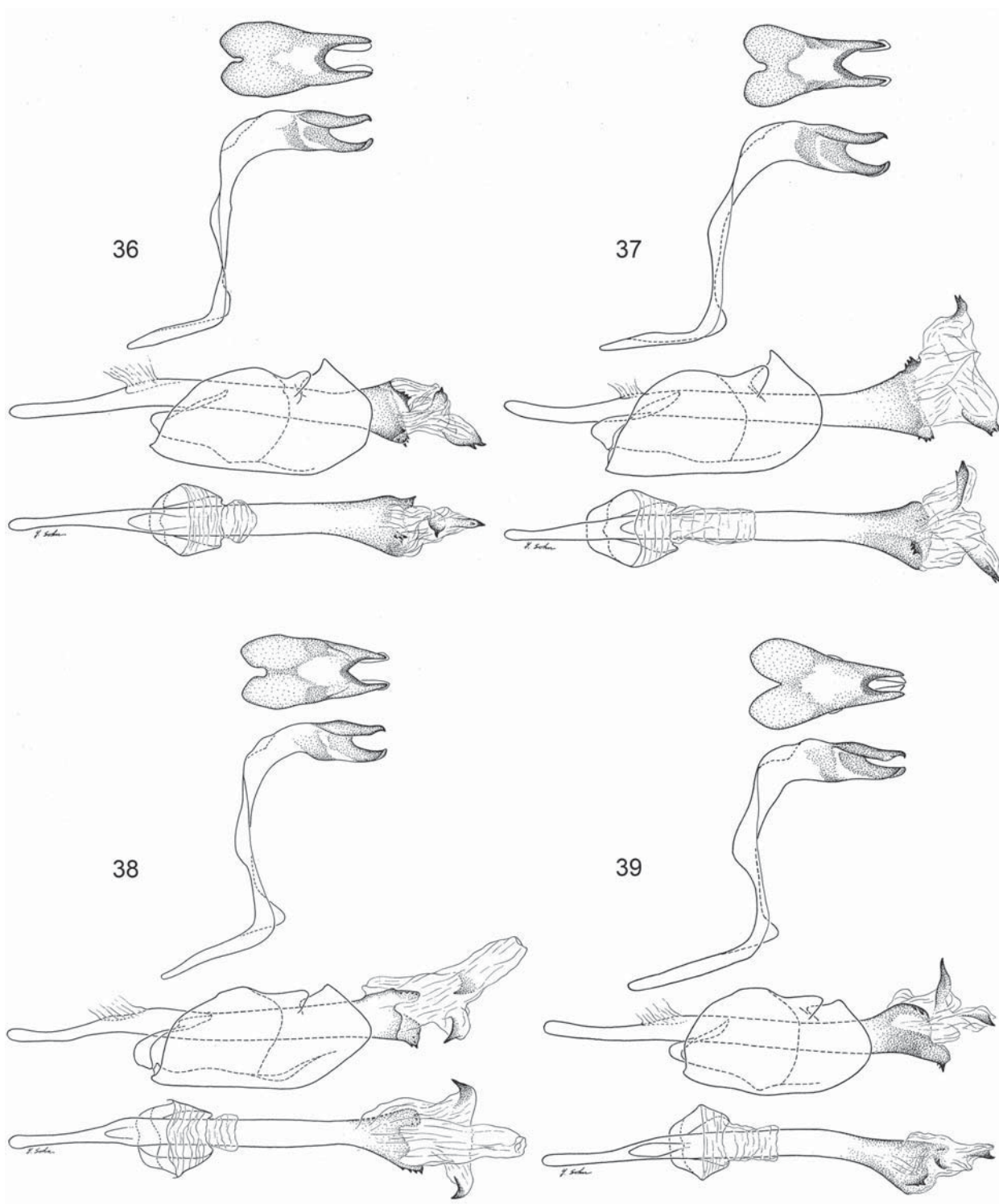
FIGS. 36–39. Male genitalia of *Atrytonopsis*. **36,** *A. vierecki*, Sitting Bull Falls, Guadalupe Mts., 4650 ft., Eddy Co., NM, 26-V-1959, X-1173 (JM & SNB). **37,** *A. deva*, 2 mi. ESE of Emory Pass, Black Range, 7000 ft., Sierra Co., NM, 27-V-1959, X-1189 (JM & SNB). **38,** *A. lunus*, Southwestern Research Station, Chiricahua Mts., Cochise Co., AZ, 6-VIII-1958, X-1179 (P. Opler). **39,** *A. pittacus*, HO Canyon, Davis Mts., 6000 ft., Jeff Davis Co., TX, 30-IV-1959, X-1181 (JM & SNB). (JM & SNB = John M. and Sarah N. Burns, collectors.)
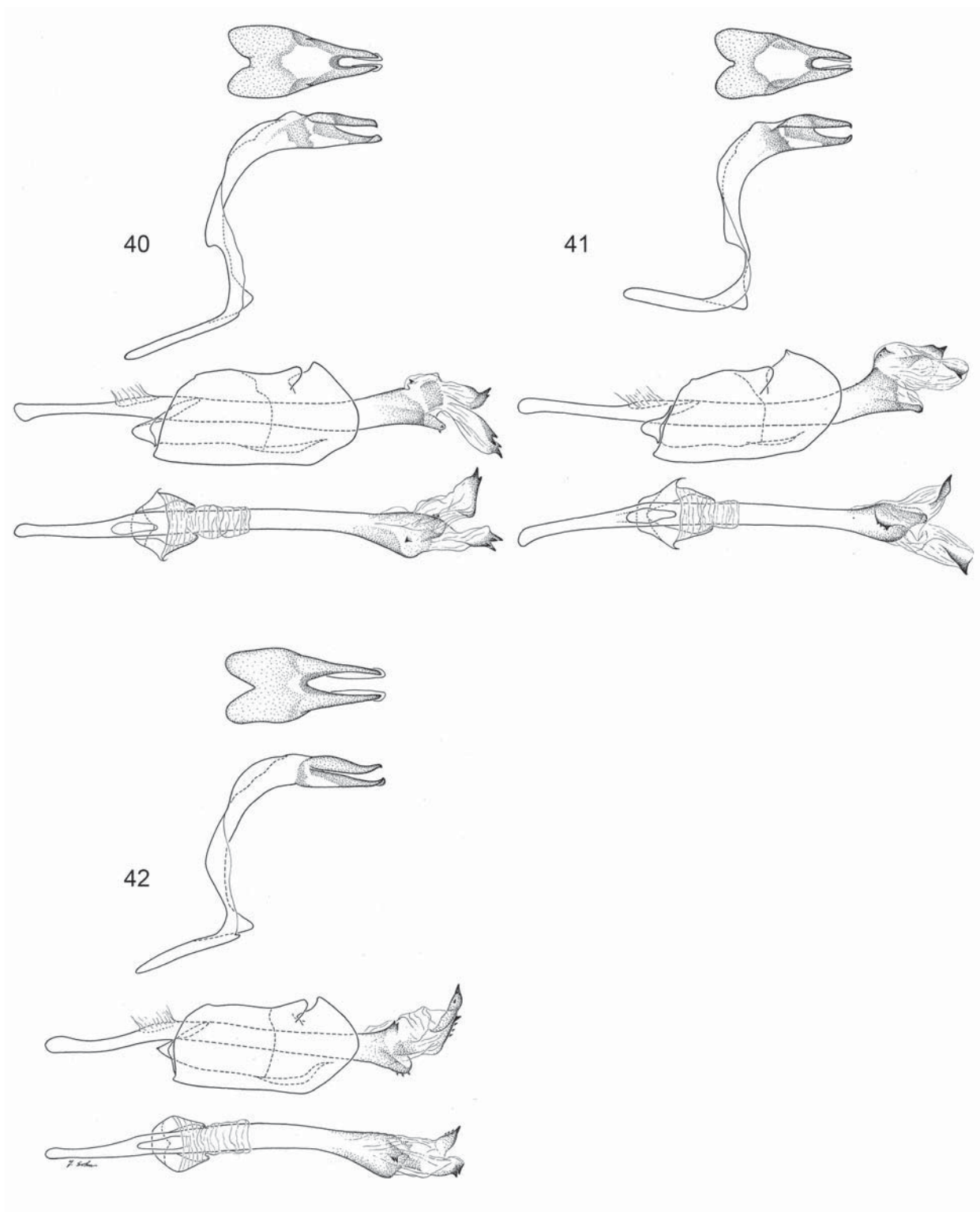
FIGS. 40–42. Male genitalia of *Atrytonopsis*. **40,** *A. python*, Palmerlee, Cochise Co., AZ, 8-V-1915, X-1131. **41,** *A. margarita*, Jemez Springs, Sandoval Co., NM, 24 to 31-V, X-1135. **42,** *A. cestus*, Baboquivari Mts., Pima Co., AZ, 15 to 30-V-1924, X-1144.
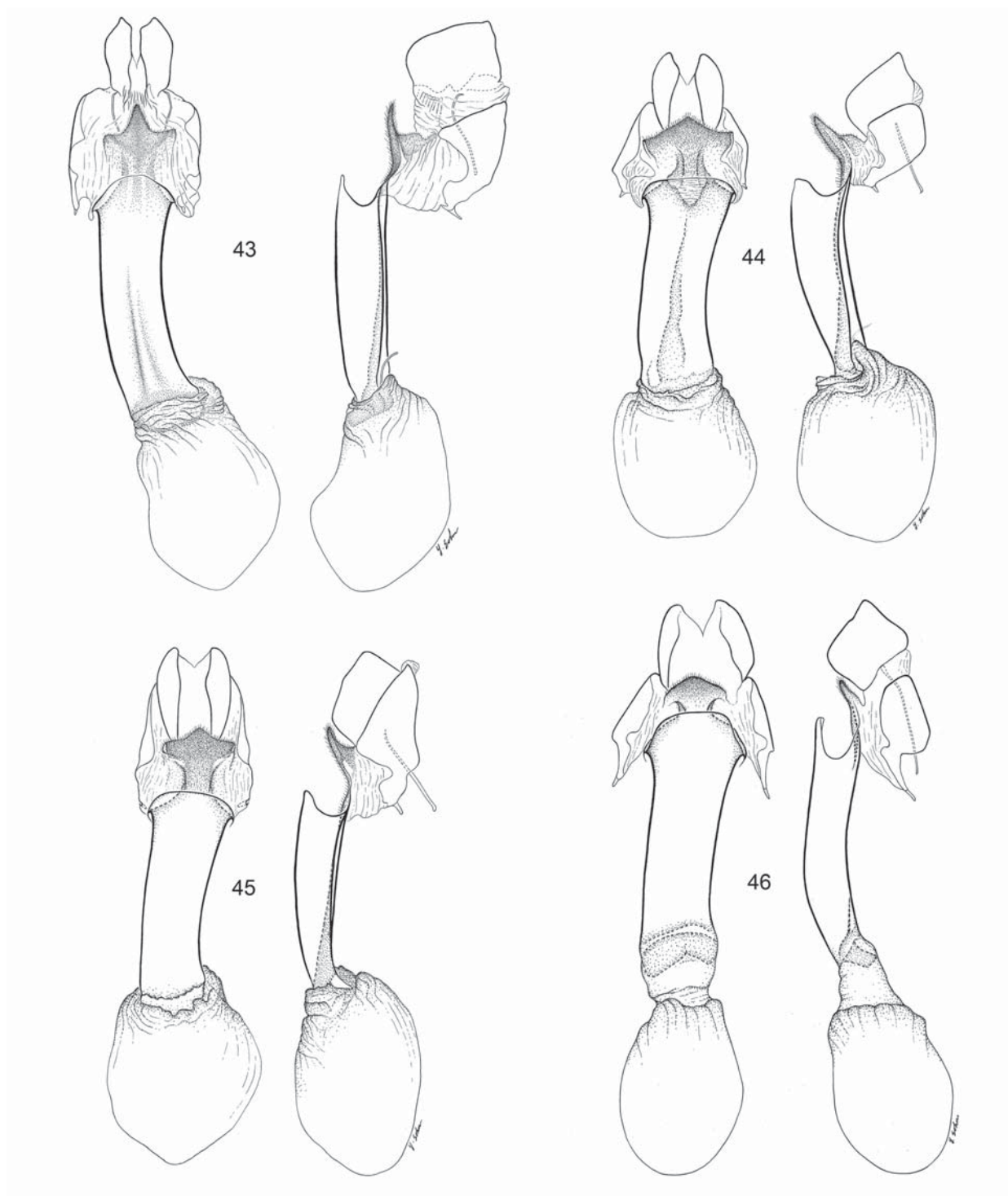
FIGS. 43–46. Female genitalia of *Atrytonopsis*. **43,** *A. quinteri*, Hammocks Beach State Park, Bear Island, Onslow Co., NC, 25-IV-1985, X-3560 (JMB). **44,** *A. hianna*, Lexington (Grant St.), Middlesex Co., MA, 2-VI-1975, X-1095 (JMB). **45,** *A. hianna*, New Berlin Rd. × Cedar Point Rd.: 0.5 mi. E of junction, northern Jacksonville, 24-III-1976, X-1195 (JMB). **46,** *A. lunus*, above Herb Martyr Camp and Dam, Cave Creek, Chiricahua Mts., 6000 ft., Cochise Co., AZ, 4-VIII-1974, X-1164 (JM & SNB).
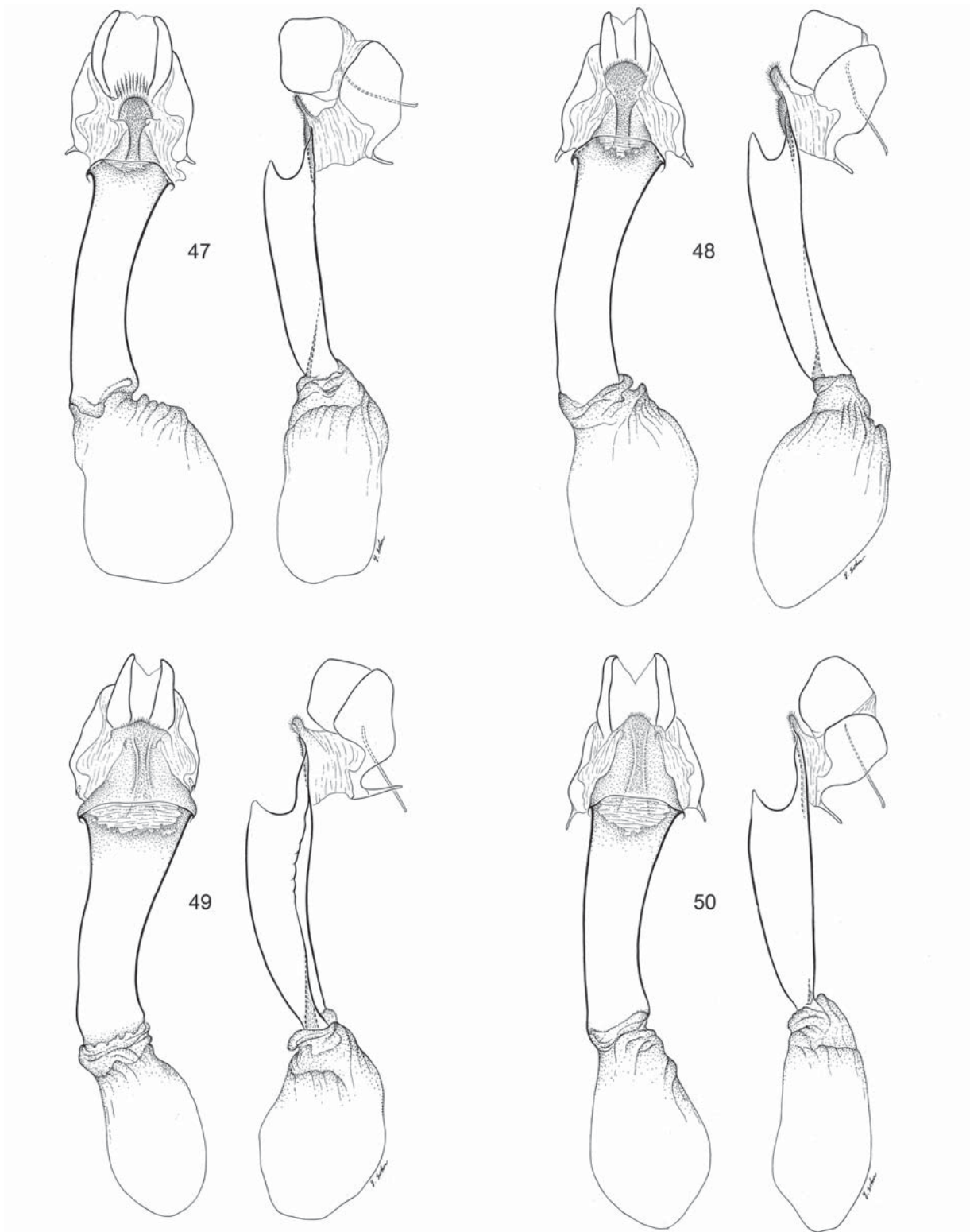
FIGS. 47–50. Female genitalia of *Atrytonopsis*. **47,** *A. python*, 2.5 mi. NE of San Lorenzo, Black Range, 6200 ft., Grant Co., NM, 28-V-1959, X-1163 (JM & SNB). **48,** *A. python*, Southwestern Research Station of AMNH, Cave Creek Canyon, Chiricahua Mts., 5400 ft., Cochise Co., AZ, 14-VI-1958, X-1155 (JM & SNB). **49,** *A. margarita*, Mount Locke, Davis Mts., 6300–6791 ft., Jeff Davis Co., TX, 4-V-1959, X-1158 (JM & SNB). **50,** *A. margarita*, Jemez Springs, Sandoval Co., NM, 24 to 30-VI, X-1209.
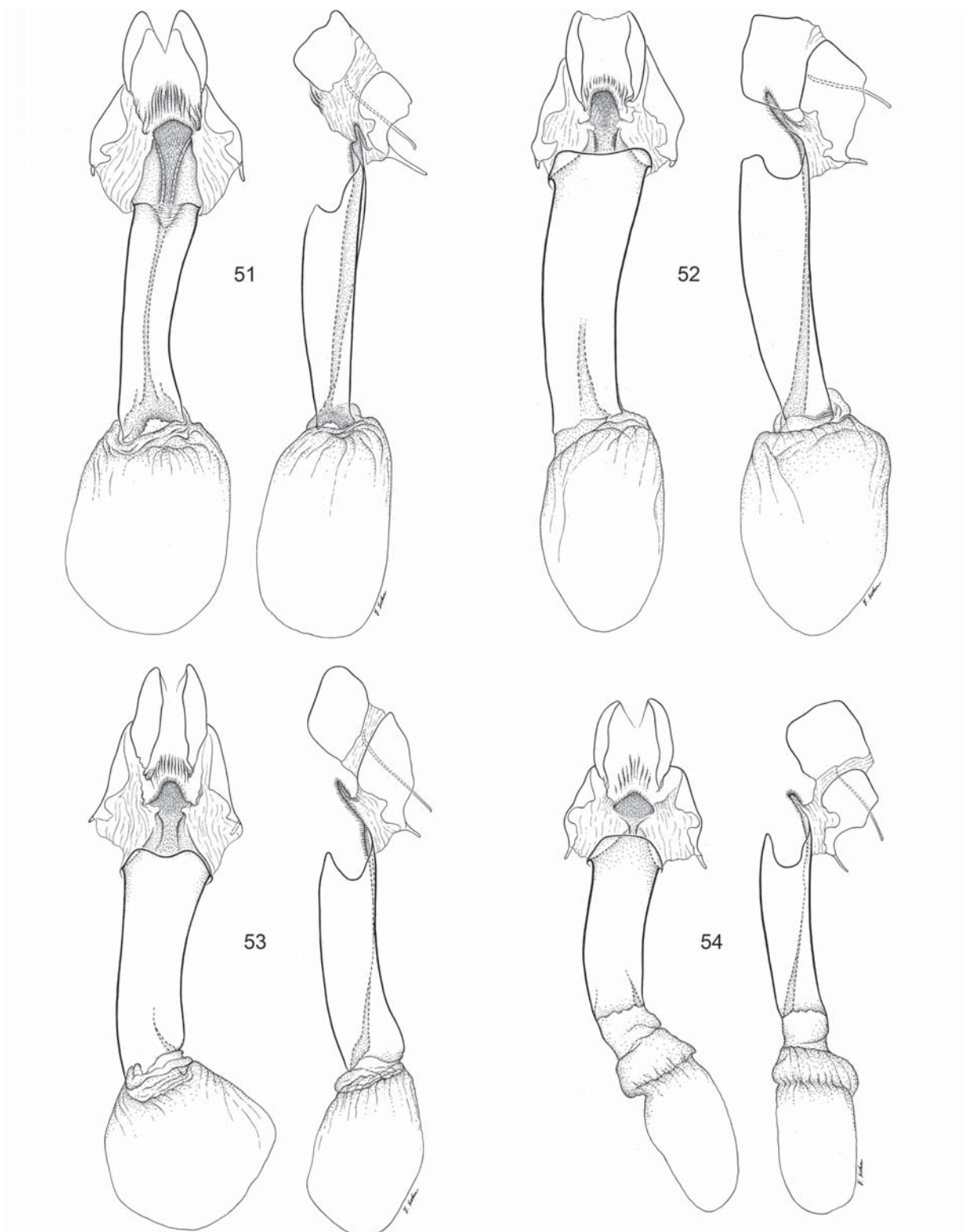
FIGS. 51–54. Female genitalia of *Atrytonopsis*. **51,** *A. pittacus*, Limpia Canyon, 4 mi. WNW of Fort Davis, Davis Mts., 5000 ft., Jeff Davis Co., TX, 28-IV-1959, X-1183 (JM & SNB). **52,** *A. deva*, Treasure Park, Pinaleno Mts., 8900 ft., Graham Co., AZ, 4-VI-1959, X-1187 (JM & SNB). **53,** *A. vierecki*, Sitting Bull Falls, Guadalupe Mts., 4650 ft., Eddy Co., NM, 26-V-1959, X-1174 (JM & SNB). **54,** *A. cestus*, 1 mi. W of Elkhorn Ranch, Sabino Canyon, Baboquivari Mts., 4200 ft., Pima Co., AZ, 20-IV-1961, X-1165 (K. Roever).
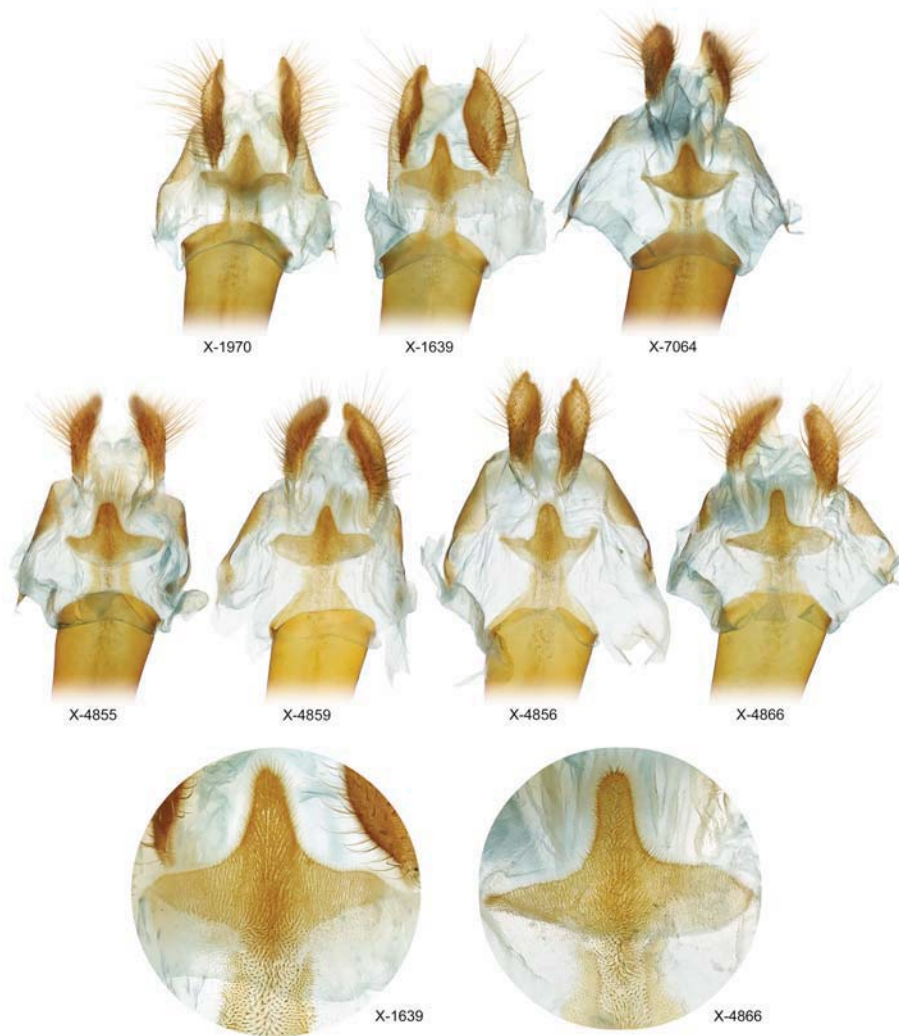
FIG. 55. Ultimate expressions of the narrow phenotype at the caudal end of the genitalia in seven females of *A. quinteri* (ventral view). Specimens denoted by their J. M. Burns genitalia dissection code. X-1970 from Hammocks Beach State Park, Bear Island, Onslow Co., NC; all others from Fort Macon State Park, Bogue Banks, Carteret Co., NC. Genitalia of two of the Ft. Macon specimens enlarged to show diverse microprojections.

as well as by cattle, goats, and sheep; I saw no skippers. On 26 and 27 August 2005, in the course of vegetation surveys on western Shackleford Banks, Leidner (pers. comm.) found the foodplant abundant in various horse exclosures that she examined; but earlier that year, when she visited the island during the spring and summer flight periods of *A. quinteri*, she did not find the skipper.

Atrytonopsis quinteri may occur c. ½ km west of Bear Island on Brown's Island, which is undeveloped. However, it belongs to the Camp Lejeune Marine Corps Base and is strictly off-limits because for decades it has been both a bombing range and a target for naval gunnery practice. (At times, when collecting on Bear Island, I flinched at the sound of nearby explosions and

hoped that the people responsible were reasonably accurate.) Having got permission from Camp Lejeune to collect in limited sections of Onslow Beach, farther southwest, I spent three hours on 26 April 1985 near Onslow North Tower and Risely Pier—areas with foodplant and suitable habitat (although it was narrower and somewhat damaged)—but saw no sign of *A. quinteri* whatsoever. On 4 and 6 May 1984, I checked much of Topsail Island, which lies even farther to the southwest in both Onslow and Pender counties, and found many areas of unspoiled habitat with much *Schizachyrium* but no *A. quinteri*.

Bogue Banks, Bear Island, and neighboring barrier islands are only 2,500–3,000 years old and extremely

dynamic (S. R. Riggs pers. comm., O. H. Pilkey pers. comm.). However, relative to their neighbors, Bogue Banks and Bear Island are tough, i.e., in the course of rapid changes in barrier islands, better able to persist (S. R. Riggs pers. comm.). In this region, major threats are erosion and/or sand deposition from frequent sizeable storms and accompanying surges, hurricanes, various human activities (which include residential and commercial development and shoreline augmentation or "stabilization"—plus, from the skipper's point of view, use of insecticides), and global warming.

In 2001 and 2002, in connection with the status and conservation of *A. quinteri*, Hall (2004) sought the skipper not only on Bear Island, Bogue Banks, and Radio Island, but also along the length of the North Carolina coast. His survey sites stretched from almost the Virginia border to the South Carolina border; and he, too, went to Shackleford Banks, Onslow Beach, and Topsail Island. Nevertheless, his study did not expand the known limits of the skipper's range. Many survey sites along the Outer Banks lacked the larval foodplant. Additional territories for *A. quinteri*—discovered in 2000 and 2003, respectively—are two more dredge spoil islands: Brandt Island, just north of Fort Macon State Park and virtually in contact with it, so that the Brandt Island skipper population is, in effect, no more than an extension of the Ft. Macon one; and Marsh Island, right next to the north edge of Morehead City. However, it is questionable whether there ever was a population on Marsh Island (only one individual was seen there) and, if so, whether it could survive recent destruction of the requisite habitat (Hall 2004). On dredge spoil high enough to support *S. littorale* at the west end of Bird Shoal (which is between Radio Island and Beaufort [and part of the Rachel Carson Reserve of the National Estuarine Research Reserve]), Leidner (pers. comm.) saw one example of *A. quinteri* on 25 April 2008 and three on 30 July 2014.

The barrier islands inhabited by *A. quinteri* closely parallel the mainland, with unsuitable salt marshes and water in between (except for some dredge spoil islands). In seeking proximate populations of *A. hianna*, I found and sampled it c. 1½ km west of Swansboro, Onslow County, a mainland locality that is only c. 5 km north of Bear Island (with some intervening dredge spoil islands, at least two of which support the larval foodplant [Hall 2004]), and at another mainland locality that is c. 9 km north of Morehead City, Carteret County. Besides those specimens of *A. hianna* (two of which appear in Figs. 15, 16, 30, 31), I took 40 males, 8 females of *A. hianna* at Holly Ridge, c. 4 km from the water in far southern Onslow County, which are also typical.

Genitalic context. Male. Setting the genitalia of *A. quinteri* in context, Figs. 32–54 show *Atrytonopsis*

genitalic morphology in both sexes of most species. The figures of male genitalia (Figs. 32–42)—with the posterior end to the right—are (except for Fig. 32) exploded views: uppermost are the uncus, gnathos, and tegumen in dorsal view; then the uncus, gnathos, tegumen, vinculum, and saccus in left lateral view (with the uncus, gnathos, and tegumen rotated 90° from their dorsal aspect); followed by the left valva, phallus (with cornuti exerted beyond its dentate distal end), and juxta in left lateral view; and finally the phallus and juxta in dorsal view.

The genitalia of *Atrytonopsis* are interspecifically conservative. Essentially, in males, the valvae (in lateral view) suggest a "roundish rectangle," with a very rounded distal end that terminates dorsally in a sharply to bluntly pointed projection, which is almost always higher than the body of the valva; the body of the valva itself ends dorsoposteriorly in a separate, rounded, thumb-like projection, which is slightly lateral to, and usually slightly overlapping, the pointed projection. Both the uncus and gnathos are divided. The distal end of each uncus prong is curved slightly downward to a pointed tip. The phallus is slender and long (longer than the valva and saccus combined), flared at the distal end, and finely dentate there, with two sizable cornuti that are sharply pointed, each with one or two (sometimes three) sharp points. The most obvious differences between a number of species involve the uncus and gnathos: the length of the prongs of the divided uncus, the horizontal distance between them, and their vertical distance from the underlying gnathos vary. Closer study indicates other, smaller interspecific differences. Some of them are obscure owing to intraspecific variation but emerge when series of genitalic dissections are compared. To make this point, I illustrated individual variation in both male and female genitalia of four species of *Atrytonopsis*: *A. lunus* (Edwards) and *A. frappenda*, which constitute the *lunus* group of *Atrytonopsis* (Burns 1982, figs. 17–28); and *A. ovinia* and *A. edwardsi* Barnes and McDunnough, which constitute superspecies *A. ovinia* (Burns 1983, figs. 28–55). These published figures and those of two recently described Mexican species of *Atrytonopsis* (*A. llorentei* and *A. austinorum* Warren 2011) are not duplicated here. Warren and Grishin (2012) showed that the Mexican species *A. zweifeli* Freeman—which Freeman described from two males, and which I included in the *lunus* group—is simply a synonym of *A. frappenda*. Male genitalia of the two species in superspecies *A. ovinia* depart significantly from the general description given above with respect to both the uncus (shallowly notched) and the phallus (great length, slight distal flare) (Burns 1983, figs. 19–27).

FIGS. 56–61. Sand dune habitat of *A. quinteri*, in which its larval food, *Schizachyrium littorale*, is the dominant plant. **56,** Fort Macon State Park, Bogue Banks, Carteret Co., NC, 27-VII-1983. **57–59,** Hammocks Beach State Park, Bear Island, Onslow Co., NC, 27-VII-1983. **60, 61,** Radio Island (a dredge spoil island), Carteret Co., NC, 29-IV-1985. (**60,** Motorcycles have worn bare paths through vegetation.)

The male genitalia of *A. quinteri*—with a deeply divided uncus, whose prongs are both widely spaced (producing a U in dorsal view) and well above the gnathos—resemble not only those of its nearest relative, *A. hianna*, but also those of other species: *A. vierecki* (Skinner), *A. deva* (W. H. Edwards), *A. lunus, A. frappenda*, and *A. llorentei*. Despite their genitalic similarity, these species differ in facies and size. In still other superficially separable species, *A. python* (W. H. Edwards), *A. pittacus, A. cestus* (W. H. Edwards), and *A. austinorum*, the uncus prongs are closer together so that the U is squeezed (it is also deeper in *A. cestus*), and the uncus is closer to the gnathos. But small interspecific differences in valval shape apparent in the various figures are generally attributable to individual variation. Given the degree of conservatism overall, it is not

surprising that the male genitalia of *A. quinteri* are like those of *A. hianna*.

Female. The figures of intact female genitalia (Figs. 43–54)—with the posterior end at the top—show the ovipositor lobes, lamella postvaginalis, and bursa copulatrix in ventral view (on the left) and in right lateral view (on the right). Always, the ostium bursae is large and the ductus bursae is wide and heavily sclerotized, and it curves a little to the left in ventral view. Obvious differences between species of *Atrytonopsis* involve a distal central strip together with the distal end of the lamella postvaginalis, which are more or less sclerotized and roughened with microprojections that range from hairs to spines to teeth (see especially Figs. 55: X-1639 and X-4866).

In both *A. quinteri* and *A. hianna*, the sclerotized distal end of the lamella postvaginalis is generally wide (Figs. 43–45)—much as it is in the *lunus* group (Fig. 46)—and, midventrally, it almost always extends to form a sort of triangle that varies greatly from wide to narrow, and from short to long, with a caudal tip that ranges from pointed to (more often) rounded or (rarely) blunt. (For a good example of an *A. lunus* female that develops a midventral triangle in the lamella postvaginalis similar to that in many females of *A. hianna* and *A. quinteri*, see Burns 1982, fig. 22.) In *A. quinteri* (43 females dissected) narrowing of the triangle may be conspicuous (Fig. 43). Figure 55 shows ultimate expressions of the narrow phenotype. However, at least half of the triangles in dissected *A. quinteri* females are within the range of expression in *A. hianna* (36 females dissected), and *A. hianna*'s triangles occasionally narrow, so that the more frequent and more extreme narrowness in *A. quinteri* is a modest difference. Despite extensive individual variation, the female genitalia of these species differ from those of other species of *Atrytonopsis* (Figs. 47–54), in which the central strip is notably narrow and its expansion into a caudal projection at the posterior end of the lamella postvaginalis, although laterally limited, is medially pronounced.

Taxonomic tangent (Figs. 47–50). However, *A. margarita* (Skinner) **revised status** is an exception (and it is not, as it has variously been called, a synonym, form, variety, race, or subspecies of *A. python* [Mielke 2005, vol. 4, p. 853]). In the female genitalia of *A. python*—the sister species of *A. margarita*—both the caudal expansion and especially the central strip are sclerotized, and the caudal expansion is usually wide enough for the two, in combination, to suggest a paddle (Figs. 47, 48). In *A. margarita*, both parts look relatively pale, despite their microprojections; and a lessening to lack of sclerotization makes the distal end of the lamella postvaginalis look relatively formless. It is particularly

significant that sclerotization flanking the central strip is wider and longer in *A. margarita* (Figs. 49, 50) than it is in *A. python* (Figs. 47, 48). Male genitalia are not helpful (taxonomically).

Superficially, these two species express to varying degrees the wingspot pattern common to most species of *Atrytonopsis*, including *A. quinteri*. Wingspots are white in *A. margarita* instead of light yellow, as they are on both wings dorsally and the forewing ventrally, in *A. python*. The brown ground color of both wings is warmer in *A. python* because their overscaling (particularly the long hairs of the dorsal hindwing) are yellower, at times imparting a faintly orange tinge. The colder brown ground color of *A. margarita* stems from overscaling that varies within individuals from paler yellow to gray. At least in the United States, these species may replace each other geographically: *A. margarita* occurs in west Texas (e.g., Big Bend, Davis Mountains, Guadalupe Mountains) and in much of New Mexico; *A. python*, in southwestern New Mexico and Arizona.

Natural history. Mating: On Bear Island at 1045 h EDT on 25 April 1985, I saw a male and female *A. quinteri* fluttering about each other below the tops of sea oats, *Uniola paniculata* L., Poaceae, and rushed over to find the pair already united, less than 60 sec. later, on the sand to which the female had dropped. On Radio Island at 1200 h EDT on 30 April 1985, I watched a female *A. quinteri* in direct flight, at a height of c. 1 m. When a perched male flew up at her, she instantly dropped, alighting on a *Schizachyrium* blade c. 5 cm aboveground. The male followed at once, lit beside her, and promptly engaged. Their speedy courtship—if any—was not elaborate. After observing them for less than 2 min., I netted and cyanided them, and their union was already firm: they remained in copula instead of coming apart.

Oviposition and ova (Fig. 62): From 1983 to 1985, in Fort Macon State Park, at Emerald Isle, and on Radio Island, I saw 15 different females oviposit: always a single egg on either the dorsal or ventral surface of a blade of *S. littorale*, c. 2–20 cm above the sand. Oviposition took place at any time of day (specific records ranged from 0848 h to 1658 h EDT). Eggs have a nubbly surface and are pale greenish cream or pale yellowish cream when laid. Within a day, they become pale orange; and in the second day, the orange intensifies (through reddish-orange to red), appearing as a spot at the micropyle and as a narrow to wide, regular to irregular, belt around the egg, all against a tan (or pale yellowish) ground. The red may shade toward a purplish-red, and the belt may cover almost all of the egg. Color fades in the last three days to tan, with the dark head of

Fig. 62. Immature stages of *A. quinteri*. **a–c,** egg (newly laid [pale] and older). **d–x,** Larval Instars: **d–i,** first; **j, k,** second; **l, m,** third; **n–q,** fourth; **r–u,** fifth; **v, w,** sixth; **x,** prepupa. **y–z1,** pupa. Note, on the front of the head in latter larval instars, the development of an odd **W** whose central pointed apex extends dorsad in a wide midcranial line longer than the sides of the **W**. In this plate, black lines within white ones demarcate three groups of photos; in each group, photos are to the same scale. (Courtesy N. V. Grishin)

the larva becoming visible beneath the micropylar area. Eclosion of first instar larvae from eggs seen laid on 25-VII-1983 occurred 9 days later. A newly eclosed larva eats most of its egg shell.

Eggs that I got from a caged female *A. hianna* from Holly Ridge, NC, were very pale green when laid and promptly developed a pale orange tinge. Then, on day two, they became uniformly light orange (and, still later,

uniformly darker orange), except for a more intense orange or red spot at the micropyle. But unlike eggs of *A. quinteri*, they never developed a belt of any kind. Heitzman and Heitzman (1974), who reared *A. hianna* many times in Missouri and Arkansas, did not see a belt either.

Development (Fig. 62): There are 6 larval instars. The shiny black head of the first instar gives way to a

matte pale brown and then light brown, on which, in latter instars, there appears a darker brown marking that looks (especially in head-on view) like a W whose central pointed apex extends dorsad in a wide midcranial line that is longer than the sides of the W. The body, fuzzy with short white hairs, becomes pink; but in the last instar the body becomes yellowish ventrolaterally. From 1 to 2½ weeks (average c. 11 days) into the last instar, wax glands appear on the ventral abdomen, traversing an anterior part of both A7 and A8. The larva coats the inside of its shelter with bright white, powdery wax.

Unlike the larvae of *A. quinteri*, those that I reared from a female of *A. hianna* did not develop the odd W marking on the head; and, in a late instar, the dense white hairs of the body were longer than those of *A. quinteri*. Heitzman and Heitzman (1974) described the head of the last instar larva of *A. hianna* as "unmarked" and the body as "covered with long yellowish white hair."

Speciation. The following scenario stresses the possibility of a novel, rigorous environment exerting strong selective pressure on a colonizer. Presumably, by whatever means, at least one fertilized female from an eastern or southeastern population of *Atrytonopsis* reached an island in the dynamic complex of barrier islands and founded a population that was genetically less variable than its source population (see, e.g., Mayr 1963), as well as geographically isolated from it to a slight but relevant extent. The new environment was bizarre because barrier islands—instead of separating from mainland—form offshore and offer harsh, unstable, sandy habitat. Some mainland species successfully invade such ecologically meager habitat, adapting to it rapidly and even differentiating to the level of new species in a short time. *Schizachyrium littorale*, which is endemic to coastal sands and rather wide-ranging today, may well have existed already on the barrier island that *A. quinteri*'s ancestor reached. It was an attractive foodplant for the immigrant skipper. (Foodplants of *A. hianna* are species of *Schizachyrium* and its close relative *Andropogon*.) Where *S. littorale* flourishes (Figs. 56–61), so does *A. quinteri*. The grass is so adjusted to hot, dry, shifting sand dunes, as well as to windblown salt spray, that it is the dominant dune plant and an abundant, concentrated food source. The skipper withstands similar conditions. Although from a broad perspective *A. quinteri* is considered rare, Leidner and Haddad (2010, 2011) estimate that local populations range in size from hundreds to thousands of adults.

Given that the combination Bogue Banks + Bear Island is only c. 2,500 to 3,000 years old (S. R. Riggs pers. comm., O. H. Pilkey pers. comm.), evolution of *A. quinteri* may have been rapid; and differentiation continues. No later than 1585 (Fisher 1962), an inlet

split Bogue Banks from Bear Island. Leidner and Haddad's (2010, 2011) use of amplified fragment length polymorphisms for genetic analysis of population differentiation across 8 and 10 sampling sites reveals three populations of *A. quinteri*, separated by natural inhibitors of dispersal. The two populations on Bogue Banks are genetically more similar to each other than they are to the population on Bear Island, which is not as genetically variable. As expected, degrees of genetic difference relate to the efficacy and age of the two dispersal inhibitors: the lesser one is an eroded 8-km stretch of Bogue Banks wherein beach abuts maritime forest (which runs along the inner side of the island) because intervening dunes and shrub thickets have been washed away; the greater one is the inlet between the two islands (Leidner & Haddad 2010, 2011).

The origin of *A. quinteri* may have been lengthier and more complex. Fuller understanding of history and relationships calls for molecular comparison of *A. quinteri* with populations of *A. hianna* from the southeastern United States as well as from the rest of that skipper's extensive range. At the very least, DNA barcodes from sizable samples would help. In general, barcodes are a powerful taxonomic tool at the species (and generic) level in hesperiids. As an example of barcodes at their best, they were the first clue that a common and widespread species of *Perichares* described in 1775 actually comprises four species with similar facies and genitalia; as it turns out, small interspecific differences in larval and pupal color patterns and big differences in foodplant selection support the barcode data (Burns et al. 2008). However, at the other extreme (which is rare), barcodes barely separate two species of *Polyctor* with distinctly different genitalia, facies, and ecosystem choice (Burns et al. 2007). Whether barcodes are helpful or not, data from nuclear DNA would be desirable for thorough analysis of the eastern American *Atrytonopsis*.

Evolution of new species in ecologically outré, often severe, sandy habitats is a common phenomenon in both plants and animals. Currently, in Lepidoptera, Metzler (2014) is documenting local differentiation in seven families of moths. In material he has amassed during six years of collecting in the gypsum dunes of White Sands National Monument, an ecologic island in the Tularosa Basin of New Mexico, he has discovered 30 new species (many now formally named). Here again, selection is strong, and differentiation has been recent and rapid: decisive geologic evidence shows that the white sands formation is only c. 8,000 years old. It seems that in some cases, speciation has occurred with the divergent population in its peculiar habitat remaining in contact with its progenitor.

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TWO NEW SPECIES OF *EUPTYCHIA* HÜBNER, 1818
(LEPIDOPTERA: NYMPHALIDAE: SATYRINAE) FROM THE GUIANA SHIELD,
WITH NOTES ON *E. MARCELI* BRÉVIGNON, 2005 AND *E. RUFOCINCTA* WEYMER, 1911

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ABSTRACT. Two new species of *Euptychia* are described: *Euptychia audacia* Brévignon, Fratello & Nakahara **n. sp.** and *Euptychia aquila* Fratello, Nakahara & Brévignon **n. sp.** These two taxa, the recently described *Euptychia marceli* Brévignon, 2005 and *E. roraima* Nakahara, Fratello & Harvey, 2014, a quartet of *Euptychia* from the Guiana Shield region, are compared morphologically. New information on *E. marceli* Brévignon, 2005 is revealed, and the taxonomic status of *E. rufocincta* Weymer, 1911 is discussed including its possible synonymy with *E. picea* Butler, 1867.

.**Additional key words:** *Euptychia picea, E. roraima, Euptychia audacia, Euptychia aquila,* Guiana subregion

For many years, the gargantuan subtribe Euptychiina (see Lamas 2004) has been the subject of taxonomic studies. However, its taxonomy has been poorly understood because of the predominance of superficial morphological homogeneity among its members (Peña & Lamas 2005). Approximately 50 genera and more than 400 species have been recognized within this subtribe (Peña et al. 2010, Freitas et al. 2011, 2012). Regarding the classification of these species, lepidopterists usually accept and follow Lamas (2004), who retained most of the genera erected by Forster (1964). This scheme of generic classification is characterized by the lack of clear-cut diagnoses. As a result, placements of taxa in these genera are usually tentative. However, because of recent work on *Euptychia* Hübner, 1818 including phylogenetic studies (e.g., Pulido-B. et al. 2011, Freitas et al. 2012), this genus has become one of the more well-defined and understood genera among Euptychiina. Though D'Abrera (1988) provisionally applied the name *Euptychia* in a very broad sense, we accept the strict definition of Forster, which restricts the genus to 18 described species (Lamas 2004, Brévignon 2005, Pulido-B. et al. 2011, Freitas et al. 2012, 2013, Neild et al. 2014, Nakahara et al. 2014).

Distributed throughout the Neotropical region, members of *Euptychia* are relatively small, almost all are marked prominently with ventral bands and submarginal eyespots and the great majority exhibit wing translucence. Almost all male *Euptychia* species that have been dissected show a conspicuous projection of the tegumen above the uncus in the male genitalia, which is possibly a diagnostic character to differentiate this genus from other genera in the subtribe (G. Lamas, pers. comm. 2008, Freitas et al. 2012, pers. obs.). The occurrence of one recurrent vein in the forewing discal cell is also considered a character shared by all *Euptychia* (Freitas et al. 2012, pers. obs.). These members of *Euptychia* also possess distinctive larval characters and use singular hostplants (DeVries 1987) for Euptychiina: Selaginellaceae (Lycopodiophyta) and Neckeraceae (Bryophyta), not seed plants which are the hostplants of most Satyrinae genera. Selaginellaceae are also the hostplants of some Oriental satyrines (Fukuda 1983), *Ragadia* Westwood, 1851 and *Acrophtalmia* C. Felder & R. Felder, 1861, but they belong to different subtribes within Satyrini (Peña et al. 2011).

Extensive fieldwork done in French Guiana in recent decades has rendered a significant increase of the

taxonomic and biological knowledge of the butterfly fauna of this country (Brévignon 1998, 2005, 2008, Brévignon & Benmesbah 2012). In a like manner, recent expeditions by the first author and partners have helped increase the knowledge of the butterflies of neighboring Guyana. This certainly applies to lowland and lower premontane Euptychiina, and particularly the genus *Euptychia*. From both recent (Brévignon 1998, 2005, 2008, Brévignon & Benmesbah 2012, Costa et al. [2014], Nakahara et al. 2014) and present studies (Costa et al. in prep.) including this article, there seems to be a considerable number of euptychiine species that appear to be endemic to the Guiana subregion of Amazonia; a high percentage (over 50%) of endemism has been detected for the *Euptychia* fauna of this region. The Guiana (or Guianan) subregion includes French Guiana, Surinam, Guyana and parts of adjacent regions of Venezuela and Brazil, and has a long historical basis for being considered a biogeographical region. According to Lim and Tavares (2012), the Guiana subregion "was first recognized as a biogeographic zone..." by Wallace (1852). We follow a modern work (Voss & Emmons 1996) that delineates the Guiana subregion as that section of Amazonia east of the Rio Negro and north of the Amazon River. The Guiana subregion coincides to a great extent with the Guiana Shield (Lim & Tavares 2012), a geological formation of ancient Precambrian basement rock. Extensive faunistic and floristic research focuses on this huge biogeographical region (e.g., Hollowell et al. 2001, Lim & Engstrom 2001) and both past and ongoing studies in numerous biological groups including Rhopalocera (e.g., Désamoré et al. 2010, Costa et al. [2014], in prep.), indicate that the Guiana subregion is a very important area for endemicity, not only for butterflies but also for many other groups of living organisms. The research of Costa et al. [2014], (in prep) focuses on the montane forests and other highland habitats of the Pantepui region where the greatest butterfly endemicity is expected, even more in its infancy is the study of butterfly endemicity of other montane forests, Amazonian forests and other lowland habitats (e.g., savannahs) encompassed within this vast biogeographical region.

Two new *Euptychia* species from the Guiana Shield region are described; both had been previously misidentified as known species.

MATERIALS AND METHODS

Identification of *Euptychia* species treated in this study was based on the information from the original descriptions (Butler (1867); Weymer (1911); Brévignon (2005); Nakahara et al. (2014)) and the examination of type material and other specimens in public and private collections (listed below). The external morphology of the described species and congeners has been studied by the authors, by examining preserved specimens from several localities spanning their known geographical range, in order to evaluate their variation and stability of characters. Abdomens were dissected using standard techniques at the USNM, with adult abdomens being soaked in hot 10% KOH for 10–15 minutes, dissected and subsequently stored in glycerine. A Wild M5 stereomicroscope was used for male genitalia dissections at the USNM and photographed with a Canon 5D camera; a LEICA MZ 16 microscope was used for male and female genitalia dissections at the MGCL, with images of female genitalia taken by using a Canon EOS 50D and stacked by using Helicon focus 6.2.2 and Helicon Remote (ver. 3.4.14). Butterfly body morphological characters were studied under magnification using these binocular microscopes. Measurements are provided as minimum–maximum values. The terminology for genital and abdominal structures largely conforms to Klots (1956), except for the term aedeagus, where we follow Peña and Lamas (2005). Nomenclature for wing venation follows the Comstock-Needham system described by Miller (1970:44), and areas and elements of wing pattern follow that of Peña and Lamas (2005) and Neild (2008). The following acronyms and abbreviations are used throughout this paper.

AMNH American Museum of Natural History, New York, USA

BMNH The Natural History Museum, London, UK

LCB Lalita & Christian Brévignon collection, Cayenne, French Guiana

MB Mohamed Benmesbah collection, Plaisance-du-Touch, France

MGCL McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, Gainesville, Florida, USA

MNHM Museum National d'Histoire Naturelle, Paris, France

MUSM Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru

USNM National Museum of Natural History, Smithsonian Institution, Washington, DC, USA

ZMHU Museum für Naturkunde der Humboldt-Universität, Berlin, Germany

ZSM Zoologische Staatssammlung München, Munich, Germany

DFW dorsal forewing

VFW ventral forewing

DHW dorsal hindwing

VHW ventral hindwing

Taxonomy

Euptychia audacia Brévignon, Fratello & Nakahara, **new species**
Figs. 1 (1–4), 2 (1–4), 3, 4 (1)

Euptychia picea; Brévignon, 1998 : 122
Euptychia sp.; Brévignon, 1998 : 123, 124
Euptychia rufocincta; Brévignon, 2005: 401: 23–26; 2008: 75, 89: 49a–c

Diagnosis. *Euptychia audacia* possesses a 'marceli-type' VHW ocelli pattern (based on the pattern of *E. marceli*); the large tornal ocellus of *E. marceli* is much larger, with a much wider yellow ring, compared to its large apical ocellus; it also lacks small satellite ocelli above the large tornal ocellus and below the large apical ocellus. Among described *Euptychia* species, *E. audacia* is the closest in both sexes to *E. marceli*, distinguished in the males by being smaller, often significantly, and slightly darker dorsally and ventrally, with the ventral brown bands less reddish. The preeminent male facies characteristic is dorsal: *E. audacia* males exhibit dark brown coloration in the FW apical area that largely obscures the prominent VFW apical ocellus from showing through; in *E. marceli* males, the DFW apical dark brown coloration is much more restricted, consequently, the prominent VFW apical ocellus is seen easily through the translucence. Female *E. audacia* are again smaller, often significantly, than *E. marceli* females, and their VHW large tornal ocellus is usually not as large compared to the VHW large apical ocellus as in *E. marceli* females, where there is always a substantial difference in size between these two ocelli. *E. audacia* females show slightly more DFW dark brown coloration, distally and apically, than *E. marceli* females, though this apical dark brown coloration is much more restricted compared to the males and does not obscure the prominent VFW ocellus from showing through the translucence, and again, the ventral brown bands are less reddish on *E. audacia*. Larger *E. audacia* and smaller *E. marceli* specimens can be very close, especially on worn specimens, so dissection would probably be necessary for determination. A further new species of *Euptychia* (see below), sympatric in the Guianan southern mountains with both *E. audacia* and *E. marceli*, also has the 'marceli–type' VHW ocelli pattern, but is very easily distinguished from *E. audacia*. Male genitalia of *E. audacia* **n. sp.** are distinguished from its congener *E. marceli* by the following characters: narrower and slightly curved uncus; a significant extention of the ventral margin of the tegumen is present (absent in *E. marceli*). Female

genitalia of *E. audacia* are distinguished from its congener *E. marceli* by the following characters: lamella antevaginalis developed, forming a plate in ventral view (not developed in *E. marceli*) (see Fig. 4). See below for male and female genitalic differences between *E. audacia* and the additional Guianan new *Euptychia* species.

Description. MALE: forewing length 16 mm
Wing shape. Forewing inner margin almost straight, outer margin almost straight, with a rounded apex. Hindwing rounded and rather elongated toward the tornus, slightly outwardly curved inner margin convex proximally to vein 3A, rounded tornus, outer margin convex, base of costa convex.
Wing venation. Forewing recurrent vein present in discal cell.
Dorsal surface of wings. Ground colour brown (R137, G98, B67), with subtle greyish overtones, slightly translucent, thus revealing dark bands and ocelli from ventral surface; apical area darker (R61, G37, B25), thus hiding preapical ocellus; fringe concolorous.
Ventral surface of wings. Ground colour brown (R178, G148, B114), lighter than dorsal surface, with five darker brown (R125, G89, B57) bands; fringe concolorous.
Forewing: a narrow band distally extended along the swollen section of subcostal vein; a regular and quite straight discal band extends from subcostal vein to just beyond vein 2A; a postdiscal band extends from the subcostal vein towards inner margin until vein 2A, in apical portion, thin and distally deviated, almost joining submarginal band, slightly broadening, thicker than discal band in its medial portion, and slightly distally deviates below Cu_2; an undulating submarginal band, curved basally in each cell, extends from near apex to near tornus, gradually broadening towards vein Cu_2 and slightly narrowing after this vein where it is distally deviated; a dark brown, narrow and wavy marginal band extends from apex towards tornus, undulating until vein Cu_1 and then straight after this vein; ocellus in cell M_1 exceeding from vein M_1 and M_2 respectively, ringed in yellow and with one centered white pupil in black area; an indistinct, faint, light brown marking visible around and below the ocellus. **Hindwing:** a slightly regular and straight band extends from costal margin to inner margin, at base of wing; discal band of same width as that of forewing, traverses straight from costal margin towards inner margin, slightly narrower in anal portion; a postdiscal band of same width as that of forewing, extends from costal margin towards inner margin, very slightly undulating, slightly narrower in anal portion; an irregular submarginal band starts from apex and traverses along margin towards tornus, broadened and M-shaped between vein M_2 and Cu_1; a dark brown marginal band, thin and very slightly undulated, traverses along distal margin from apex towards tornus and almost fuses to postdiscal band in cell 2A; a submarginal ocellus, smallest of three, in cell Rs, shows one centered white pupil in black area; larger ocellus in cell M_1, ventrally exceeding from vein M_2, encircled by yellow ring and with one centered white pupil in black area; largest ocellus, ringed in yellow, with one centered white pupil in black area in cell Cu_1, exceeding from vein Cu_1 and Cu_2 respectively; an indistinct, faint, light brown marking is visible around this ocellus.
Head. Antenna light orange brown with darker base and apex, about 7 mm long; eyes entirely blackish, hairy, a fringe of creamy scales along posterior lateral edge of eye; palpus 2.5 mm long, covered with long hairy scales, creamy proximally and brownish distally; frons brown.
Thorax. Dark brown dorsally, with creamy hair ventrally. Foreleg covered by long light brown hairy scales.
Abdomen. Dark orange brown dorsally, with long creamy hairy scales ventrally.
Genitalia. (three specimens prepared: vial LCB PAG 276; vial #2013-03 and #2013-04 (USNM)): uncus narrow, curved downward in lateral view, tapered posteriorly, almost evenly broad in dorsal view; tegumen dorsally flattened in lateral view, rather short conspicuous posterior projection above uncus, approximately one third length of
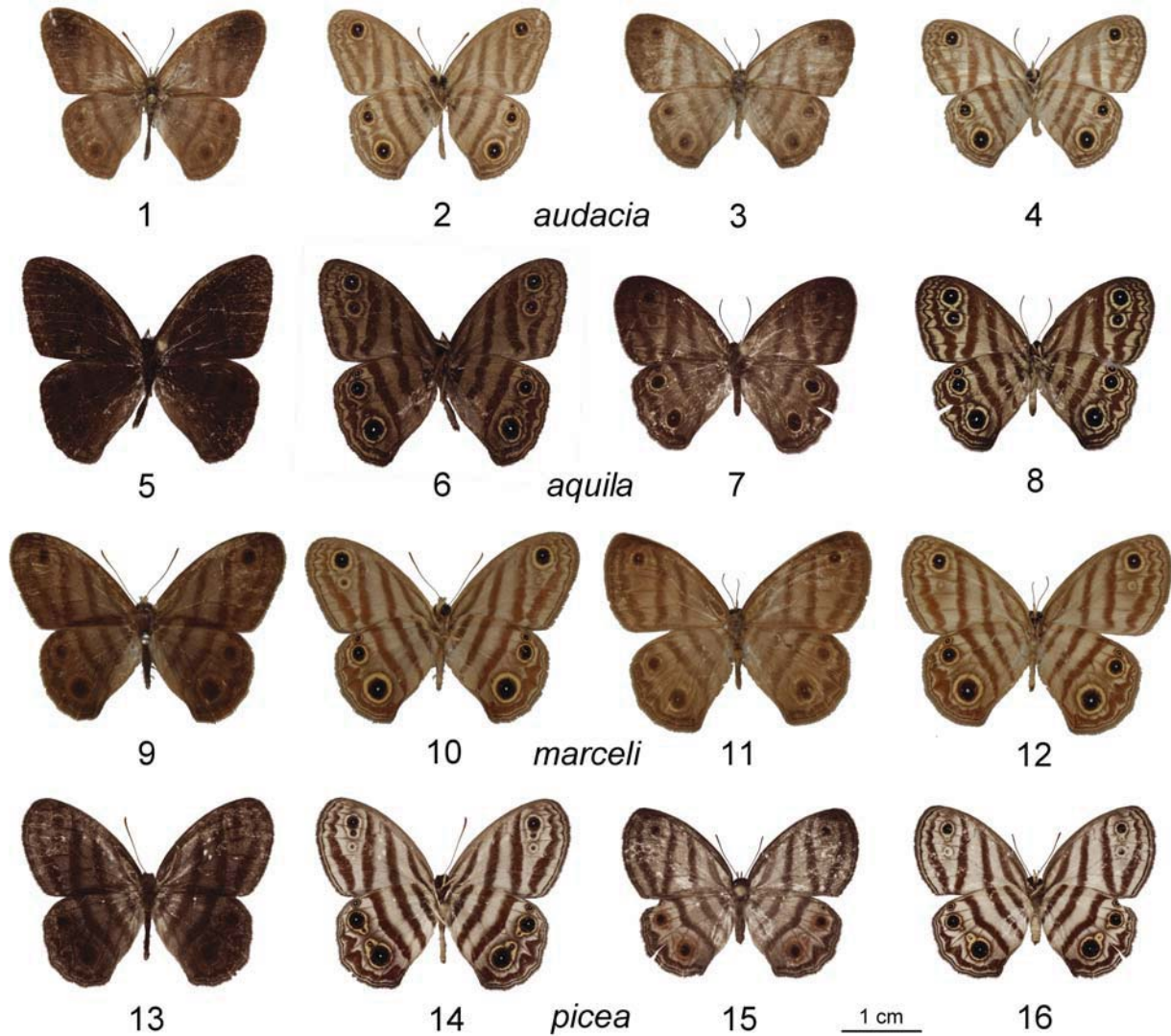
FIG. 1. *E. audacia*, *E. aquila* and *E. marceli* holotypes and allotypes, plus *E. picea* male and female form *rufocincta*: **1**. Dorsal and **2**. Ventral; *E. audacia* male holotype, Saül, French Guiana **3**. Dorsal and **4**. Ventral; *E. audacia* female allotype, Saül, French Guiana **5**. Dorsal and **6**. Ventral; *E. aquila* male holotype, E. Kanuku Mts., Guyana **7**. Dorsal and **8**. Ventral; *E. aquila* female allotype, Acarai Mts., Guyana **9**. Dorsal and **10**. Ventral; *E. marceli* male holotype, Maripasoula, French Guiana **11**. Dorsal and **12**. Ventral; *E. marceli* female allotype, Galion, Roura, French Guiana **13**. Dorsal and **14**. ventral; *E. picea* male, nr. Iquitos, Peru **15**. Dorsal and **16**. Ventral; *E. picea* female form *rufocincta*, Rondonia, Brazil
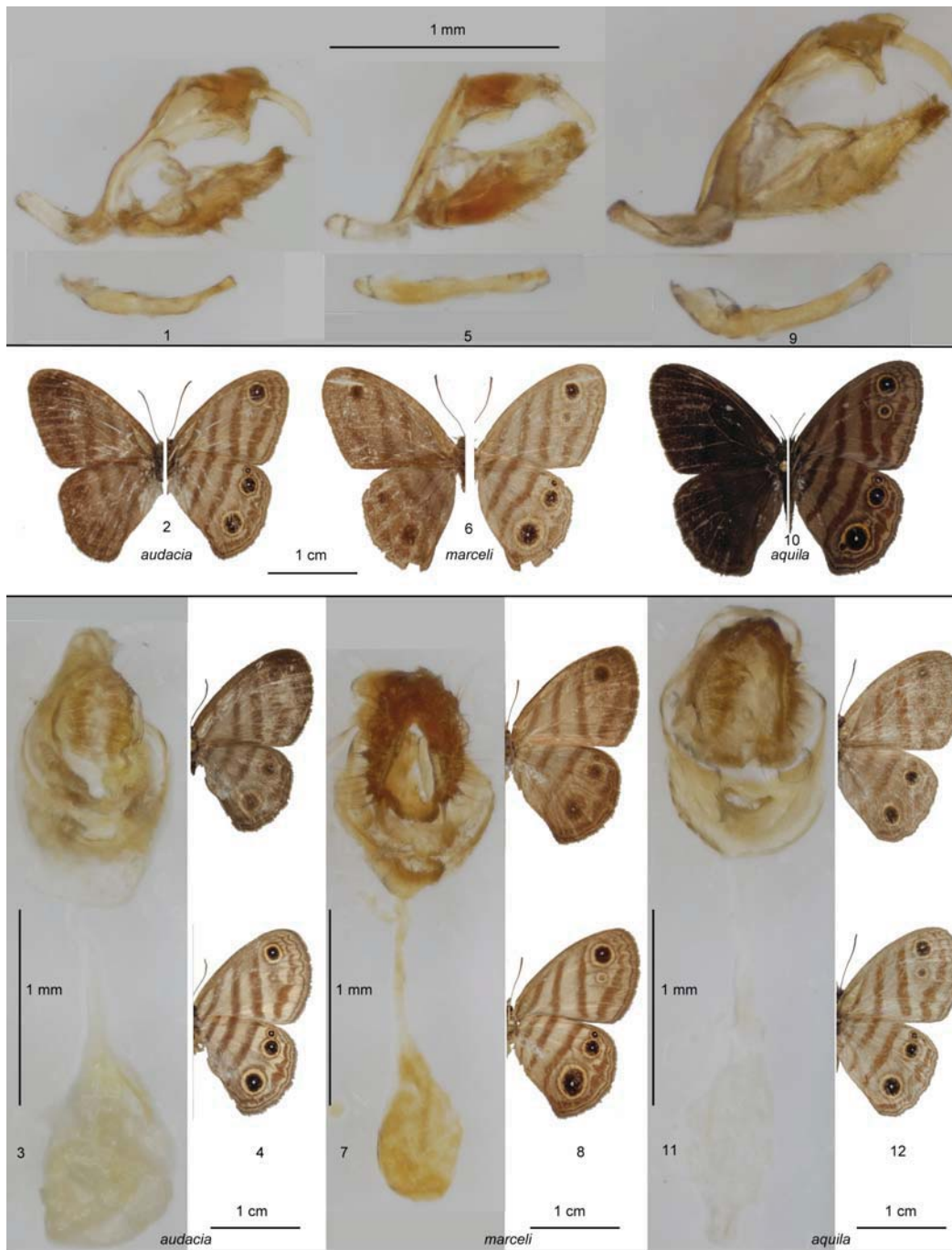
FIG. 2. Male and female genitalia of *E. audacia*, *E. aquila*, and *E. marceli*, with dissected specimens.
1-4 : *Euptychia audacia*. **1, 2** : male ; 1 : genitalia (PAG 276) of specimen 2, PK27 route de Kaw, Roura, French Guiana, 24-VIII-1993, n° 540, collection L. & C. Brévignon. **3, 4** : female ; **3** : genitalia (PAG 1105) of specimen **4**, Massif du Mitaraka, Borne 1, 2°13'N 54°26'30"W, 23-IX-2006, French Guiana, J.-P. Champenois leg, n° 22660 PAG 1105. **5-8** : *Euptychia marceli*. **5, 6** : male ; **5** : genitalia (PAG 277) of specimen 6, Galion, Roura, French Guiana, 1-V-1990, n° 559, collection L. & C. Brévignon. **7, 8** : female ; **7** : genitalia (PAG 1104) of specimen **8**, Saint-Georges-de-l'Oyapock, French Guiana, 30-V-1985, n°563, collection L. & C. Brévignon. **9-12** : *Euptychia aquila*. **9, 10** : male ; **9** : genitalia (PAG 1005) of specimen **10**, Massif du Mitaraka, Borne 1, 2°13'N 54°26'30"W, 27.IX.2006, French Guiana, J.-P. Champenois leg, n° 22653, collection B. Hermier. **11, 12** : female ; **11** : genitalia (PAG 1107) of specimen **12**, Massif du Mitaraka, Borne 1, 2°13'N 54°26'30"W, 29.IX.2006, French Guiana, J.-P. Champenois leg, n° 22663, collection B. Hermier.

FIG. 3. *Euptychia audacia* male genitalia in dorsal and lateral views (DJH-2013-3) Acarai Mts./ridge, Sipu R. 2500'-3700'.

uncus, ventral margin concave, prominent projection extending ventrally from posterior margin, subtriangular and somewhat rounded in lateral view, tegumen semi-elliptic in dorsal view; vinculum fused to anterior margin of tegumen; saccus slightly rounded, almost same length as uncus, dorsally thin and evenly broad; valva sparsely hairy, posterior quarter tapered and its apex rounded, long anterior section almost parallelogram shaped, slightly narrowing posteriorly in lateral view, curved inwards at obtuse angle in dorsal view; aedeagus tubular in dorsal view, with straight and broadening anterior portion, in lateral view one third posterior narrower and positioned at approximately 30° angle, slightly broadening anteriorly, slightly longer than length of uncus plus tegumen.

FEMALE: forewing length 14.5 mm. Similar to male except as follows.

Wing shape. Forewing costa convex, inner margin almost straight, outer margin rounded; apex and tornus rounded. Hindwing rounded and less elongated than male.

Dorsal surface of wings. Ground colour brown, lighter than male (R153, G127, B92), with darker apex (R108, G78, B52) but dark brown apex coloration much more restricted than in male.

Ventral surface of wings. Ground colour lighter brown than male (R179, G158, B140), with five darker brown bands appearing more contrasted and broader than in male (R137, G106, B77).

Genitalia. (three specimens prepared: PAG 1105 LCB; SN-14-81; SN-15-24): papillae anales hairy, adorned with setae on their internal side; lamella antevaginalis sclerotized, developed, forming a plate in ventral view; weakly sclerotized 'ring' around basal side of 8th segment, less sclerotized at top, developing from lamella antevaginalis; ductus bursae very thin getting slightly broader anteriorly; corpus bursae broad with two linear signa.

Holotype. 1♂, French Guiana: Saül, 21.VII.1991, collection L. & C. Brévignon, n°31.

Allotype. 1♀, French Guiana: Saül, 21.VII.1991, collection L. & C. Brévignon, n°35.

Paratypes. 1♂, French Guiana: Galion, Roura, 12.VII.1990°, n°543; 1♂, French Guiana: Matoury, 26.IV.1990°, n°554; 1♂, French Guiana: Mont Matoury, 19.I.2010; 1♂, French Guiana: Route de Kaw, pk27, Roura, 24.VIII.1993, n°540 (genitalia dissection: PAG 276); 1♂, French Guiana: Route de Kaw, pk38, Roura, 19.XII.2010; 7♂, French Guiana: Saül, 15, 20, 21(3).VII.1991, 26.X, 2.XI.1999; 5♀, French Guiana: Matoury, 22.XII.1985, 2.III.1986, 29.V, 12(2).VI.1990°, collection L. & C. Brévignon; 1♀, French Guiana: Matoury, 15.I.1987; 1♀, French Guiana: Mitaraka, 23.IX.2006, collection B. Hermier; 1♀, French Guiana: Route de Kaw, pk27, Roura, 8.VIII.1999; 1♀, French Guiana: Route de Kaw, pk32, Roura, 17.VI.2012; 1♀, French Guiana: Saül, 29.X.2011, collection L. & C. Brévignon. Guyana: 9♂, Iwokrama Rainforest Res., Iwokrama Mt. 2450–3150', 28.lll.-1.lV.2001, 4°19.82'N 58°47.91'W, Leg. S. Fratello (genitalia dissection for one male: 2013-4 Donald J. Harvey); 3♂, 1♀: Guyana: Acarai Mts./Ridge, Sipu River 2500-3000', 31.X.-10.XI.2000, 1°22.2'N 58°47.91'W, Leg. S. Fratello et al; 2♂: Guyana: Acarai Mts./Ridge, Sipu River 2500-3700', 6–9.XI.2000, 1°20'N 58°57'W, Leg. S. Fratello et al (genitalia dissection for one male: 2013-3 Donald J. Harvey); 2♂: Guyana: Acarai Mts., Sipu River 2000-2500', 4–10.XI.2000, 1°21.3'N 58°57.4'W, Leg. S. Fratello et al; 1♀: Guyana: Acarai Mts., Sipu River 900-2500', 29.X.–12.XI.2000, 1°23.2'N 58°56.8'W, Leg. S. Fratello et al; 1♂: Guyana: Two Hat Mt., E. Kanukus, S. Rupununi, S. Slope Summit 2300–2600', 23–28.IX.2000, 3°8.8'N 59°6.9'W, Leg. S. Fratello et al; 1♂: Guyana: Region 9, Kanuku Mts., Nappi Mt., 2700'–3300', 03°18.8'N 59°33.9'W, 21 Feb–10 Mar 1999, leg. S. Fratello, R. Hanner, S. Hendricks, R. Williams; 2♀: Guyana: Region 9, Kanuku Mts., Nappi Creek, 500'–1,000', 03°N 59°34.2W, 21 Feb–10 Mar 1999, leg S. Fratello, R. Hanner, S. Hendricks, R. Williams; 1♂: Guyana: Region 7, Mt. Ayanganna, Kuiewa R., 2500'–3300', 05°26.0'N 60°00.4'W, 2-25 Apr 1999, leg. S. Fratello, R. Hanner, W. Prince, R. Williams; 1♂: Guyana: Cuyuni River, Kamaria Falls 100', 30.XI-5.XII.2000, 6°24'N 58°54.6'W, Leg. S. Fratello et al (all previous Guyana Paratypes: USNM). 1♂: Guyana: Bartica, B. Guiana, H. S. Parish, Joicey Bequest. Brit.Mus. 1934-120., BMNH; 2♂: Guyana: Kaieteur Falls, British Guiana, Feb.-Mar., 1936, A. Hall., BMNH; 1♀: Guyana: Demerara R., Crowley Bequest, 1901-78., BMNH; 1♀: Guyana: Carimang R., B. Guiana. H. Whitely. Godman-Salvin Coll. 1904.-1. *Euptychia picea*, Butl., BMNH; 1♀: Guyana: Br. Guiana, Parish. Ex. Grose Smith 1910. Joicey Bequest. Brit. Mus. 1934-120., BMNH.

Paratypes marked with ° show on ventral hindwing a satellite ocellus, in cell M_3, of the ocellus in cell Cu_1.

Etymology. The specific epithet *audacia* means audacity in Latin, a quality needed to go further in the knowledge of Neotropical butterflies, especially when it concerns very common butterflies, as *E. audacia* in French Guiana. These common sibling species in less showy and popular groups have been neglected for centuries.

Distribution. Widely distributed in French Guiana and Guyana, from the northern lowlands of the coast to the southernmost mountains. In Guyana, it appears to be most common on the upper slopes and high ridges of the mountain ranges in Guyana's southern half. Guyana specimens from the Pacaraima Mts. of the Guyana tepui region are known at elevations up to approximately 900m. Though the authors know of no Surinamese specimens, based on its extensive range in French Guiana to the east and Guyana to the west, it seems probable that this taxon also occurs in Suriname. Photographic evidence of live and dry, unset specimens (A. Neild & M. Costa, pers. comm.) suggests *E. audacia* could occur in Venezuela: the live specimen from lowland forest near the Cuyuni River in easternmost Venezuela, close to Guyana, the unset specimens from the tepui region and at elevations above 1,000m. We sustain this affirmation also because this species has been collected on Mt. Ayanganna, Guyana, not far east of the Venezuelan border. The high Acarai Mt. ridges where some specimens were collected constitute the border between Guyana and Pará, Brazil. *Euptychia audacia* should occur in other localities in Pará's Acarai Mts., probably also in the mountains of Pará, Brazil adjoining Suriname, in the mountains of Amapá state,

FIG. 4. Ventral view of lamella antevaginalis: **1**. *Euptychia audacia* (SN-14-81) Relais de Patawalodge, Kaw Mountains, Cayenne, French Guiana (FLMNH voucher 191766); **2**. *Euptychia aquila* (SN-15-23) Acarai Mts./ridge, Sipu River (USNM ENT 00233743); **3**. *Euptychia marceli* (SN-14-79) 85km. S El Dorardo (nr Las Claritas Hotel), Bolívar, Venezuela (FLMNH voucher 191015).

Brazil contiguous with French Guiana, in the mountains of Roraima state, Brazil adjacent to Guyana's easternmost Acarai Mts., and possibly in the tepui region of Roraima state. It could also occur in the lowlands of Amapá, Brazil which are contiguous with the French Guiana lowlands, in the lowlands of Pará, and possibly in the lowlands of Amazonas state, Brazil adjoining Pará and Roraima states.

Behavior & habitat. In French Guiana, *E. audacia* has been observed in primary and secondary forests, mostly during the rainy season. It occurs with equal frequency in lowland or hill forest, flying in both the morning and the afternoon with no seeming preference. In French Guiana, the phenology of *E. audacia* differs from that of sympatric *E. marceli*, which flies all year long and is sometimes frequent on hilltops early in the morning (6:30–8:00AM). During the recent Guyana expeditions undertaken by the first author and partners, far more males (n = 20) were collected compared to females (n = 4). Only one of these specimens (a male) was collected in lowland forest; one (a male) was collected on a tepuian plateau at approximately 900m, all others came from the slopes and high ridges of mountain ranges at elevations from approximately 150 to approximately 1,000m (e.g., Fig. 5). About two thirds of these specimens, all males except for one female, were collected on the high ridges of these mountain ranges above approximately 750m; three out of four females were from lower slopes, two at approximately 150–300m. These data suggest that at least in Guyana, *E. audacia* is more prevalent or concentrated in hill forest compared to lowland forest, the males most common on high ridges. Some other Euptychiina of different genera collected during these expeditions also followed this pattern. Whether this distribution pattern reflects hill-topping behavior by the males or an actual greater prevalence of *E. audacia* in Guyana at these higher elevations is a subject for future study. With three out of four females taken on lower slopes suggests possible hill-topping behavior for this species. In Guyana, *E. audacia* seems to be predominantly a hill forest species that ranges into lower premontane forest in the mountains including the Pantepui. Typical of many Euptychiina, males perched/rested on top of leaves within one and a half meters of the forest floor, their flight not fast but erratic and their daily flight activity of substantial duration.

Euptychia aquila Fratello, Nakahara & Brévignon, new species
Figs. 1 (5-8), 2 (9-12), 4 (2), 6, 7

Euptychia picea; Brévignon, 2012: 43: 9-12; 45: 10; 49.

Diagnosis. *Euptychia aquila*, like *E. audacia*, possesses a '*marceli*-type' (see above) VHW ocelli pattern. Male *E. aquila* are easily distinguished from sympatric *E. marceli* and *E. audacia*, and all other known *Euptychia* besides *E. roraima*, by an entirely dark brown dorsum that exhibits very little translucence. In addition, male *E. aquila* is darker ventrally than *E. audacia* and *E. marceli* and shares with female *E. aquila* a few other characters that differentiate it from *E. audacia* and *E. marceli*: there is usually a prominent second VFW apical ocellus in cell M_3 that is much less prominent and often faint in *E. audacia* and *E. marceli*; it usually has a very small satellite (sometimes extremely tiny and inconspicuous) above the VHW large tornal ocellus (sometimes contained within the yellow ring of the large ocellus) that is lacking on most *E. audacia* and all *E. marceli*; it almost always has a VFW submarginal band that angles strongly inward below vein Cu_1, this is more variable on *E. marceli* and *E. audacia* and usually does not angle inward as prominently as on *E. aquila*. Female *E. aquila*

FIG. 5. West Kanuku Mts. from Nappi Peak (approximately 1,000m), Guyana ; over 30 Euptychiina species occur on these and nearby forested slopes and ridges, including *E. audacia*, *E. aquila* and probably *E. marceli*.

are similar in size to *E. marceli* females and usually larger than *E. audacia* females, and their most distinguishing character is that they possess two large distal ocelli on the DHW lacking on *E. marceli* and *E. audacia*, where the two large ventral ocelli show through the translucent wings. As noted above, *E. roraima* also manifests a dark brown dorsum, though it is somewhat lighter on the distal third of both the forewing and hindwing; it is equally dark ventrally compared to *E. aquila* but there are significant wing shape and ventral wing pattern differences between *E. roraima* and *E. aquila* elucidated in the original description of *E. roraima*. The male genitalia of *E. aquila* differ from the genitalia of *E. marceli* by having a slightly curved and narrower uncus; a conspicuous postero-ventral wedge-shaped projection of the tegumen; a rather triangular distal half of the valvae; an anteriorly curved aedeagus. The male genitalia of *E. aquila* differ from the genitalia of *E. audacia* by the conspicuous postero-ventral wedge-shaped projection of the tegumen being narrower and longer in *E. aquila*. The female genitalia of *E. aquila* are distinguished from

its congeners *E. marceli* and *E. audacia* by the following characters: lamella antevaginalis wide and sclerotized, shaped as a ventral escutcheon (thin and not sclerotized in *E. marceli*, not escutcheon shaped in *E. audacia*) (see Fig. 4).

Description. MALE: forewing length 17 mm.

Wing shape. Forewing inner margin almost straight, outer margin almost straight, with rounded apex. Hindwing rounded and elongated towards tornus, slightly outwardly curved inner margin convex proximally to vein 3A, rounded tornus, outer margin convex, rounded apex, base of costa convex.

Wing venation. Forewing recurrent vein present in discal cell.

Dorsal surface of wings. Ground colour dark brown (R23, G18, B17), hardly translucent; fringe concolorous.

Ventral surface of wings. Ground colour dark brown, lighter than dorsal surface (R88, G58, B44), with five dark reddish brown bands (R54, G24, B18); fringe concolorous.

Forewing: a narrow band extends distally along swollen section of subcostal vein; a regular and quite straight discal band extends from subcostal vein to just beyond vein 2A; a postdiscal band, almost parallel to discal band and thicker, extends from subcostal vein and traverses towards inner margin until vein 2A, slightly broadening to end and markedly distally deviated below vein Cu_2; an undulating submarginal band extends from near apex to near tornus, gradualy broadening towards vein Cu_2 and slightly narrowing after this vein, curved basally in each cell, proximally displaced below Cu_1; narrow marginal band extends from apex towards tornus, very weakly

FIG. 6. *Euptychia aquila* male genitalia in dorsal and lateral views (DJH-2013-1) Two Hat Mt, E. Kanukus, S. Rupununi, S. Slope Summit 2300-2600'.

undulating until vein Cu$_1$ and then straight after this vein; ocellus in cell M$_1$ exceeding vein M$_1$ and M$_2$ respectively, ringed in yellow and with one centered white pupil in black area; smaller ocellus located in cell M$_3$, ringed in yellow and with one centered white pupil in black area; indistinct, faint, dark brown marking is visible around ocelli. Hindwing: regular band extends from costal margin to inner margin, at the base of hindwing; discal band, same width as that of forewing, traverses straight from costal margin towards inner margin, narrower in its anal portion; a postdiscal band of the same width as that of the forewing, extends from the costal margin towards the inner margin, very slightly distally curved, slightly narrower in its anal portion; irregular submarginal band starts from apex and traverses along margin towards tornus, broadened and M-shaped between vein M$_2$ and Cu$_1$; marginal band, thin and very slightly undulated, traverses along distal margin from apex towards tornus and almost fuses to postdiscal band in cell 2A; submarginal ocellus in cell Rs, the smallest of all, shows one centered white pupil in black area; a larger ocellus in cell M$_1$, ventrally exceeding from vein M$_2$, encircled by yellow ring and with one centered white pupil in black area; largest ocellus, ringed in yellow with one centered white pupil in black area in cell Cu$_1$, exceeding from vein Cu$_1$ and Cu$_2$ respectively; a satellite minute ocellus present on the apical side of this ocellus; indistinct, faint, dark brown marking visible around this ocellus.

Head. Antenna about 7.5 mm long, dark brown dorsally with base of antennomeres and tip of the club orange, orange ventrally; eyes entirely dark red brown with black hair; palpus 2.5 mm long, covered with long hairy scales cream at base and blackish distally.

Thorax. Dark brown dorsally with multicolored long hairy scales (green, yellow, orange, red), more densely on its anterior portion near head, with light brown hairy scales ventrally.

Abdomen. Brown dorsally, darker on first three segments with long multicolorous hair on the first segment, with long creamy hair scales ventrally.

Genitalia. (three specimens prepared: vials # PAG 1005 (LCB); vial #2013-01 and #2013-02 (USNM)): uncus rather narrow, curved downward in lateral view, tapered posteriorly, evenly broad in dorsal view; tegumen dorsally convex, somewhat rectangular in dorsal view, posterior projection of the tegumen visible above uncus, approximately one fourth length of uncus, ventral margin concave with conspicuous postero-ventral projection wedge-shaped, subtriangular, with rather tapered distal edge in lateral view; vinculum fused to anterior margin of tegumen; saccus rather angular, almost same length as uncus, dorsally broad, shrinking progressively anteriorly; valva sparsely hairy, posterior fifth triangular with pointed apex, middle section broadest, anterior section tapered, hooked right-angled inwards forming a boot-shape in dorsal view; aedeagus tubular, strongly curved in its anterior quarter in lateral view, and uniform width in its posterior three quarters.

FEMALE: forewing length 15 mm. Similar to the male except as follows:

Wing shape. Forewing costa convex, inner margin almost straight, outer margin rounded, apex and tornus rounded. Hindwing rounded and less elongated than male.

Dorsal surface of wings. Ground color much paler brown than the male (R172, G155, B137), both wings translucent. Hindwing with two large, yellow-ringed, white-pupiled black ocelli in the distal third of the wing, one in apical area, the other in tornal area.

Ventral surface of wings. Ground color lighter brown than dorsal ground color and much paler than male (R173, G161, B138), bands lighter than those of male (R157, G130, B84), in other respects wing pattern very similar to male except size difference between the large HW tornal ocellus, and the larger HW apical ocellus, not as significant as in male.

Genitalia. (two specimens prepared: PAG 1107 LCB; SN-15-23): Papillae anales hairy, adorned with setae on their external side; lamella antevaginalis sclerotized and developed, shaped as a ventral escutcheon, forming a sclerotized 'ring' around basal side of 8th segment; ductus bursae not sclerotized, thin, getting progressively broader anteriorly; corpus bursae long with two linear signa.

Holotype. 1♂, Guyana: Two Hat Mt. E. Kanukus, S. Rupununi, S. Slope 1200–2300', 23–28.IX.2000, 3°8.8'N 59°6.9'W, Leg. S. Fratello et al (USNM)

Allotype. 1♀, Guyana: Acarai mts./ridge, Sipu R. 2500–3700', 6–9.XI.2000, 1°20'N 58°57'W, Leg. S. Fratello et al (USNM)

Paratypes. FW length: 12♂, 16–19mm, 11♀, 15–19mm. 4♂: Guyana: Two Hat Mt, E. Kanukus, S. Rupununi, S. Slope Summit 2300–2600', 23–28.lX.2000, 3°8.8'N 59°6.9'W, Leg. S. Fratello et al (genitalia dissection for one male: 2013-1 Donald J. Harvey); 5♂: Guyana: Acarai Mts./ridge, Sipu River 2500–3000', 31.X.–10.XI.2000, 1°22.2'N 58°57.9'W, Leg. S. Fratello et al (genitalia dissection for one male: 2013-2 Donald J. Harvey); 1♂, 1♀: Guyana: Acarai mts./ridge, Sipu R. 2500–3700', 6–9.Xl.2000, 1°20'N 58°57'W, Leg. S. Fratello et al (genitalia dissection: SN-15-23); 1♀: Guyana: Region 9, Kanuku Mts., Nappi Mt., 1500'–2700', 03°18.8 59°33.9'W, 21 Feb–10 Mar 1999, leg. S. Fratello, R. Hanner, S. Hendricks, R. Williams; 1♀: Guyana: Region 9, Kanuku Mts., Nappi Mt., 1000'–1500', 03°19.5'N 59°33.5W, 21 Feb–10 Mar 1999, leg S. Fratello, R. Hanner, S. Hendricks, R. Williams (all previous Guyana Paratypes: USNM); 3♀: Guyana – Brit. Guiana: Kutari Sources. Jan–Feb. 1936. G.A. Hudson. B.M. 1936-360. (BMNH); 2♂: French Guiana: Massif du Mitaraka, Borne 1, 2°13'N 54°26'30"W, 20, 27.IX.2006, J.-P. Champenois leg, n°22653, 22654, collection B. Hermier (genitalia dissection for one male: PAG 1005); 3♀: French Guiana: Massif du Mitaraka, Borne 1, 2°13'N 54°26'30"W, 26, 28, 29.IX.2006, J.-P. Champenois leg, n°22661, 22662, 22663, collection B. Hermier (genitalia dissection for one female: PAG 1107); 1♀: French Guiana: Massif du Mitaraka, Sommet en cloche, 2.233848 / -54.46057, 22-III-2015, M. Benmesbah (MNHM); 1♀: French Guiana: Massif du Mitaraka, Sommet en cloche, 2.233848 / -54.46057, 22-III-2015, M. Benmesbah (MB).

Etymology. *aquila*, is the feminine form of the Latin masculine adjective aquilus, meaning dark colored, thereby corresponding with the Latin feminine noun *Euptychia*. Male *E. aquila* have the darkest

dorsal surface of any known *Euptychia*, entirely dark brown with only very slight translucence. The male ventral surface is also darker than almost all other *Euptychia*.

Distribution. At present known from three mountain ranges in southern Guyana, the Kanukus, both East and West, and Acarais, most specimens from the upper slopes and high ridges, 700m-1,150m, and a single specimen from mountains near the Kamoa River, approximately 700m, and in French Guiana in the extreme south of the department, in the Tumuc-Humac Mounts. The high Acarai Mt. ridges where some specimens were collected constitute the border between Guyana and Pará, Brazil. Its range should include other higher mountain ranges in southernmost Guyana (e.g., Wassarai and Kamoa Mts.), the mountains of southern Surinam, other localities in Pará's Acarai Mts., and the mountains of Amapá and Roraima states, Brazil, adjacent to the Guianan southern mountains. Approximately one week of collecting in two seasons: March–April and November, on the high slopes and ridges in Guyana's Iwokrama Mts. (approximately 110k north of the Kanuku Mts., highest summits approximately 925m), has not yielded this species.

Behavior & habitat. All known specimens of *E. aquila* are from hill to lower premontane forest (e.g., Fig. 5); none are known from lowland forest, which has been extensively collected in both Guyana and French Guiana (although in southern Guyana and French Guiana, where *E. aquila* has been found, the flatlands have been much less sampled than in northern regions). Present evidence strongly suggests that *E. aquila* is a hill-lower premontane species restricted to the Guianan southern mountains. In Guyana's Acarai Mts., which are higher than the Tumac-Humac Mounts of French Guiana, *E. aquila* is found, besides lowland hill forest, in lower premontane forest at approximately 1,000m and somewhat higher. In Guyana, 10 out of 11 males and two out of five females were collected on the highest slopes and summit ridges of the East Kanuku Mts. (700–800m) and Acarais (750–1,150m). Whether these records entail male hill-topping behavior is subject to further investigation. The lowest recorded elevation for Guyana specimens, a female from the West Kanukus, is 300–450m. Guyana specimens were all probably collected in the low understory within a couple of meters of the forest floor.

<center>DISCUSSION</center>

Both *E. audacia* and *E. aquila* are described in this genus due to their morphological resemblance to *E. marceli* and some other *Euptychia*. The placement of these new species in the genus *Euptychia* is reinforced by the presence of a projection of the tegumen above the uncus; as mentioned above, this character is thought to be a possible diagnostic character that differentiates this genus from other genera in this subtribe (Freitas et al. 2012). Whether this genitalic structure is a unique trait for *Euptychia* will be ascertained when all Euptychiina, including many undescribed taxa, are dissected. It is worth noting that this structure varies widely among known *Euptychia*, as

FIG. 7. *Euptychia aquila* male from the Tumuc-Humac Mts., French Guiana, the only known *E. aquila* specimen manifesting a satellite ocellus below the large VHW ocellus. This is a good example of the type of individual variation seen in *Euptychia* ventral ocelli patterns even among taxa like *E. aquila*, where this pattern is uniform to a large degree.

the drawings in Forster (1964) reveal, also comparing the modest projection of *E. audacia* and *E. aquila* with the very long projection of *E. cesarense* Pulido, Andrade, Peña & Lamas, 2011 (Pulido-B. et al. 2011). In addition, the presence of a recurrent vein in the FW discal cell in both new species should support their placement in *Euptychia*, as mentioned above this trait is also thought to be a shared character for *Euptychia* (but as mentioned before, broader study is needed including whether this character is unique to *Euptychia*). Early stage biology would also reinforce the placement of *E. marceli*, *E. audacia* and *E. aquila* in the genus *Euptychia*. Although hostplants and early stages are known for several *Euptychia* species (Singer et al. 1983, DeVries 1987, Beccaloni et al. 2008, Brévignon 2008), the early stage biology of the majority of taxa is presently unknown, especially regarding Amazonian species (Beccaloni et al. 2008, Brévignon 2008). The majority of *Euptychia* taxa with known nonseed hostplants and early stages possess whitish phenotypes (one taxon with white females, grayish males): *E. mollina* Hübner, 1818 and a few similar taxa (Beccaloni et al. 2008, Brévignon 2008). *Euptychia insolata* Butler & Druce, 1872 is one of only two *Euptychia* with a known nonseed hostplant, manifesting a quite different phenotype, and notable that it alone has been recorded feeding on bryophytes (Neckeraceae). This taxon (resident in south Central America and northwestern

South America) resembles the allopatric *E. marceli*, *E. audacia* and *E. aquila*, most similar to *E. marceli*. *Euptychia insolata* has a marked *marceli*-type VHW ocelli pattern; its tornal ocellus is notably large for a small butterfly and the larger apical ocellus is smaller than on *E. marceli*, resulting in a great difference in size considering these two ocelli. *E. insolata* exhibits a striking sexual dimorphic coloration, males are brown and females whitish, in addition to other subtle external differences. *E. aquila* is sexually dimorphic regarding coloration as well but in a different manner, males are dark brown dorsally, females a translucent light brown. The male genitalia of *E. insolata* are similar to those of *E. marceli*, *E. audacia* and *E. aquila* but with some obvious distinctions: absence of the conspicuous postero-ventral projection of the tegumen present in *E. audacia* and *E. aquila*; shape of the valvae. We assume *E. marceli*, *E. audacia* and *E. aquila* are by varying degrees closely related to *E. insolata* and infer they should also utilize nonseed hostplants, possibly bryophytes.

Concerning facies solely, *E. audacia* closely resembles *E. marceli* in many respects, though usually obviously smaller. *E. aquila* resembles *E. marceli* as well, especially females, but less closely than does *E. audacia*: for males, particularly because of the dark brown dorsum and darker brown venter; for females in possessing two DHW ocelli. The male genitalia of *E. audacia* and *E. aquila* possess a conspicuous postero-ventral projection of the tegumen, a significant character that is lacking in *E. marceli*. This character is also found in at least four other *Euptychia* species: two Guianan species, the recently described *E. neildi* Brévignon, 2005 (Brévignon 2008: fig. 52) and *E. roraima* (Nakahara et al. 2014: fig. 3); the wide ranging *E. mollina* and *E. hannemanni* Forster, 1964, a taxon known from a restricted range (both figured in Forster 1964: p. 81). Whether this character is more prevalent in Guianan species and whether it is an important character for determining relationships in the genus, should be elucidated when a complete generic revision is undertaken including many undescribed species. It is noteworthy that *E. roraima*, though possessing unique facies, beyond the shared conspicuous postero-ventral projection of the tegumen, also has male genitalia very similar to *E. audacia* and *E. aquila*, and is perhaps closely related to them. As already related previously, it is also possibly deserving notice that this taxon is a very dark *Euptychia*, akin to *E. aquila* in this respect. The relationships among *E. marceli*, *E. audacia*, *E. aquila* and *E. roraima* will hopefully be discerned in this future generic revision, though the strong male genitalic and phenotypic evidence presently infer the

Fig. 8. *Euptychia picea* female form *rufocincta* illustration from Weymer (1911).

possible close relationship of *E. aquila* and *E. roraima*.

Until it was described by the third author (Brévignon 2005), *E. marceli* had been misidentified as *E. picea* for many years. In fact, Guianan *Euptychia* specimens misidentified as *E. picea* in the BMNH (photos provided by A. Neild, pers. comm.), including specimens collected over a hundred years ago, represent *E. marceli*, *E. audacia*, *E. aquila* and at least one other undescribed *Euptychia* and no true *E. picea*. Most astounding of these embedded species in the BMNH collection are three *E. aquila* females collected in 1936 from the Kutari Sources, British Guiana, as it was assumed that this species was unknown until collected recently in very remote, little-or-never explored mountain ranges in southern Guyana (Kanuku and Acarai Mts.) and southern French Guiana (Tumuc-Humac Mts.); the Kutari Sources are in the easternmost district of Guyana's Acarai Mts., very close to the border of Surinam, an area expected to be part of this taxon's range and also very remote.

Even after the description of *E. marceli*, the confusion has persisted in museum collections, SF separating *E. marceli* from *E. picea* very recently in three major museum collections, AMNH, USNM and MGCL, with the differentiation of these two taxa ongoing at the BMNH (A. Neild, pers. comm.). Comparing the respective VHW ocelli pattern of each taxon actually accounts for a very easy separation of the two (see Fig. 1). The large tornal ocellus of *E. marceli* is much larger, with a much wider yellow ring, compared

to its large apical ocellus; on *E. picea*, the large tornal and large apical ocellus are usually much closer in size and the yellow ring around the tornal ocellus is hardly wider than the yellow ring around the apical ocellus. *Euptychia picea* also has a small satellite ocellus above the large tornal ocellus and usually has a small satellite ocellus below the large apical ocellus; *E. marceli* lacks these VHW satellite ocelli. The VHW ocelli pattern just described for *E. marceli* is the so-called *marceli*-type pattern described above. As noted above, both *E. audacia* and *E. aquila* possess this *marceli*-type ocelli pattern, though the size difference between the large tornal and apical ocelli and greater width of the tornal ocellus yellow ring is not as prominent on these two new species, especially in the females, and to an even lesser degree, especially for female *E. aquila*; in addition, *E. aquila* usually has a very small to tiny satellite ocellus above the VHW large tornal ocellus and rarely, *E. audacia* also does. Because of the long historic confusion concerning these taxa, it is worth noting that there are a small number of undescribed taxa that could be confused with *E. marceli*, *E. audacia* and female *E. aquila*; specimens representing these taxa were shared with us by our colleagues or uncovered during our own research. Among them are some small *Euptychia*, like *E. audacia*, whose males are indistinguishable dorsally from this species, and some Brazilian lower Amazonian specimens seemingly important to understanding the relationship of *E. marceli* and *E. picea*.

On the Identity of *Euptychia rufocincta* Weymer, 1911 and a Possible Future Neotype Designation

Further confusion concerning the Guianan '*marceli*-type' species resulted from the poor condition, missing specimens, and mistakes concerning *E. picea* form *rufocincta* (Weymer 1911) type material. In 1911, Weymer described *rufocincta* as a form of *E. picea* based on a specimen he presumed was from Surinam. A notable feature of this form *rufocincta* and the reason for this appellation, is the presence of two rufous rings on the DHW, these rings surrounding the two large VHW ocelli showing through the DHW translucence (Fig. 1 (15)); this notable feature is clearly mentioned in the original description and also figured in that work (Weymer 1911) (Fig. 8). Form *rufocincta* was raised to species rank by Lamas (2004), and has been treated as a species by several authors (e. g. Pulido-B et al. 2011). However, the syntypes of *E. rufocincta* have not been found yet, and a putative type specimen illustrated in Warren et al. (2014) is a specimen in ZSM, which had erroneously been labelled as 'paratype' by Forster (G. Lamas, pers. comm.). In addition, there is no evidence

that this specimen was actually examined by Weymer, especially because the dorsal hindwing rufous rings are hardly evident on this specimen. In addition, our examination of *Euptychia* specimens photographed at the ZMHU and ZSM did not result in the discovery of the syntype of *E. rufocincta*. These facts and subsequent confusion resulted in tentatively using the name *E. rufocincta* for the taxon now being described as *E. audacia*, when describing *E. marceli* (Brévignon 2005). Analysis done during work on this present manuscript has shown that *E. rufocincta* is actually female *E. picea*, concerning certain Amazonian populations of *E. picea*, a conclusion probably reached by other researchers as well and seeming close to Weymer's original intent when he described *E. picea* form *rufocincta*. Regarding these populations of *E. picea*, the main reason for this conclusion is that only male *E. picea* and female *E. rufocincta* have been found in the collections we studied and their ventral patterns correlate extremely well. What is currently considered *E. picea* includes populations whose females lack the dorsal rufous rings (A. Neild and K. Willmott, pers. comm.). Until the Amazonian *E. picea* complex is studied further, we decided it is prudent to not synonymize *E. rufocincta* with *E. picea* at this time. There remains the possibility that in the future, the name *rufocincta* might be used for certain populations of *E. picea*, at least to the level of subspecies. In addition, a future neotype designation for *E. rufocincta* might preclude further confusion concerning this 'taxon'.

Also in question is the provenance of Surinam for both *E. picea* form *rufocincta* given in the original description and the false 'type'; as extensive collecting in French Guiana and Guyana has never produced any *E. picea*, and no other similar looking specimens are known from Surinam (H. Gernaat, pers. comm.), the only logical conclusion is that Surinam is a mistaken locality for this taxon. Present evidence points to *E. picea* having a widespread Amazonian distribution outside the Guiana subregion, probably allopatric to *E. marceli*, *E. audacia* and *E. aquila*, all sympatric in the Guianan southern mountains, *E. marceli* and *E. audacia* sympatric widely elsewhere in the Guianas, and all three taxa probably endemic to the Guiana subregion. Beyond the French Guiana localities given for *E. marceli* in the original description (Brévignon 2005) and additional French Guiana localities, *E. marceli* is found widely in Surinam and Guyana and has been collected in eastern Venezuela not too distant from Guyana (A. Neild, pers. comm.); as in *E. audacia*, there is the possibility that *E. marceli* is more widespread in the Guiana subregion.

Conclusion and Future Research

Mainly because of recent extensive collecting efforts in French Guiana and Guyana, three distinct Guianan *Euptychia* species long hidden among museum specimens of *E. picea* have been discerned: first *E. marceli* (Brévignon 2005) and now *E. audacia* and *E. aquila*. With this progress comes many additional questions that will hopefully be answered with subsequent research. Outside the scope of this manuscript but of interest to the authors, is the relationship of the aforementioned *E. insolata* and the undescribed species with *E. marceli*, *E. audacia* and *E. aquila*. The description of these undescribed taxa by our colleagues and one of us (SN) will differentiate them from known taxa and represent another advance. We look forward to the morphological, genetic and early stage biology studies, larger in scope, that will clarify relationships and increase ecological knowledge concerning these attractive small denizens of Neotropical rainforest understories.

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TWO NEW YELLOW-BANDED SISTER SPECIES OF *SYNTOMAULA* MEYRICK (LEPIDOPTERA: GELECHIOIDEA: COSMOPTERIGIDAE) FROM PAPUA NEW GUINEA ASSOCIATED WITH RUBIACEAE

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ABSTRACT. Two new species, *Syntomaula xanthofasciata* **n. sp**. and *S. flavoangulata* **n. sp.** (Lepidoptera: Gelechioidea: Cosmopterigidae) are described from Papua New Guinea and are associated with *Neonauclea obversifolia* (Valeton) Merr. & L.M. Perry, *Uncaria appendiculata* Benth., and *Uncaria cordata* (Lour.) Merr. (Rubiaceae). Macromorphological features and DNA barcodes provide corroborative evidence to diagnose these similarly patterned species. Illustrations of the wing pattern, wing venation, and male and female genitalia are provided. The distinctive yellow and brown forewing coloration is discussed with regard to potential mimicry.

Additional key words: Cosmopterigidae, DNA barcode, Gelechioidea, Malesia, Papua New Guinea, Rubiaceae, Mimicry, Taxonomy

The genus *Syntomaula* was established by Meyrick (1914) with the description of its type species, *S. tephrota* from Sri Lanka. *Syntomaula* contains seven described species: one species is from southeast Asia and the other six species are from Sri Lanka, Japan, and New Guinea. Walker (1864) described *Cryptolechia simulatella* and *C. niveosella* from Sarawak. Later Meyrick (1916) transferred *C. simulatella* to *Bathraula*. And Diakonoff (1968) transferred *Bathraula simulatella* to *Syntomaula* (Scaeosophinae) and synonymized *Cryptolechia niveosella* with *S. simulatella*. Diakonoff (1968) also synonymized *Bathybalia* Diakonoff, 1954 with *Syntomaula*, transferring *B. microsperma* Diakonoff, 1954 to *Syntomaula*. Later Sinev (2002) synonymized *Protorhiza* Diakonoff, 1968 with *Syntomaula*, transferring *Protorhiza cyanosticta* Diakonoff, 1968 to *Syntomaula*. Moriuti (1977) described *Syntomaula cana* from Yakusima Island in Japan, documenting the first known host associations (Rubiaceae) for the genus.

Meyrick (1914) initially treated *Syntomaula* as part of the Oecophoridae. He (1932) later reconsidered the genus part of the Scaeosophidae, but Clarke (1955) transferred it to the Cosmopterigidae. Diakonoff (1968) agreed with Clarke's placement of the genus in Cosmopterigidae but recognized Meyrick's (1922) "*Scaeosophides*-group", which *Syntomaula* originally was part of, and upgraded its status to Scaeosophinae.

Currently, there is no phylogenetic analysis that defines the Scaeosophinae or the genera within. Meyrick (1922), Sinev (2002), and Li et al (2012) defined the Scaeosophinae by the synapomorphy, hindwing with an elliptical unscaled area on both surfaces posterior of the cell. This feature is not present in all *Syntomaula* but this genus shares several features of the male and female genitalia with other scaeosophine genera, i.e.,

Scaeosopha (Li et al., 2012) that we consider important enough to keep the genus in the Scaeosophinae. These features include; tegumen with two elongate, opposable dorsolateral lobes; valvae basally bearing an elongate spinelike or digitate process; female with a sclerotized margin of ostium; and corpus bursae with paired signa. We tentatively define *Syntomaula* as having asymmetrical valvae, elongate asymmetrical basal processes of the valvae, imbricate cornuti in a row within the vesica of the phallus, a shortened part of the ductus bursae posterior to the bulla, and a widened part of the ductus bursae (possibly the corpus bursae) anterior to the bulla.

The two new species of *Syntomaula* described herein originated from a massive program of rearing caterpillars in Papua New Guinea, with an international group of collaborators focusing on the ecology of herbivorous insects, their host plants, and their parasitoides (Miller et al. 2003, Craft et al. 2010, Novotny et al., 2007, 2010, Hrcek et al., 2011, Hrcek et al. 2013). These new taxa were found during a project at Wanang, in lowland rainforest in the Sepik River Basin, near Madang, Papua New Guinea. These species are known only from reared adult specimens, and we are not able to find specimens collected as adults in major collections of New Guinea moths.

The purpose of this study is to: 1) describe two new species of *Syntomaula* from Papua New Guinea using collaborative techniques such as macromorphology and DNA barcode data from Cytochrome c Oxidase I sequences, 2) to hypothesize relationships of these two new taxa not only by morphology but by associations from host-plant data, and 3) to discuss the distinctive forewing color pattern relative to other sympatric moths in Papua New Guinea.

MATERIALS AND METHODS

Field and laboratory studies follow Basset et al. (2000, 2004), Miller et al. (2003, 2013) and Craft et al. (2010). Cytochrome c Oxidase I ("DNA barcode") sequences were prepared by the Biodiversity Institute of Ontario, University of Guelph, following the protocols in Craft et al. (2010) and Wilson (2012). Data for 30 sequences have been deposited in GenBank as accession numbers HM906298, HM900661-4, HQ946812-33, JF847961, including the standard fields for the BARCODE data standard (Benson et al. 2012) and more data, including images and host plants, are available in the Barcode of Life Database (BOLD, www.boldsystems.org; Ratnasingham and Hebert, 2007, 2013), in a dataset accessible using a DOI (dx.doi.org/10.5883/DS-NGSYNTOM). Neighbor-joining (NJ) trees were generated from nucleotide sequences using the BOLD aligner as implemented in BOLD (Ratnasingham and Hebert, 2007, 2013).

Morphological observations and measurements of the wings were made using a Leitz RS dissecting microscope with a calibrated ocular micrometer. Genitalia were dissected as described by Clarke (1941), except mercurochrome and chlorazol black were used as stains. The Methuen Handbook of Colour (Kornerup and Wanscher, 1978) was used as a color standard. Holotypes are deposited in the National Museum of Natural History (USNM), Smithsonian Institution, Washington, DC. Paratypes are distributed among USNM, the Papua New Guinea National Agriculture Research Institute (NARI), and the Natural History Museum (NHM), London, United Kingdom. Data of all specimens examined in this study are summarized in Table 1.

In addition to the morphological differences noted in the descriptions below, DNA barcode sequences from the two new species described here differ from each other by 6.222–6.908% (calculated using the BOLD aligner as implemented in BOLD), clearly indicative of species level divergence in Lepidoptera (Craft et al. 2010, Ratnasingham and Hebert 2013).

RESULTS

Syntomaula xanthofasciata Adamski, **n. sp.**
(Figs. 1–2, 4–6, 10)

Diagnosis. *Syntomaula xanthofasciata* is similar to *S. flavoangulata* in acies but differs from the latter by having a more deeply emarginate posterior margin of the eighth tergum, a wider apical part of the dorsolateral processes of the tegumen of the genital capsule, a broader apical part of the valva, more asymmetrically shaped basal processes of the valvae, a longer part of the phallus with cornuti, a wider membranous space

FIG. 1. *Syntomaula xanthofasciata* Adamski (Paratype, USNM ENT 00697920).

between ventral parts of the eighth tergum in the female, and a more reticulated bulla and corpus bursae in the female.

Description. *Head*: vertex and frontoclypeus yellow; outer surface of labial palpus yellow except, basal segment pale brown, inner surface pale yellow; scape basal 1/3 flagellum brown, distal 2/3 pale brown; proboscis pale yellow.

Thorax: Tegula brown; mesonotum brown, demarcated posteriorly by a narrow, transverse, dark-brown band adjacent to a yellow-tufted, posterolateral margin. Femur and tibia of foreleg pale brown, brown, or with brown scales with distal margin pale brown; tarsomeres 1 and 4–5 dark brown on dorsal surface, pale yellow beneath; tarsomeres 3–4 pale yellow; basal 1/2 of midfemur pale yellow, distal 1/2 brown; midtibia as above except, with a suffused pale-yellow band near midlength; tarsomeres as above; femur and tibia of hindleg pale brown, tarsomeres pale yellow except, dorsal surfaces of tarsomeres 3–5 dark brown. Forewing (Fig. 1): Length 5.1–7.9 mm (n = 11), with a broad, median, and oblique, yellow band, juxtaposed basally by a brown fascia, extending anterodiagonally with 2–3 irregular crenulations to 1/3 costal length; median fascia juxtaposed distally at 2/3 length by a brown band; each band demarcated by a narrow row of dark-brown scales; submarginal and fringe scales with basal 1/2 pale brown, distal 1/2 brown. Undersurface brown, gradually darkening from midlength of radial and medial veins to submarginal line; radial and medial veins pale brown along subapical length, appearing as narrow streaks; area posterior to CuP pale yellowish brown. Venation (Fig. 2) with M_2 about equidistant from M_1 and M_3; CuA_1 about 3× as divergent distally than from base. Hindwing: translucent pale brown, apical fringe scales brown. Venation (Fig. 2) with frenulum with a single acanthus in males, 4 acanthae in females; M_2 about 2.5× as divergent distally than from base, and closer to M_1 than from M_3; M_3 and CuA_1 basally connate, CuA_2 absent.

Abdomen (Fig. 6): with eighth tergum deeply emarginate posteriorly forming two long posteriolateral subtriangular processes, and widely emarginate anteriorly forming two subparallel digitate processes. **Male Genitalia** (Figs. 4–5): Tegumen with two elongate, opposable dorsolateral lobes; lobes widened basally, gradually narrowed to slightly beyond 1/2, deeply notched along inner margin of a clavate apical part. Vinculum broad, U-shaped. Valvae basally parallelsided, apiclly elliptical, asymmetrical, with right valva slightly less emarginate than left; right valval base bearing a large, elongate, setose, digitate process; left valval base bearing a large setose, outwardly curved spinelike process. Juxta thin, apically rounded, setose. Phallus bulbous basally, produced into a tubular, single-coiled apical process; vesica with many imbricate cornuti in a narrow row about as long as 1/2 length of tubular part. **Female Genitalia** (Fig. 10): Papillae anales lobelike, setose. Ovipositor telescopic with 3

membranous subdivisions; apophysis posterioris slightly longer than 1.5× length of apophysis anterioris. Eighth segment ringlike extending ventrally, forming two free, broadly rounded parts. Ostium demarcated by a widened rim with a posteriorly produced narrow process, within membrane, flanked by large triangular plates formed by a mesially emarginate seventh sternum. Ductus bursae smooth posteriorly, dilated near posterior end of corpus bursae, forming a large reticulated bulla; inception of ductus seminalis on posterior end of bulla. Corpus bursae reticulated throughout, gradually widening from posterior end to near 1/2 length, ovoid on anterior end, with two opposable subequal signa; signa elongate, wider anteriorly than posteriorly, each with a mesolongitudinal ridge, produced into a single spinelike process on anterior end.

Holotype ♂, "Papua New Guinea, Madang Province, Wanang Village, 05°15'S, 145°16'E"; "Manumbor, Sau, Isua, Mogia, Sosanika, Idigel, Keltim, Kua, Bito"; "Sp. 125, WP-3D-0734 [*Neonauclea obversifolia* (Valeton) Merr. & L.M. Perry (Rubiaceae)], CATX 087, 23 Jan[uary] 2007"; "USNMENT: PNG, Madang Ecology Project, 00659673"; "♂ Genitalia Slide by DA, USNM 84164"; "DNA" [USNM].

Paratypes (5 ♂, 5 ♀): 1 ♂, 3 ♀, same data as holotype except, "00659672", "♀ Genitalia Slide by DA, USNM 84165; "00659666", "00659674", "00659677" [specimens not dissected]: 1 ♂, same data as above except, "WP-5B-1122, CATX 291, 9 Oct[ober] 2007"; "00667632"; "♂ Genitalia Slide by DA, USNM 83527": 1 ♂, 1 ♀, same data as above except, "WP-3E-0807, CATX 103, 24 Oct[ober] 2006"; "00659676", [specimen not dissected], "00659671"; "♀ Genitalia Slide by DA, USNM 84166": 1 ♂, 1 ♀, same data as above except, "Auga, Molem, Tamtiai, Lilip, Ibalim, Posman, Rimandai, Brus, Novotny, Hrcek lgt"; "WP-3C-0663, CATX 075, 23 Apr[il] 2007"; "00697920" [specimen not dissected]; "05°15'S, 145°17'E"; WP-3A-574, CATX 469, 14 Jul[y] 2007"; "00667636"; "♀ Wing Slide by DA, USNM 83520"; "DNA 2010" [specimen not dissected]: 1 ♂, same data as above except, "05°15'S, 145°17'E"; "WP-5C-1098, CATX 185, 20 Jun[e] 2007"; "00669354" [specimen not dissected, abdomen in gelatin capsule].

Etymology. The species epithet, *xanthofasciata*, is a compound word formed from the Greek *xantho* meaning yellow and the Latin *fascia* meaning banded, referring to the large median yellow band of the forewing.

Biology. *Syntomaula xanthofasciata* is known only to feed on *Neonauclea obversifolia* (Valeton) Merr. & L.M. Perry (Rubiaceae).
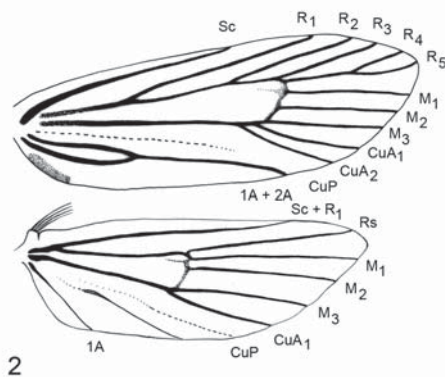
Fig. 2. Forewing and Hindwing venation of *Syntomaula xanthofasciata* Adamski (USNM 83520).

Fig. 3. *Syntomaula flavoangulata* Adamski (Paratype, USNM ENT 00697223).

Syntomaula flavoangulata Adamski, **n. sp.**
(Figs. 3, 7–9, 11)

Diagnosis. *Syntomaula flavoangulata* is similar to *S. xanthofasciata* in facies but differs from the latter by having a more shallowly emarginate posterior margin of the eighth tergum, a narrower apical part of the dorsolateral processes of the tegumen of the genital capsule, a narrower apical part of the valva, less asymmetrically shaped basal processes of the valvae, a shorter part of the phallus with cornuti, a narrower membranous space between ventral parts of the eighth tergum in the female, and a less reticulated bulla and corpus bursae in the female.

Description. *Head*: Vertex and frontoclypeus yellow; outer surface of labial palpus yellow except, basal segment pale brown, inner surface pale yellow; scape basal 1/3 flagellum brown, distal 2/3 pale brown; proboscis pale yellow.
Thorax: Tegula brown; mesonotum brown, demarcated posteriorly by a narrow, transverse, dark-brown band adjacent to a yellow-tufted, posterolateral margin. Femur and tibia of foreleg pale brown, brown, or with brown scales with distal margin pale brown; tarsomeres 1 and 4–5 dark brown on dorsal surface, pale yellow beneath, tarsomeres 3–4 pale yellow; basal 1/2 of midfemur pale yellow, distal 1/2 brown; midtibia as above except, with a suffused pale-yellow band near midlength; tarsomeres as above; femur and tibia of hindleg pale brown, tarsomeres pale yellow except, dorsal surfaces of tarsomeres 3–5 dark brown. Forewing (Fig. 3): Length 6.2–8.1 mm (n = 14), with a broad, median, and oblique, yellow band, juxtaposed basally by a brown fascia, extending anterodiagonally with 2–3 irregular crenulations to 1/3 costal length; median fascia juxtaposed distally at 2/3 length by a brown band; each band demarcated by a narrow row of dark-brown scales; submarginal and fringe scales with basal 1/2 pale brown, distal 1/2 brown. Undersurface brown, gradually darkening from midlength of radial and medial veins to submarginal line; radial and medial veins pale brown along subapical length, appearing as narrow streaks; area posterior to CuP pale yellowish brown. Venation similar to *S. xanthofasciata*. Hindwing as in *S. xanthofasciata*.
*Abdomen* (Fig. 9): with eighth tergum shallowly emarginate medioposteriorly forming two short posteriolateral lobelike extensions, and broadly emarginate anteriorly between two short lateral processes.
Male Genitalia (Figs. 7–8): Tegumen with two elongate, opposable dorsolateral lobes; lobes nearly parallelsided from a widened base, each bearing a large toothlike process near 2/3 length. Vinculum broad, U-
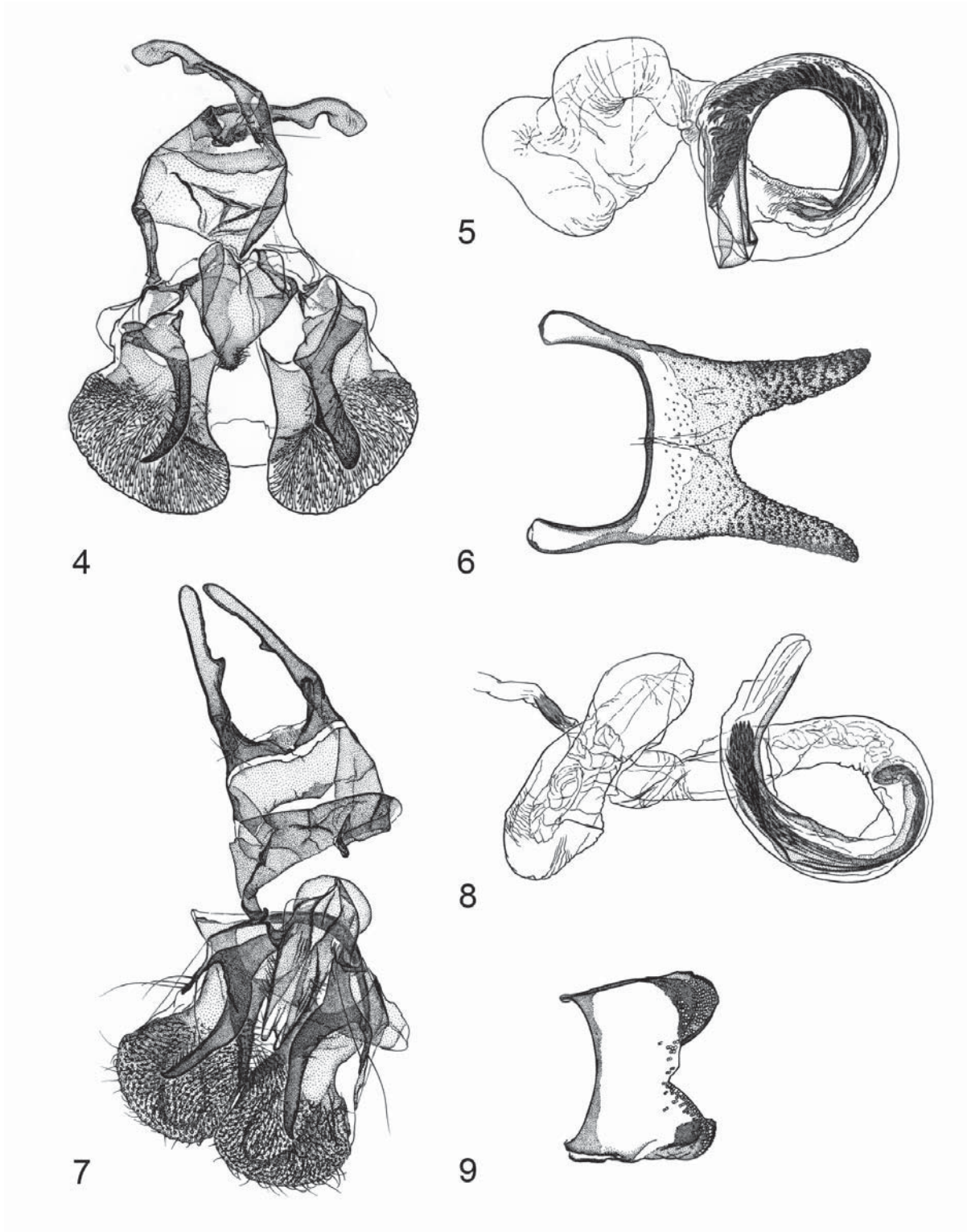
FIGS. 4–9. Male genitalia and eighth tergum of *Syntomaula* spp. Figs. **4–6,** *S. xanthofasciata* Adamski (Holotype; USNM 84164). **4,** Genital capsule. **5,** Phallus. **6,** Eighth tergum. Figs. **7–9**, *S. flavoangulata* Adamski (Holotype; USNM 84167). **7,** Genital capsule. **8,** Phallus. **9,** Eighth tergum.
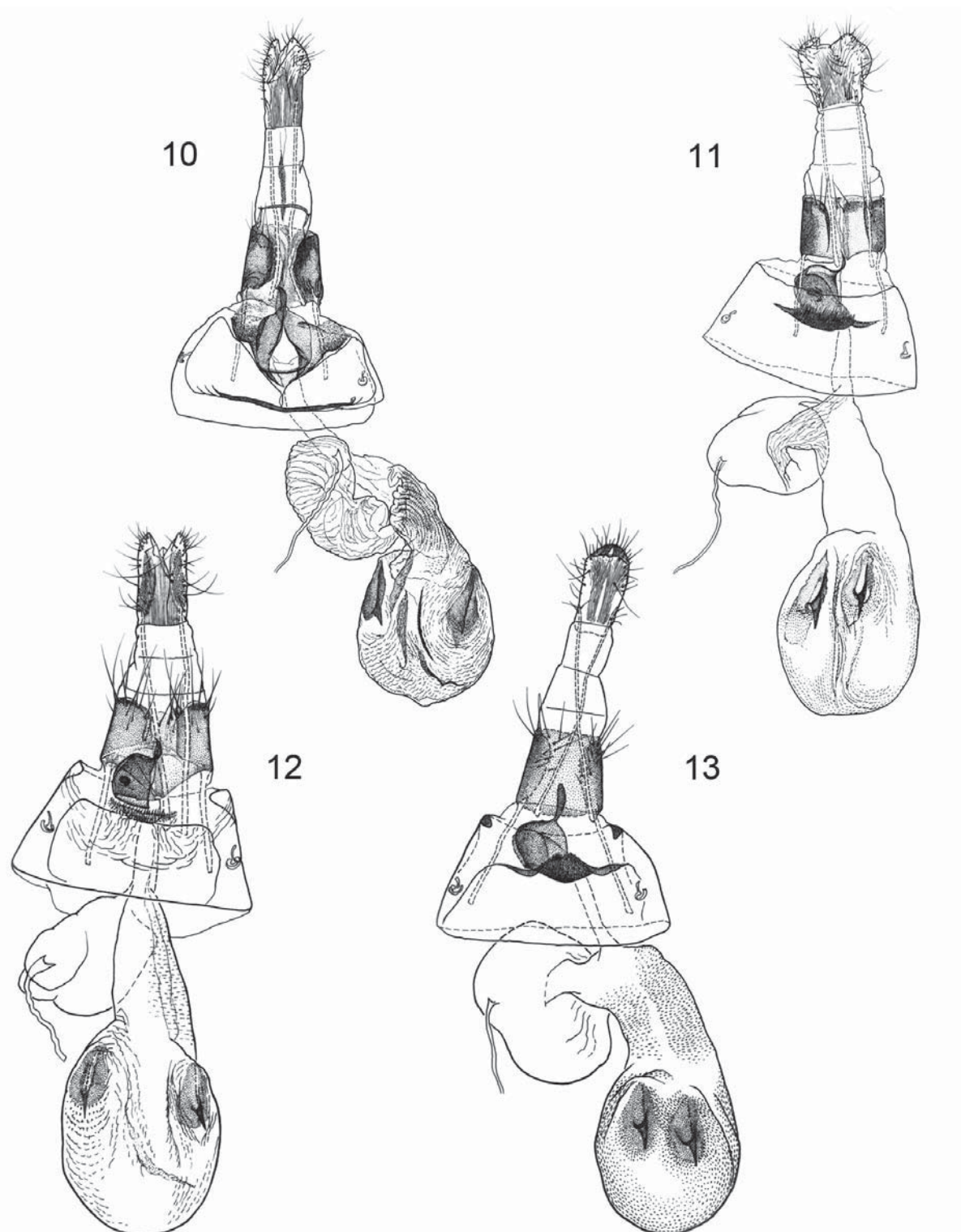
Figs. 10–13. Female genitalia of *Syntomaula* spp. **10**, *S. xanthofasciata* Adamski (USNM 84165). **11,** *S. flavoangulata* Adamski (USNM 83532). Figs. **12–13,** Varients of *Syntomaula flavoangulata* or singletons of one or two additional *Syntomaula* (USNM 84168 and USNM 83533).

TABLE 1. Summary of specimen data.

Specimen	Species	Status	Sex	Genitalia Slide	Plant Number
USNM ENT 00659677	*xanthofasciata*	paratype	M		WP-3D-0734
USNM ENT 00659676	*xanthofasciata*	paratype	M		WP-3E-0807
USNM ENT 00697920	*xanthofasciata*	paratype	M		WP-3C-0663
USNM ENT 00659673	*xanthofasciata*	holotype	M	USNM 84164	WP-3D-0734
USNM ENT 00659674	*xanthofasciata*	paratype	F		WP-3D-0734
USNM ENT 00659671	*xanthofasciata*	paratype	F	USNM 84166	WP-3E-0807
USNM ENT 00659666	*xanthofasciata*	paratype	F		WP-3D-0734
USNM ENT 00659672	*xanthofasciata*	paratype	F	USNM 84165	WP-3D-0734
USNM ENT 00667632	*xanthofasciata*	paratype	M	USNM 83527	WP-5B-1122
USNM ENT 00669354	*xanthofasciata*	paratype	M		WP-5C-1098
USNM ENT 00667636	*xanthofasciata*	paratype	F	USNM 83520	WP-3A-574
USNM ENT 00697223	*flavoangulata*	paratype	F		WS-1Z-3445
USNM ENT 00659464	*flavoangulata*	holotype	M	USNM 84167	WS-4A-2163
USNM ENT 00667869	*flavoangulata*	paratype	M		WS-4A-2163
USNM ENT 00659467	*flavoangulata*	paratype	F	USNM 83534	WS-4A-2137
USNM ENT 00667861	*flavoangulata*	paratype	F	USNM 83509	WS-4A-2163
USNM ENT 00667822	*flavoangulata*	paratype	M	USNM 83507	WS-4A-2163
USNM ENT 00667853	*flavoangulata*	paratype	M	USNM 125655	WS-4A-2163
USNM ENT 00697222	*flavoangulata*	paratype	F		WS-1Z-3445
USNM ENT 00667857	*flavoangulata*	paratype	M	USNM 83506	WS-4A-2163
USNM ENT 00667806	*flavoangulata*	paratype	F	USNM 83535	WS-4A-2163
USNM ENT 00659466	*flavoangulata*	paratype	F		WS-4A-2163
USNM ENT 00659465	*flavoangulata*	paratype	F	USNM 83532	WS-4A-2163
USNM ENT 00667849	*flavoangulata*	paratype	F	USNM 83508	WS-4A-2163
USNM ENT 00667865	*flavoangulata*	paratype	F		WS-4A-2163
USNM ENT 00704492	BIN AAL8374	larva	-		WP-4W-0849
USNM ENT 00667894	BIN AAN2759	adult	F	USNM 84168	WS-4A-2163
USNM ENT 00667873	BIN AAN2760	adult	F	USNM 83533	WP-2D-0340
ZMA.INS.765353	BIN ACD3489	adult	?		
ZMA.INS.765354	BIN ACD3571	adult	?		

Table 1. Summary of specimen data.(continued)

Plant species	Date	Genbank	Locality	Lat	Lon	Elev
Neonauclea obversifolia	23-Jan-2007	HQ946816	Wanang	-5.25	145.27	115
Neonauclea obversifolia	24-Oct-2006	HQ946814	Wanang	-5.25	145.27	115
Neonauclea obversifolia	23-Apr-2007	HQ946813	Wanang	-5.25	145.27	115
Neonauclea obversifolia	23-Jan-2007	HQ946812	Wanang	-5.25	145.27	115
Neonauclea obversifolia	23-Jan-2007	HQ946822	Wanang	-5.25	145.27	115
Neonauclea obversifolia	24-Oct-2006	HQ946820	Wanang	-5.25	145.27	115
Neonauclea obversifolia	23-Jan-2007	HQ946823	Wanang	-5.25	145.27	115
Neonauclea obversifolia	23-Jan-2007	HQ946825	Wanang	-5.25	145.27	115
Neonauclea obversifolia	09-Oct-2007	HM900661	Wanang	-5.25	145.27	115
Neonauclea obversifolia	20-Jun-2007	HQ946815	Wanang	-5.25	145.27	115
Neonauclea obversifolia	14-Jul-2007	JF847961	Wanang	-5.25	145.27	115
Uncaria caudata	30-Apr-2008	HQ946818	Wanang	-5.25	145.27	115
Uncaria appendiculata	12-May-2006	HQ946827	Wanang	-5.25	145.27	115
Uncaria appendiculata	12-May-2006	HQ946832	Wanang	-5.25	145.27	115
Amomum aculeatum	12-May-2006	HQ946830	Wanang	-5.25	145.27	115
Uncaria appendiculata	12-May-2006	HQ946828	Wanang	-5.25	145.27	115
Uncaria appendiculata	12-May-2006	HM900663	Wanang	-5.25	145.27	115
Uncaria appendiculata	12-May-2006	HM900664	Wanang	-5.25	145.27	115
Uncaria cordata	30-Apr-2008	HQ946826	Wanang	-5.25	145.27	115
Uncaria appendiculata	12-May-2006	HM900662	Wanang	-5.25	145.27	115
Uncaria appendiculata	12-May-2006	HQ946833	Wanang	-5.25	145.27	115
Uncaria appendiculata	12-May-2006	HQ946819	Wanang	-5.25	145.27	115
Uncaria appendiculata	12-May-2006	HQ946829	Wanang	-5.25	145.27	115
Uncaria appendiculata	12-May-2006	HQ946817	Wanang	-5.25	145.27	115
Uncaria appendiculata	12-May-2006	HQ946824	Wanang	-5.25	145.27	115
Neonauclea obversifolia	28-Oct-2006	HM906298	Wanang	-5.231	145.182	100
Uncaria appendiculata	12-May-2006	HQ946821	Wanang	-5.25	145.27	115
Uncaria appendiculata	08-Aug-2006	HQ946831	Wanang	-5.25	145.27	115
	19-Nov-2011	KR736046	Maripi	-0.91667	133.967	112
	26-Oct-2008	KR736047	Lelambo	-4.01667	139.783	900

shaped (not shown). Valvae slightly asymmetrical, basally parallelsided, apically subtrapezoidal; base of valvae bearing from base a large, subequal forklike process, inner part much larger than outer part; inner part setose. Juxta thin, apically rounded, setose. Phallus bulbous basally, produced into a tubular, single-coiled apical process; vesica with many imbricate cornuti in a wide row about as long as 1/5 length of tubular part. **Female Genitalia** (Fig. 11): Papillae anales lobelike, setose. Ovipositor telescopic with 3 membranous subdivisions; apophysis posterioris about 2X length of apophysis anterioris. Eighth segment ringlike extending ventrally, forming two free, closely opposable parts. Ostium demarcated by a widened, twisted rim with a posteriorly produced broadly produced, narrow process, within membrane, posterior to entire, seventh sternum. Seventh sternum with a densely setose elongate ridge on posterior 1/3. Ductus bursae smooth, dilated near posterior end of corpus bursae, forming a large bulla; inception of ductus seminalis on posterior end of bulla. Corpus bursae, gradually widening from posterior end to near 1/2 length, ovoid and finely reticulate on anterior end, with two opposable subequal signa; signa elongate, wider anteriorly than posteriorly, each with a mesolongitudinal ridge, produced into a single spinelike process on anterior end.

Holotype ♂, "Papua New Guinea, Madang Province, Wanang Village, 05°15'S, 145°16'E"; "Manumbor, Sau, Isua, Mogia, Sosanika, Idigel, Keltim, Kua, Bito"; "Sp. 125, WS-4A-2163 [*Uncaria appendiculata* Benth. (Rubiaceae)], CATX 263, 12 May 2006"; "USNMENT: PNG, Madang Ecology Project, 00659464"; "♂ Genitalia Slide by DA, USNM 84167"; "DNA" [USNM].

Paratypes (4 ♂, 9 ♀): 2 ♂, 4 ♀, same data as holotype except, "00667857"; "♂ Genitalia Slide by DA, USNM 83506"; "00667869", [*Uncaria appendiculata* [specimen not dissected]; "00659465", "♀ Genitalia Slide by DA, USNM 83532"; "00659467", [ex. *Amomum aculeatum* Roxb. (Zingiberaceae)]; "♀ Genitalia Slide by DA, USNM 83534"; "00667865", "00659466" [ex. *Uncaria appendiculata*]; [specimens not dissected]; 2 ♀, same data as above except, "WS-1Z-3447, CATX 0469, 30 Apr[il] 2008", "00697222", "00697223", [ex. *Uncaria cordata* (Lour.) Merr. (Rubiaceae)]; [specimens not dissected]; 2 ♂, 3 ♀, same data as above except, "Auga, Molem, Tamtiai, Lilip, Ibalim, Posman, Rimandai, Brus, Novotny, Hrcek"; "00667822"; [ex. *Uncaria appendiculata*]; "♂ Genitalia Slide by DA, USNM 83507"; "00667853"; [ex. *Uncaria appendiculata*]; "♂ Genitalia Slide by LEH, USNM 125655"; "00667849"; [ex. *U. appendiculata*]; "♀ Genitalia Slide by DA, USNM 83508"; "00667861"; [ex. *Uncaria appendiculata*]; "♀ Genitalia Slide by DA, USNM 83509"; "00667806"; [ex. *Uncaria appendiculata*]; "♀ Genitalia Slide by DA, USNM 83535."
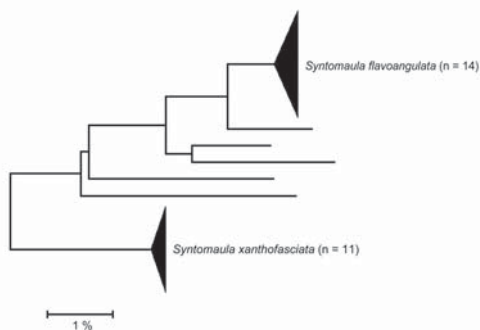
FIG. 14. A compressed subtree sequence data of *Syntomaula xanthofasciata* Adamski and *S. flavoangulata* Adamski taken from 25 samples, and *Syntomaula* spp. taken from 5 samples of 4 adults and one larva based upon neighbor-joining analysis. Subtrees are compressed into triangles with a vertical scale of 10 pixels per specimen; the horizontal scale corresponds to divergence. Two female specimens (HQ946821 and HQ946831) are very similar morphologically to the above described species. They are illustrated in Figs. 12–13.

Etymology. The species epithet, *flavoangulata*, is a compound word formed from the Latin *flavus* meaning yellow and the Latin *angulatus* meaning angled, referring to the large angular median yellow band of the forewing.

Biology. Most specimens of *Syntomaula flavoangulata* have been reared from *Uncaria appendiculata*, but it has also been reared twice from *U. cordata* (Lour.) Merr. (Rubiaceae), and once from *Amomum aculeatum* Roxb. (Zingiberaceae). The *Amomum* record may be a mistake.

Remarks: Macromorphological evidence is corroborated by a compressed subtree of DNA sequence data (Fig. 14), showing over a 1 per cent difference between samples of *Syntomaula xanthofasciata* and *S. flavoangulata*, in addition to other *Syntomaula* spp. (see Table 1).

DISCUSSION

Forewing coloration and mimicry

Syntomaula xanthofasciata and *S. flavoangulata* have a distinctive forewing color pattern shared by many other small moths of New Guinea. This pattern is characterized by the upper side of the forewing having the distal 1/3–1/2 brown, and the basal 2/3–1/2 yellow or orange, and most of the body brown. Some species have the base of the forewing brown. The hindwing is usually brown, although it can be paler in some species. In addition to Cosmopterigidae (*Syntomaula*), we have observed this color pattern in at least four other moth families:

Erebidae: Arctiinae: Lithosiini: Many species in many genera, not listed here because the generic concepts need revision, but examples are illustrated in Draudt (1914). *Trischalis splendens* de Vos and van Mastrigt (2007) is a recently described species that appears to fit this pattern.

Oecophoridae: Stathmopodinae: Several species in the genus *Stathmopoda*, including *Stathmopoda aurifera* Walker (Robinson et al. 1994:55), which may be a species complex (Miller et al. 2014).

Tineidae: Several species of the genus *Edosa* (Perissomasticinae), see Robinson 2008:320, 366; 2009: Figs. 287–288, and several species of the genus *Opogona* (Hieroxestinae), see Robinson and Tuck (1997).

Tortricidae: Olethreutinae: Several species of *Loboschiza*, including *Loboschiza mediana* (Walker) (Horak 2006:266), and an unidentified *Loboschiza* also reared at Wanang (project morphospecies TORT204).

Some species of *Idiophantis* (Gelechiidae: Anacampsinae) are similar in pattern, although the basal brown coloration is more dominant than the distal brown coloration. These include *Idiophantis thiopeda* Meyrick,

Idiophantis pandata Bradley (1961: pl. 5, fig. 13), and *Idiophantis* n. sp. (project morphospecies XXXX124).

We suspect that this yellow and brown pattern in moths may be mimicry of Chrysomelidae that may be distasteful. When the wings of these moths are closed at rest, the patterns resemble those of some beetles, and some of the moths even fold the angles of the wings to yield a more oval (beetle-like) shape when at rest. Chrysomelidae with similar patterns in New Guinea include members of three subfamilies (some illustrated in Gressitt and Hornabrook 1977): Chrysomelinae: *Promechus* species (Gressitt and Hart 1974); Galerucinae: *Aulacophora* species such as *Aulacophora pallidifasciata* Jacoby (Gressitt and Hornabrook 1977:62); and Hispinae: *Hispodona chapuisi* Gestri (Gressitt and Samuelson 1988), *Callistola* species (Gressitt 1960), and *Promecotheca* species. While collecting on flowers at Wau in 1983, Miller (unpublished) netted what he thought was a microlepidopteran, and it turned out to be a chrysomelid, so evidently vertebrates can be tricked by these color patterns. Mimetic relationships between beetles and moths have been described elsewhere by Linsley et al. (1961) and Balsbaugh and Fauske (1991).

Meyrick (1938: 503) and Diakonoff (1955: 183; 1956) have commented on the frequent occurrence in New Guinea of moths with a white ground color and black markings of particular patterns, and suggested that it could have a protective function, but we are not aware of previous discussion of the yellow and brown color pattern in New Guinea.

The yellow and brown color pattern appears to be a subset of the *"Damias* type" of mimetic pattern characterized by Holloway (1984) and Yen et al. (2005:198) by "several large bright colour patches (red, yellow, white) with black or white background colour." In New Guinea we have also found a pattern of red, yellow, and black in a new genus of Oecophorinae (reared as morphospecies TORT144, being described by Vitor Becker, Scott Miller and Shen-horn Yen), a new species of *Lactura* (Lacturidae), *Spoladea mimetica* Munroe (illustrated by Munroe 1974:23; Crambidae: Spilomelinae), and *Bursadella anticeros* (Meyrick) and *B. proceros* (Meyrick) (illustrated by Clarke 1969:103, 148; Immidae). This pattern differs from that in our two new *Syntomaula* by including red, and the moths are often larger. Beetle models have not yet been associated with the mimetic pattern that includes red, although similar chyrsomelid beetles are a possibility.

Related species

We have two reared females that appear, based on DNA and genitalia, to be additional undescribed species,

but we refrain from describing them based on single females, because they may represent variation. One is specimen USNM ENT 00667894, genitalia slide 84168 (figure 12) and the other is USNM ENT 00667873, genitalia 83533 (figure 13), both reared from *Uncaria appendiculata.*

We are also aware of three additional specimens with unique DNA sequences that might also represent undescribed species. One is known only from a larva collected on *Neonauclea obversifolia* (Rubiaceae) (plant WP4E0849) at Wanang, specimen USNM ENT 00704492, our morphospecies CATX469 (Miller et al., 2013), Genbank accession HM906298. The other two are specimens collected at light in Indonesian New Guinea, now in the Naturalis Biodiversity Center, Leiden. We have seen images of the wings, but have not examined the genitalia. They are ZMA INS 765354 from Lelambo, Jayawijaya Mountains, and ZMA INS 765353 from Maripi, Arfak Mountains (Genbank accessions KR736047 and KR736046).

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THREE NEW SPECIES OF *IDAEA* TREITSCHKE (GEOMETRIDAE: STERRHINAE) FROM THE SOUTHWESTERN UNITED STATES AND NORTHERN MEXICO.

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ABSTRACT. Three new species of *Idaea* Treitschke, 1825 (Geometridae: Sterrhinae) are described and illustrated: *Idaea knud-sonaria* **n. sp.**, type locality Sierra Diablo Wildlife Management Area, Culberson County, Texas; *Idaea kendallaria* **n. sp.**, type locality Santa Ana Refuge, Hidalgo County, Texas; and *Idaea elizabetharia* **n. sp.**, type locality Madera Canyon, Santa Cruz County, Arizona. *I. kendallaria* has been reared on southern live oak, *Quercus virginiana* Miller.

Additional key words: *Idaea skinnerata*, *Idaea demissaria*, *Idaea asceta*, North America, inchworm

Idaea Treitschke 1825 is a large genus in the geometrid, or inchworm, moth subfamily Sterrhinae, containing about 680 species worldwide (Hausmann, 2004) and 30 in America north of Mexico. These include the 26 species listed in Hodges et al. (1983), *Idaea asceta* (Prout 1910) added by Covell (2011), and the three new species described here. The moths are moderately small and usually white, tan or gray. The forewing and hindwing are similar in color and pattern, and have only medial and postmedial lines, the medial line "at a rather proximal position" (Hausmann, 2004). Areas of darker shading present or absent, mostly between lines or distal to postmedial line when present. Small dark discal dots are present on all wings in many species. Antennae fasciculate in males, simple in females. The male hind tibia is often modified with or without hair pencils. Male genitalia are rather simple, with gnathos opposing the uncus and valves usually undivided but variable in width and shape. Sheet-like and spine-like cornuti are present or absent. The ductus bursae and/or corpus bursae of the female usually contain patches, bands, or a lining of spines and/or tiny pointed spicules.

During the course of revisionary studies of North American Sterrhinae the following three species came to light as undescribed. All are similar to each other in some maculation and/or genital features and also to several other species, such as *I. demissaria* (Hübner 1831), *I. celtima* (Schaus, 1901), *I. basinta* (Schaus. 1901), and *I. skinnerata* (Grossbeck, 1907). Since the ranges of at least two of them extend into Mexico, study of types of similar neotropical *Idaea* species was necessary before the new species could be described.

MATERIALS AND METHODS

Specimens used in this study are deposited in the following collections. They are listed with their acronyms which are given in parentheses following paratype and other data to indicate ownership or deposition of those paratypes.

AMNH American Museum of Natural History, New York, NY
GJB George J. Balogh collection, Portage, MI
CNC Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, Ontario
CSU Gillette Museum, Colorado State University, Ft. Collins, CO
CUIC Cornell University Insect Collection, Ithaca, NY
ECK Edward C. Knudson Collection, Houston, TX
JRH J. Richard Heitzman Collection, Independence, MO (partly now at MGCL)
LACM Natural History Museum of Los Angeles County, Los Angeles, CA
MCZ Museum of Comparative Zoology, Harvard University, Cambridge, MA
MGCL McGuire Center for Lepidoptera & Biodiversity, Florida Museum of Natural History, Gainesville, FL
NSM Nova Scotia Museum of Natural History, Halifax, Nova Scotia, Canada
TAMU Texas A & M University Insect Collection, College Station, TX
UCB Essig Museum of Entomology, University of California, Berkeley, CA
UCD Bohart Entomological Museum, University of California, Davis, CA
USNM United States National Museum of Natural History, Smithsonian Institution, Washington DC
TNHC Texas Natural History Collections, Integrative Biology, University of Texas at Austin

I. kendallaria **n. sp.** was compared with holotypes of the following species in the The Natural History Museum, London, England, by the late D. S. Fletcher: *Acidalia spernata* Walker (1861), *Acidalia botydaria* Walker (1867), *Ptychopoda limitata* Warren (1897) and *Anteois pygmeata* Warren (1901) (all described from Venezuela). I compared it with the syntype ♂ of

Ptychopoda clothula Dyar (1914, type locality Panama) and the syntype ♂ of *Ptychopoda rufarenaria* Warren (1906, type locality Cayenne, French Guiana), both in the USNM. I compared *I. elizabetharia* **n. sp.** with the holotype ♂ of *I. skinnerata* (Grossbeck, 1907) from Arizona in the AMNH. I am convinced that *I. kendallaria* **n. sp.** and *I. elizabetharia* **n. sp.** are distinct from the species mentioned above.

Idaea knudsonaria Covell, **new species**
(Figs. 1 ♂ – 2 ♀, 13–14, 23)

Diagnosis: The sharply defined, nearly straight brown medial line on forewing and hindwing, and the terminal line, widest toward the forewing apex, are distinctive. Hindwing discal dot red. Male and female genitalia similar to *I. demissaria* (Figs. 17–18); valve broader-based and phallus with 35 or more spine-like cornuti (3 in *I. demissaria*); female ductus bursae shorter than that of *I. demissaria*, and straight; corpus bursae pyriform instead of ovate and recurved basally, projecting at an angle to ductus bursae; sclerotized strap-like process in corpus bursae (spinose in *I. demissaria*); corpus bursae lacks spicule lining present in *I. demissaria*.

Description (Figs. 1, 2): Head, antenna, thorax and abdomen yellowish buff; antenna fasciculate in male, simple in female. Front dark brown, interantennal fillet yellowish buff. Legs buff; male hindleg extremely reduced, with tibia subequal to tarsus in length, and both together shorter than middle tibia; no hair pencil. Forewing with one areole (accessory cell), which may not be closed. Wings pale yellowish buff. Forewing with narrow brown edging along costa; medial line absent; postmedial line brown, nearly straight; broader terminal line evenly narrowing from apex to tornus; discal dot slightly darker brown than medial line and sometimes partially enclosed in it. Pattern of hindwing a continuation of that on the forewing; postmedial line straight, with obscure discal dot represented by a few dark red scales within the postmedial line; terminal line moderately wide and fairly even. Fringe scales very long, yellowish buff. Underside glistening off-white, with pattern of upper side faintly expressed. Wing length: 6.5 – 8.5 mm.

Male genitalia (Fig. 13): Tegumen rounded, very similar to *I. demissaria* (Fig. 17) and related species. Uncus broad-based, curving ventrally, narrowing to a fine, sclerotized point; valve broad-based, slightly sinuous as it narrows to a slightly out-turned pointed apex; gnathos heavily sclerotized centrally, opposing uncus; juxta membranous; vinculum moderately deep and broadly rounded (lobe-like in *I. demissaria*); phallus dorsally recurved anterior to juncture with ductus ejaculatorius, and straight posterior to that juncture; one anterior and three posterior patches of 35–55 variably sized, similarly shaped, spine-like cornuti.

Female genitalia (Fig. 14): Somewhat similar to *I. demissaria* (Fig. 18), ductus bursae moderately long, straight, much more narrow than in *I. demissaria*. A wide heavily sclerotized band extends the length of the ductus bursae and into the pyriform corpus bursae; this band is recurved in corpus bursae where it is heavily spinose; no tiny spicules line corpus bursae.

Immature stages: Unknown.

Holotype (Fig. 1). ♂, Sierra Diablo Wildlife Management Area, 6000', Culberson Co., Texas, 29 May 1973, A. & M. E. Blanchard (USNM).

Paratypes (9): TEXAS. 1 ♂, same data as holotype, C. V. Covell Jr.

genitalia slide #1,225 (USNM); 1 ♀, same location and collectors as holotype, 30 May 1973, C. V. Covell Jr. genitalia slide #1,226 (USNM); 1 ♂, Sierra Diablo WMA, Culberson Co., 27 June 1981, E. C. Knudson, C. V. Covell Jr. genitalia slide #1,359 (ECK); 1 ♀, same locality and collector as preceding, 11 June 1982, C. V. Covell Jr. genitalia slide #1,357 (ECK); 1 ♂, 3 ♀♀, same locality and collector as preceding, 18 August 1984 (ECK). MEXICO. 1 ♀, 6 mi. E[ast of] Est. [Estacion ?] Roberto, Nuevo Leon, 27 May 1981, J. Doyen, C. V. Covell Jr. genitalia slide #1,356 (UCB).

Distribution and flight period (Fig. 23): Known only from the type locality and an unidentified site in Nuevo Leon, Mexico. Collected between late May through June and in August.

Discussion: The distinctive wing pattern is unlike that of any other known nearctic or neotropical Geometridae.

Etymology: This species is named in honor of Edward C. Knudson, who collected some of the type series and who has made many important contributions to our knowledge of American Lepidoptera—particularly those of Texas.

Idaea kendallaria Covell, **new species**
(Figs. 3 ♂ – 4 ♀, 15–16, 24)

Diagnosis: This species is very similar to reddish-shaded specimens of the common and widespread North American *I. demissaria* (Hübner 1831) in color, pattern and genital features. *I. kendallaria* is distinguished from most *I. demissaria* by being slightly smaller on average, with browner (less reddish) shading, and sharper contrast between the forewing pattern basad and distad of the postmedial line (Figs. 3–6). Females are often almost concolorous brown—a dimorphism absent in *I. demissaria*. The patch of ground color at the apex of the male forewing tends to terminate more cleanly above R_3, with subterminal shading appressed to outer side of postmedial line all the way to inner margin (often thin edging of ground color along outer side of posterior portion of postmedial line in *I. demissaria*). Hindwing without broad, subterminal reddish border of shaded specimens of *I. demissaria* (some variants lack shading). Male genitalia (Figs. 15, 17) with gnathos about half length of uncus (subequal in *I. demissaria*); broad costal spine of *I. demissaria* valve absent. Posterior end of cornutus terminates in two rounded nubs (two small sharp spines in same position in *I. demissaria*). The female genitalia with much wider ductus bursae than *I. demissaria* (Figs. 16, 18); with small spinose patch at basal end of corpus bursae (in *I. demissaria* there is only a vague sclerotized patch without spines); small membranous sac (appendix bursae) extends distally from the corpus bursae, not bearing spines—a structure absent in *I. demissaria*.

Description (Figs. 3–4): Head, thorax and abdomen orangish buff with front brown; antenna fasciculate in male, simple in female, orangish buff. Interantennal fillet and legs yellowish buff; male hind tibia greatly reduced, slightly shorter than length of tarsus, without hair pencil. Single areole of the forewing not closed in specimens
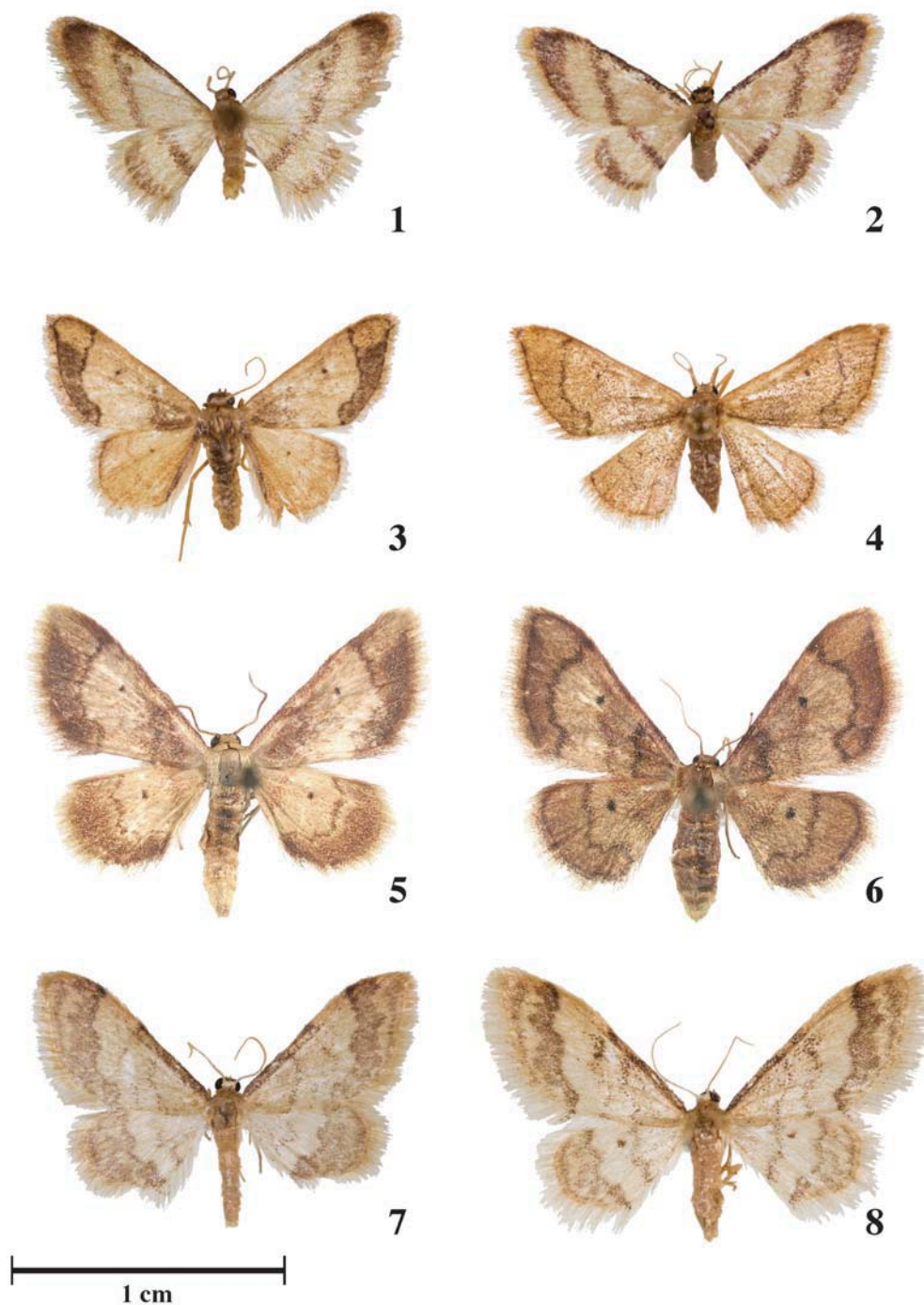
FIGS. 1–8. **1.** *Idaea knudsonaria*, **n. sp.** , holotype ♂, Sierra Diablo Wildlife Management Area, Culberson Co., TX **2.** *Idaea knudsonaria*, **n. sp.** , ♀, same locality as holotype **3.** *Idaea kendallaria* **n. sp.** , holotype ♂, Santa Ana Refuge, Hidalgo Co., TX **4.** *Idaea kendallaria* **n. sp.** ♀, Mountain View Acres, Bexar Co., TX **5.** *Idaea demissaria* (Hübner), ♂, Fluker, Tangipahoa Parish, LA **6.** *Idaea demissaria* (Hübner), ♀, Wedge Plantation, McClellanville, SC **7.** *Idaea elizabetharia* **n. sp.** , holotype ♂, Madera Canyon, Santa Cruz Co., AZ **8.** *Idaea elizabetharia* **n. sp.** , ♀, same locality as holotype

FIGS. 9–14. **9.** *Idaea skinnerata* (Packard), ♂, Cochise Co., AZ **10.** *Idaea skinnerata* (Packard), ♀, Palmerlee, AZ **11.** *Idaea elizabetharia*, ♂ antenna **12.** *Idaea skinnerata*, ♂ antenna **13.** *Idaea knudsonaria* **n. sp.** , ♂ genitalia **14.** *Idaea knudsonaria* **n. sp.** , ♀ genitalia

FIGS. 15.–18. *Idaea kendallaria* **n. sp.** , ♂ genitalia, **16.** *Idaea kendallaria* **n. sp.** , ♀ genitalia, **17.** *Idaea demissaria* (Hübner), ♂ genitalia, **18.** *Idaea demissaria* (Hübner), ♀ genitalia
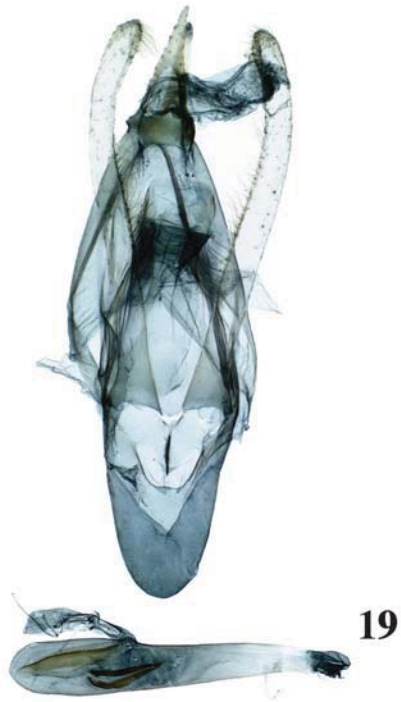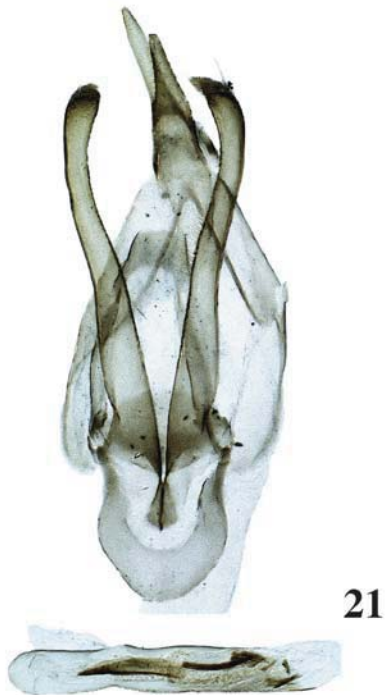
Figs. 19–22. **19.** *Idaea elizabetharia* **n. sp.** , ♂ genitalia, **20.** *Idaea elizabetharia* **n. sp.** , ♀ genitalia, **21.** *Idaea skinnerata* (Grossbeck), ♂ genitalia **22.** *Idaea skinnerata* (Grossbeck), ♀ genitalia

Fig. 23. *Idaea knudsonaria* distribution map
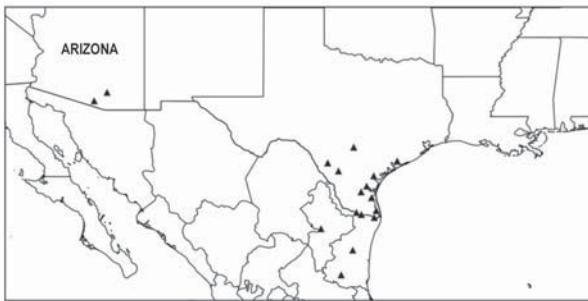
Fig. 24. *Idaea kendallaria* distribution map
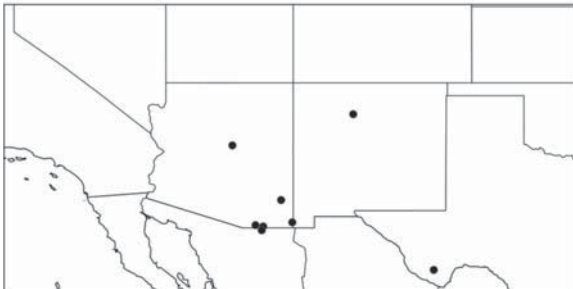
Fig. 25. *Idaea elizabetharia* distribution map

examined. Wings orangish buff with scattered dark reddish brown scales in male, uniformly suffused with brown in female; antemedial line straight, dark brown, not complete to costa; faint trace of brown median line in posterior half of forewing; postmedial line sharp, complete, finely scalloped, dark brown; terminal line dark brown. Male with dark reddish brown shading in posterior half of basal area and distad of postmedial line except for a small elongate patch of orangish buff below apex. Fringe orangish buff, with diffuse brownish spots at ends of veins. Hindwing colored as forewing, with medial and postmedial lines often obscure. Small, sharply defined blackish discal dot on forewing and usually larger one on hindwing. Underside glistening yellowish with markings of the upperside repeated faintly. Long yellowish hair pencil from male hindwing base, appressed along anal margin. Forewing length: 6.0–8.0 mm.

Male genitalia (Fig. 15): Uncus rounded at apex, narrower than gnathos. Gnathos broad-based, narrowing to a blunt tip and one-half to two-thirds length of uncus. Valve simple, rounded terminally, fused with other valve at base; broad sclerotized spine absent. Large tuft of long hair-scales inserted laterally at valve base (easily lost during dissection). Phallus large, longer then genital capsule, with large, complex cornutus with an anteriorly twisted heavily sclerotized, plate-like structure pointed at its basal corners; middle portion is marked by many very small spicules; and two short, rounded to bluntly pointed spines at posterior end. Dense expandable tufts of deciduous hair scales on 8th segment.

Female genitalia (Fig. 16): Ductus bursae short, wide, heavily sclerotized, flared at ostium, opening to wider, elongate basal portion of corpus bursae in which is a small basal plate of spines; narrower portion of the corpus bursae doubles back and widens to form ovoid terminal sac; a long, moderately sclerotized, heavily spinose band lines the corpus bursae, ending in terminal sac lined with many small spicules and moderately large spines. A small, membranous sac (appendix bursae) projects from curved portion of corpus bursae..

Immature stages: The late Roy O. Kendall reared this species on southern live oak, *Quercus virginiana* Miller, but did not make notes on the life stages (R. O. Kendall pers. comm.).

Holotype (Fig. 3). ♂, Santa Ana Refuge, Hidalgo County, Texas, 13 Nov., 1971, A. & M. E. Blanchard (USNM).

Paratypes (77): ARIZONA. 1 ♂, Baboquivari Mts., Pima Co., 15–30 Aug., 1923, O. C. Poling (USNM); 1 ♂, Tucson, Pima Co., 6600 N Galaxy Rd., UV, 1 Nov., 1999, C. V. Covell Jr. genitalia slide #1377 (MGCL). TEXAS. 1 ♀, Artesia Wells, La Salle Co., June 12, 1972, D. C. Ferguson (USNM); 2 ♀♀, same locality and collector, June 13, 1972 (USNM); 1 ♂, 1 ♀, same locality and collector, June 20, 1972 (USNM); 3 ♂♂, same locality and collector, June 21, 1972, (USNM); 1 ♂, Bentson Rio Grande State Park, Hidalgo County, 9 Oct. 1985, T. C. MacRae (GJB); 1 ♂, Aransas Co., Goose Island State Park north of Aransas Pass, June 13, 1968, J. R. Heitzman (JRH); 1 ♂, same locality as preceding, June 13, 1969, R. L. Heitzman (JRH); 2 ♂♂, Hidalgo Co., Bentsen-Rio Grande Vlly. SP, Oct. 11, 1980, E. C. Knudson (ECK); 1 ♂, same locality, 15 Nov. 1990, P. A. Opler (CSU); 3 ♂♂, Laguna Atascosa, Cameron County, 9 March 1975, A. & M. E. Blanchard (one is C. V. Covell Jr. genitalia slide #1521) (USNM); 1 ♂, Santa Ana Wildlife Ref. (Hidalgo), 18 Nov. 1966, A. & M. E. Blanchard, (USNM); 1 ♂, same locality, Oct. 27, 1979, E. C. Knudson (ECK); 1 ♂, same locality, Nov. 18, 1984, E. C. Knudson (ECK); 2 ♂♂, Deutschburg, Jackson Co., 7 Oct. 1974, A. & M. E. Blanchard (USNM); 1 ♂, Brownsville, "5 – 11", Geo. Dorner, (F. H. Benjamin genitalia slide #651) (USNM); 1 ♂, same locality, 10 March 1929, O. Bucholz coll., C. V. Covell Jr. genitalia slide #847 (AMNH); 1 ♂, same locality, 22 May 1928, F. H. Benjamin (AMNH); 1 ♂, same locality, 18 Oct. 1939, J. Sperry (AMNH); 1 ♂, same locality, 8 March (no year), J. A. Grossbeck (AMNH); 1 ♂, same locality, 9 Nov. 1969, A. & M. E. Blanchard (USNM); 1 ♂, same locality, 4 March 1937, T. N. Freeman (CNC); 1 ♂, same locality and collector, 22 March 1937 (CNC); 5 ♂♂, 3 ♀♀, Mtn. View Acres, Bexar Co., June 20, 1972, C. V. Covell Jr., (MGCL); same locality and collector, June 21 1972, C. V. Covell female genitalia #1254 (MGCL); 1 ♂, Mtn. View Acres, Ebony Hill Research Station, Bexar Co., 1 Sep. 1971, R. O. and C. A. Kendall (TAMU); 1 ♂, same locality and collectors, 29 Sept. 1973 (TAMU); 2 ♂♂, same locality and collectors, 27 March 1972 (TAMU); 1 ♂, ex ovum, *Quercus virginiana*, WWFR, San Patricio Co., 31 May 1962 (TAMU); 1 ♂, same locality, host plant and collectors, 1 June 1962 (TAMU); 1 ♂, same locality and collectors *ex* foodplant *Quercus virginiana*, 3 June 1962, C. V. Covell Jr. genitalia slide #849 (AMNH); 1 ♂, same locality, host plant and collectors, 5 June 1962, C. V. Covell Jr. genitalia slide #1562 (TAMU); 1 ♂, same locality, host plant and collectors, 19–20 June, 1962, C. V. Covell Jr. genitalia slide #668 (AMNH); 1 ♂, Welder Wildlife Refuge nr. Sinton, San Patricio Co., 6 July 1963, R. O. & C. A. Kendall, (TAMU); 3 ♂♂, same locality and collectors, 14 Oct. 1963 (AMNH); 1 ♀, same locality, collectors and date, with note "feeds on *Quercus* in larval stage", C. V. Covell Jr. genitalia slide #855 (AMNH); 1 ♂, Crystal City, Zavala Co., 26 June 1969, Barry Wright (NSM); 1 ♂, Chaparral Wildlife Management Area, near Artesia Wells, 12 June 1972, Barry Wright (NSM); 1 ♀, same locality and collector, 11 June 1972 (NSM); 1♂, Kingsville, Kleburg Co., 1971, J. E. Gillaspy (UTA); 1 ♂, same locality and collector, 6 July 1981 (UTA); 2 ♂♂, same locality and collector, 12 Nov 1980 (one is C. V. Covell Jr. genitalia slide #1349) (UTA); 1 ♂, same locality and collector,

13 June 1989 (UTA); 1 ♂, same locality and collector, 22 July 1973 (UTA); 1 ♂, same locality and collector, 14–17 March 1982 (UTA); 1 ♂, same locality and collector, 30 March 1981, C. V. Covell Jr. genitalia slide #1348 (UTA); 1 ♀, same locality and collector, 10 June 1985, C. V. Covell Jr. genitalia slide #1256 (UTA); 1 ♂, Brooks Co., Falfurrias, 18 May 1983, Cavasos and Gillaspy (UTA); 2 ♂♂, 2 ♀♀, same locality and collectors, 18 June 1983, C. V. Covell Jr. ♂ genitalia slide #1253 and ♀ genitalia slides #1255 and #1350 (UTA); 1 ♂, Pharr, 30 March 1948, O. Bucholz, C. V. Covell Jr. genitalia slides #848 (AMNH); 1 ♂, Kenedy Co., Riskin Ranch, 17 Aug. 1976, J. E. Gillaspy (UTA); 1 ♂, Hidalgo Co., Santa Ana NWR, 14 Nov. 1990, P. A. Opler (CSU); 1 ♂, 1 ♀, same locality and collector, 30 Nov. 1990 (CSU); 1 ♂, Cattail Lake, same locality and collector as preceding, 13 Nov. 1990 (CSU). MEXICO. 1 ♂, Nuevo Leon, door light, Cola de Caballo (horsetail falls), 27 Oct. 1979, R. O. & C. A. Kendall (TAMU); 1 ♂, 1♀, Tamualipas, Nacimiento del Rio Frio, Gomez Farias, 16 March 1981, Gillaspy and Lara (UTA); 1♂, same locality and collectors, 30 March 1983 (UTA); Tamualipas, Rio Vergel, 25 km SW C. Victoria, 14–17 March 1982, J. E. Gillaspy (UTA).

Distribution and flight period (Fig. 24). This species is known from southern Texas (north to the vicinity of San Antonio, Bexar County) and northern Mexico, west into Arizona. It can be common in southern Texas. Capture records are for February into November.

Discussion: While in North America *I. kendallaria* most closely resembles the widespread *Idaea demissaria* (Hübner, 1831)—the only species with which it can easily be confused—*I. kendallaria* is also very similar in size, color, and pattern to other species not yet recorded in the United States. *Idaea spernata* (Walker, 1861)—and its synonyms, *I. botydaria* Walker (1863), *I. limitata* Warren (1897) and *I. pygmeata* Warren (1901)—all described from Venezuela, and *I. clothula* (Dyar, 1914) from Panama, resemble *I. kendallaria*. Their types differ in genital features from both *I. kendallaria* and *I. demissaria*.

Etymology: This species is named in fond memory of the late Roy O. Kendall, who with the help of his wife Connie contributed immensely to the knowledge of the Lepidoptera of Texas and northern Mexico.

Idaea elizabetharia Covell, **new species**
(Figs. 7 ♂ – 8 ♀, 11, 19–20, 25)

Diagnosis: Very similar in size, color and pattern to *Idaea skinnerata* (Grossbeck, 1907) (Figs. 9 ♂ and 10 ♀, 12, 21, 22), but male antenna has most segments with two pairs each of long setae, while antennal segments of *I. skinnerata* have fascicles of many and much shorter setae. Antemedial line of *I. elizabetharia* forewing usually indistinct or absent, but straight if present, not sharply angled in anterior third as in *I. skinnerata*. Basal area of *I. elizabetharia* has no darker brown shading as has *I. skinnerata*. Postmedial line of *I. elizabetharia* less strongly sinuous than in *I. skinnerata*, especially toward inner margin where that of *I. skinnerata* makes a strong curve toward wing base; *I. elizabetharia* has no dark outer shading of anterior two thirds of postmedial line as in most *I. skinnerata*. Male genitalia very similar to those of *I. skinnerata* (Fig. 21), but valve straight and blunt terminally in *I. elizabetharia* while that of *I. skinnerata* is bent dorsad and ends in a point. Phallus of *I. elizabetharia* has three large cornuti, two almost identical in size and curved alike and lying close

together; that of *I. skinnerata* has two large cornuti and two clusters of many small straight, spine-like cornuti. Ductus bursae of *I. elizabetharia* shorter and less heavily sclerotized than that of *I. skinnerata* (Fig. 22); corpus bursae long, basally narrow, recurved and lined except in ovate terminal end with many small spines. Corpus bursae in *I. skinnerata* much shorter, pyriform, not recurved, with two semicircular patches of numerous moderately large spines.

Description (Figs. 7–8): Moderately small with body, legs and wings pale grayish tan. Front and palpi dark brown; interantennal fillet and antenna white to whitish tan. Male antenna with two triplets of long setae on most segments, each seta more than twice the length of antennal width; female antenna simple. Male hind tibia reduced but not flattened, and with neither spurs nor hair pencils. Maculation slightly contrasting with the ground color. Forewing brown along costa, heaviest toward base. Antemedial and medial lines faint, light brown, sometimes obscure, nearly straight; no basal dark brown shading. Discal dots present or absent. Postmedial line heaviest and most complete line, doubly bulging outward, then curved in toward base before reaching inner margin. Brown shading beyond postmedial line most extensive in anterior half of subterminal area, leaving a narrow band of ground color before outer margin. Hindwing pattern continues that of forewing. Underside shiny yellowish tan with postmedial line and shading pale brown. Forewing length: 8.0–9.5 mm.

Male genitalia (Fig. 19): Capsule very small, narrow with very large, straight phallus. Valve slightly turned inward, setose along inner side, rounded terminally. Uncus and gnathos oppose each other, uncus slightly longer than gnathos. Juxta subrectangular, membranous. Vinculum narrow and deep. Phallus with one large plate-like, spiculate cornutus and two medium-sized, nearly identical curved, pointed cornuti lying closely together in uninverted vesica.

Female genitalia (Fig. 20): Papillae anales each divided into two lobes. Small ostium bursae opens into evenly wide, moderately sclerotized ductus bursae; long basal neck of the corpus bursae narrower than ductus bursae, heavily spined, and recurved like letter "J" before swelling to a subovoid, relatively small membranous sac; ductus seminalis arises from the corpus bursae opposite its connection with the ductus bursae. Signum absent, but some spines line corpus bursae in no definite pattern.

Immature stages: Unknown.

Holotype (Fig. 7). ♂, Madera Canyon, 5600', Santa Rita Mts., Santa Cruz Co., Ariz., 25 June 1963, J. G. Franclemont (CUIC).

Paratypes (27): ARIZONA. 1 ♀, Madera Canyon, 5600', Santa Rita Mts., Santa Cruz Co., 26 June 1963, J. G. Franclemont (CUIC); 1 ♂, Ash Canyon, Cochise Co., 23 June 1988, C. V. Covell Jr., C. V. Covell Jr. genitalia slide #1360 (MGCL); 1 ♀, Cave Creek, Chiricahua Mts., Cochise Co., 21 Aug. 1951, Lloyd Martin (LACM); 2 ♂♂, 1 ♀, Pine Crest, Mt. Graham, Pinaleno Mts., Graham Co., 7300', June 28, 1955, Lloyd M. Martin, C. V. Covell Jr. genitalia slide #1233 (LACM); 1 ♂, same location, June 29, 1955, Wm. Rees, C. V. Covell Jr. genitalia slide #1231 (LACM); 3 ♂♂, 1 ♀, camp, Oak Creek Canyon, Coconino Co., 5000', July 19, 1957, R. H. Leuschner, C. V. Covell Jr. ♂ genitalia slides #1362 & #1365 (MGCL); 1 ♂, 1 ♀, Oak Creek Canyon, Coconino Co., 5500', 11 July 1988, R. H. Leuschner, C. V. Covell Jr. ♀ genitalia slide #1368 (MGCL); 1 ♂, 1 ♀, Madera Cyn., Santa Cruz Co., 5600 ft., 6 July 1963, W. R. Bauer and J. S. Buckett, C. V. Covell Jr. ♂ genitalia slide #1367 (UCD); 1 ♀, Madera Cyn., Santa Cruz Co., 4880 ft., 6 July 1963, W. R. Bauer and J. S. Buckett (UCD); 5 ♂♂, Stewart campground, Portal, 5000 ft., Cochise Co., 2–3 July 1987, J. B. Heppner, C. V. Covell Jr. genitalia slide #1366 (MGCL); Palmerlee, Cochise Co. (USNM); 1 ♂, Miller Canyon, Huachuca Mts., Cochise Co., June 25, 1955, Lloyd Martin, C. V. Covell Jr. genitalia slide #1373 (LACM); Sierra Anche Exper. Sta. El. 5000', Gila Co., August 23–25, 1958, R. H. Leuschner, Coll., C. V. Covell Jr. genitalia slide #1375 (MGCL); Tonto Creek Camp Ground, near Kohls Ranch, Gila Co., June 28, 1956, L. M.

Martin, J. A. Comstock and W. A. Rees (LACM). NEW MEXICO. 1 ♀, Jemez, July 25, '19, C. V. Covell Jr. genitalia slide #1370 (MCZ). TEXAS. 1 ♂, Davis Mtns., 6000', J. Davis Co., 13 Aug. 1987, R. L. Leuschner, C. V. Covell Jr. genitalia slide #1374 (MGCL); 1 ♂, Dog Canyon, 6400 ft., Guadalupe Mts. N.P., Culberson Co., 7–9 June 1991, E. C. Knudson (ECK).

Distribution and flight period (Fig. 25). Western Texas through New Mexico into Arizona. June to late August.

Discussion: These two species are sympatric in a large portion of their known ranges, although *I. skinnerata* has been found as far north as Colorado but not *I. elizabetharia*. On the basis of specimens examined, the flight information differs slightly: *I. skinnerata* has been collected from July 22 to Sept. 2, while *I. elizabetharia* has been recorded from June 23 to Aug. 23. Recorded altitudes differ slightly: *I. skinnerata*, 5,000–8,400 ft. elev.; *I. elizabetharia*, 4,880–7,300 ft. elev.

Etymology: I take great pleasure in naming this species in honor of my dear wife Elizabeth Barnes Covell, with thanks for her many years of devoted support of my entomological pursuits.

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ZERENE CESONIA LIMONELLA LAMAS (PIERIDAE): FIRST DISTRIBUTION RECORD
IN CHILE AND FIRST HOST PLANT RECORD

Additional key words: Andes, Coliadinae, *Dalea pennellii*, Fabaceae, *Zerene cesonia cesonides*

Zerene Hübner, [1819] (Lepidoptera: Pieridae: Coliadinae) is a small New World butterfly genus including two species, both commonly known as the dogfaces: *Zerene cesonia* (Stoll, 1790) and *Zerene eurydice* (Boisduval, 1855) (Lamas 2004).

Zerene cesonia, the Southern Dogface, is broadly distributed in the Neotropical Region, from the southern USA to Argentina, with six valid subspecies recognized along this extensive geographic range (Lamas 2004). One of these, *Zerene cesonia cesonides* (Staudinger 1894), has been mentioned as an occasional member of the northern Chilean butterfly fauna, based on collections of adult specimens (Ureta 1956, Peña & Ugarte 1996, Benyamini et al. 2014). Rearing records of this butterfly have never been reported from this region, and its presence in Chile has been assumed to be a result of sporadic migrations from the eastern slopes of the Andes (Peña & Ugarte 1996). However, the male specimen illustrated by Peña & Ugarte (1966) undoubtedly does not belong to cesonides, but to *Zerene cesonia limonella* Lamas, 1981.

In January 2013, as a part of a sampling of Lycaenidae larvae on inflorescences of *Dalea pennelli* var. *chilensis* Barneby (Fabaceae) in the neighborhood of the Socoroma village, Parinacota Province, located at about 3,000 m altitude in the western slopes of the Andes of northern Chile, one egg of a Pieridae species was fortuitously found on a leaflet of this plant. The leaf containing the egg was collected and brought to the laboratory in a plastic vial to wait for eclosion and subsequently to rear the larva with leaves of the same plant. As a result, a female adult was obtained in February 2013 and identified as *Z. c. limonella* (Fig. 1, 2), which has its type locality in Surco, Lima, Peru, and is also known from western Ecuador (Lamas 1981).

This is the first record of *Z. c. limonella* in Chile, expanding its geographic range to the south. Furthermore, although *Dalea* and other genera of Fabaceae were already mentioned as host plants for other subspecies of *Zerene cesonia* (Beccaloni et al. 2008), this is the first record of a host plant for the immature stages of *Z. c. limonella*.

Interestingly, this first Chilean record of *Z. c. limonella* is based on one field-collected egg on a native plant, and the subsequent laboratory rearing of the larva. This fact suggests the adequacy of the sampling site for the presence of this butterfly, ruling out the possibility of just a vagrant adult not associated with the vegetation of the study site. Two additional surveys for *Z. c. limonella* were performed in the same sampling site, in February 2013 and March 2014. On each occasion, ten *D. pennellii* plants were randomly selected and their leaves carefully examined, but no additional eggs, larvae or pupae were found. Similarly, adults were searched for without success. The absence of immature stages and adults in both surveys suggests that the population density of *Z. c. limonella* could be extremely low.

The Fabaceae genus *Dalea* is well represented along the Peruvian range of *Z. c. limonella* (Baldeón et al. 2006), where several other potential hosts are available for this butterfly. At the local level, *D. penelli* var. *chilensis* was recently recorded as a host plant for flower-feeding larvae of three Lycaenidae species in the same study site (Vargas 2014), highlighting the importance of this little studied native plant as a host for native butterflies.

FIG. 1, 2. Female adult of *Zerene cesonia limonella* Lamas, 1981 reared from egg collected on *Dalea pennellii* var. *chilensis* in Socoroma, Parinacota Province, western slopes of the Andes of northern Chile. **1**) Dorsal view; **2**) ventral view.

The discovery of *Z. c. limonella* increases the butterfly fauna of Chile with one more representative from the northern area of this country. This fact, together with other recent additions, both from the western slopes of the Andes (Vargas 2013) and from the coastal valleys of the Atacama Desert (Vargas & Lamas 2011), highlights the necessity of additional sampling in order to characterize better the butterfly fauna of these arid environments of northern Chile and the adjacent area of the neighboring countries, as a similar scenario has been mentioned for the butterfly fauna of southern Peru (Cerdeña et al. 2015).

Material examined. One female, Socoroma, Parinacota, Chile, February 2013; H.A. Vargas coll.; reared from egg on *Dalea pennellii* var. *chilensis*, January 2013.

The voucher specimen will be deposited in the Colección Entomológica, Universidad de Tarapacá (IDEA), Arica, Chile.

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MORPHOLOGY AND ANTIPREDATOR BEHAVIOR IN LARVAL *ORGYIA LEUCOSTIGMA* (LEPIDOPTERA: LYMANTRIIDAE)

Additional key words: caterpillar, costs, defense, tussock moth

Predation pressure usually leads to selection for prey adaptations that reduce susceptibility to predation. These often include behavioral and morphological defenses (Endler 1986, Lima 1998). Behavioral defenses can involve reduced activity levels, fleeing, hiding, and confrontation (Gross 1993, Greeney et al. 2012). Morphological defenses such as spines, hairs, and thick sclerotized cuticles are often post-contact defenses that typically reduce predation risk by making prey more difficult to handle or to kill, thereby increasing their probability of escaping if attacked or captured (Gross 1993, Greeney et al. 2012).

Studies on antipredator defenses in terrestrial insect prey have often focused on either behavior or morphology separately, even if both traits are frequently related (DeWitt et al. 1999, Johansson & Mikolajewski 2008). For example, the effectiveness of prey morphological defenses such as mimesis and crypsis can depend on behavior (Castellanos & Barbosa 2006, Iannou & Krause 2009). Similarly, antipredator behavior may depend on modified morphology such as the hypertrophied abdominal setae used by some species of caterpillars to detect the presence of predators (Rota & Wagner 2008).

There is evidence that prey defensive behavior and antipredator morphology such as hairs, spines, and thick sclerotized cuticles, are also related. Several studies have shown that morphologically defended prey have reduced antipredator behavior compared to morphologically undefended prey (Peckarsky 1996, Mikolajewski & Johansson 2004, Boyero et al. 2012, Vogelweith et al. 2014), suggesting that morphologically undefended prey depend strongly on behavioral antipredator defense in order to compensate for their relative vulnerability (DeWitt et al. 1999, Stankovich & Blumstein 2005). Most of the evidence that supports the contention that there is a negative relationship between antipredator behavior and antipredator morphology in insects comes from studies comparing different aquatic species that vary in their morphology (Mikolajewski & Johansson 2004, Vogelweith et al. 2014). Relatively few studies have compared these relationships in individuals of the same species (but see Stoks 1999). In this study, we experimentally manipulated individual prey morphology to determine if predation risk assessment behavior by prey is altered as a consequence of changes in antipredator morphology. We conducted our experiments with larvae of the white-marked tussock moth *Orgyia leucostigma* (J. E. Smith) (Lepidoptera: Lymantriidae), which are covered with conspicuous defensive hairs (Payne 1917, Castellanos et al. 2011b), and display antipredator behavior responses that include walking away and dropping from the host plant leaf (Castellanos et al. 2011a, b).

The defensive hairs of larvae of *O. leucostigma* were removed in order to test if individuals without hairs would be more vulnerable to predation and would alter their behavioral response to predation risk due to *Podisus maculiventris* (Say) (Hemiptera: Pentatomidae). The behavioral responses were compared to those of individuals with hairs. Caterpillar antipredator behaviors depend on their relative vulnerability to predators, as well as, over an evolutionary time scale, the costs of the behavior (Stamp 1986, Castellanos & Barbosa 2006, McClure & Despland 2011). Thus, we hypothesized that caterpillars without hairs would be more vulnerable to predation than individuals with hairs and that morphologically defended *O. leucostigma* would escape by dropping from host plant less often than morphologically undefended individuals.

Orgyia leucostigma are external polyphagous, solitary foliage feeders of a large number of species in various tree genera (Payne 1917). *Orgyia leucostigma* larvae used in the experiments originated from a laboratory colony established from field collections at Patuxent Wildlife Refuge Research Center (PWRRC) (39º 02' 30" N latitude, 76º 47' 30" W longitude), Maryland, USA. Larvae eclosing from egg masses were reared individually in 237-ml plastic containers, and fed *Acer negundo* L. (Aceraceae) (box elder) foliage.

The stink bug *P. maculiventris* is a generalist predator that feeds primarily on larval Lepidoptera and Coleoptera (McPherson 1982), and is a common member of the insect community in PWRRC. It actively searches for prey while walking on the foliage of plants, and is able to perceive prey within a few millimeters, or after physically contacting the prey (Evans 1982). Upon encountering prey, *P. maculiventris* extend their proboscis and slowly attempt to insert it into the nearest prey tissues (Evans 1982, I. Castellanos personal observation). *Podisus maculiventris* individuals used in

the experiments originated from adults collected in early spring at PWRRC and were fed with lymantriid, noctuid, geometrid and tenebrionid larvae, as well as water and green beans (Mallampalli et al. 2002). Prior to the experiment, hunger level was standardized for each predator by starving individuals for 24 hours.

Experimental procedure. The dorsal, lateral, anterior, and posterior hairs of 29 fifth-instar *O. leucostigma* were cut (hair removal treatment) using curved dissecting scissors, leaving approximately 0.10 cm long hair shafts. An additional 30 larvae were used with "intact" hairs. Intact caterpillars had dorsal, lateral, anterior, and posterior hairs with lengths of 0.82 ± 0.04, 0.64 ± 0.03, 0.84 ± 0.04, and 0.90 ± 0.06 cm, respectively (Mean ± SE, n = 10); hair length was measured under a microscope while caterpillars remained motionless on a box elder leaf. In order to control for the possible effect of the procedure of hair cutting per se, we cut approximately 0.10 cm of the tips of the hairs of 22 fifth-instar individuals (clipping control) and compared their antipredator behavioral responses to those of intact caterpillars. Treated and clipping control larvae were allowed to recover for a period of five hours before being exposed to a predator.

Caterpillars belonging to the three treatments were individually placed on the leaf of an *A. negundo* branch inserted into a vial with water and positioned 0.5 m above a laboratory bench, and allowed to acclimate for a period of thirty minutes. After the acclimation period, a single adult *P. maculiventris* was placed on a vertical stem in contact with the experimental leaf. After the predator began walking on the experimental leaf, the stem was removed. The defensive behaviors (i.e., walking away from the predator, dropping from the leaf, or confrontation) of caterpillars that survived the attacks, as well as those that tried to escape but failed and were predated upon, were recorded. Confrontation behavior consisted of the prey moving its head from side to side or attempting to bite or biting the predator until the predator left the leaf. Head movement commonly occurred for several minutes, which discouraged continual stalking by predators. We also observed the prey body parts (hairs or cuticle) with which the predator's proboscis came in contact. A caterpillar was recorded as a survivor if the predator or the caterpillar left the leaf, with the caterpillar left unharmed. All trials were conducted with different *P. maculiventris* adults and *O. leucostigma* larvae, in the laboratory at an ambient room temperature of 25 ± 2°C. The frequencies of different behavioral responses of caterpillars, as well as their survival, were compared using chi-square tests of independence or Fisher's exact tests when the assumptions of the chi-square test were
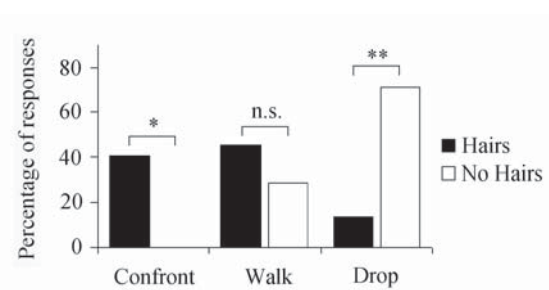
FIG. 1. The behavioral responses of surviving fifth-instar *Orgyia leucostigma* with hairs (hairs) and with their hairs removed (no hairs) that were exposed to *Podisus maculiventris* on an *Acer negundo* leaf (*P < 0.05, **P < 0.01, and n.s. is not significant).

not met (Agresti 2007). The family-wise error rate for multiple comparisons was controlled using a Bonferroni correction (Sokal & Rohlf 1995).

Results. Upon encountering caterpillars both with and without hairs, *P. maculiventris* approached individuals with their same stereotypic behavior, extending their proboscis and slowly attempting to insert it into the nearest part of the prey (Evans 1982, I. Castellanos personal observation). The behavioral responses of *O. leucostigma* larvae to predators occurred when their hairs or cuticle were contacted. Caterpillars with intact hairs that responded by confronting or walking did so when predators contacted their hairs. However, caterpillars with intact hairs that responded by dropping did so when the predator's proboscis contacted a caterpillar's cuticle, which occurred when *P. maculiventris* was able to reach the ventral (unprotected) cuticle of larvae, typically when they were at the edge of a leaf and the predator was on the opposite side of the leaf. Caterpillars without hairs responded by walking or dropping when the stink bug's proboscis contacted their cuticle. Predators interacted with caterpillars in all trials except in three occasions, one belonging to the hair removal treatment and two to the intact caterpillar treatment; these trials were discarded from the analyses.

There was no significant effect of hair clipping (clipping control) on the behavioral defenses of *O. leucostigma* caterpillars in response to *P. maculiventris* when compared with intact caterpillars (Fisher's Exact Test: $P = 0.837$). Overall, there was a significant effect of hair removal on caterpillar vulnerability to predation ($c^2 = 4.98$, df = 1, $P = 0.026$): caterpillars with their hairs removed suffered greater predation (14 out of 28, or 50%) compared to intact caterpillars (6 out of 28, or 21.4%). The removal of hairs had a significant effect on the type of defensive behavior exhibited by surviving caterpillars ($c^2 = 14.27$, df = 2, $P = 0.001$) (Fig. 1). The

percentage of intact caterpillars that survived by confronting the predators (9 out of 22, or 40.9%) was significantly greater than the percentage of caterpillars with their hairs removed that survived through that same defensive behavior (0 out of 14, or 0%) (Fisher's Exact Test: P = 0.018), whereas the percentage of intact caterpillars that dropped (3 out of 22, or 13.6%) was significantly smaller than the percentage of caterpillars with hairs removed that dropped (10 out of 14, or 71.4%) (c^2 = 12.39, df = 1, P = 0.003) (Fig. 1). The percentage of caterpillars that escaped predation by walking away was greater for intact individuals (10 out of 22, or 45.5%) than for individuals with their hairs removed (4 out of 14, or 28.6%), however, this difference was not statistically significant (c^2 = 1.03, df = 1, P = 0.933) (Fig. 1). Of the 6 caterpillars with intact hairs that were predated, 2 tried to escape by walking and 1 by confronting, but failed and were predated, and the predators were able to pierce the epidermis of the other 3 caterpillars without eliciting a defensive response. Of the 14 caterpillars without hairs that were predated, 3 tried to escape by walking, but failed and were predated, and the epidermis of the other 11 caterpillars was pierced by *P. maculiventris*. Once *P. maculiventris* is able to pierce the epidermis of its prey with its proboscis, it causes prey paralysis and immobilization, apparently by injecting a toxin (Berenbaum et al. 1992), and the proboscis also anchors the prey with its teeth and rasps (Cohen 1998).

Discussion. Most studies on antipredator defenses in terrestrial insect species have focused on either behavior or morphology, and given little consideration to the interplay between these two functional characteristics. Our results show that for larvae of *O. leucostigma*, morphology and behavior can act in a compensatory manner, providing evidence that both are important. That is, larvae without hairs were more susceptible to predation by invertebrate predators and dropped more often in the presence of predatory stink bugs. In contrast, the antipredator behavior exhibited by individuals with intact hairs most frequently involved confronting or walking away. Since piercing the cuticle by invertebrate predators is likely to represent a higher predation risk than contact with hairs, the caterpillars exhibit the strongest, and potentially, the most costly response (i.e., dropping from the plant), in order to compensate for a relatively greater vulnerability when predators contact the cuticle. Dislodged larvae may be exposed to adverse abiotic conditions (Roitberg & Myers 1978), must climb the original tree or reach another host tree (Castellanos et al. 2011a) and thus could be subjected to ground predation (Losey & Denno 1998), starvation (Nelson 2007), or reduced fitness if they access host trees of inferior quality (Stamp & Bowers 1991).

Our results show that morphological antipredator defenses can influence how caterpillars perceive threats and how perceived threats can influence the magnitude of their behavioral response, and suggest that future research on antipredator defenses in terrestrial insect species should consider the combined role of behavior and morphology. It has been argued that the intensity of a prey's behavioral defenses should be inversely related to the effectiveness of its morphological defenses due to the costs associated with antipredator behavior (Peckarsky 1996, Johansson & Mikolajewski 2008). Since relatively small increments in hair length can improve protection from predators (Sugiura & Yamazaki 2014), it is plausible that small differences in caterpillar hair length within species or between closely related species might also be associated with differences in the magnitude of a defensive behavior.

An interesting area for future research would be to compare the behavioral responses of terrestrial insect individuals of the same or closely related species that vary in antipredator morphology (or chemistry) in order to determine if there are differences in investment into morphological (or chemical) versus behavioral defenses as has been shown to occur in other systems (Stankovich & Blumstein 2005, Johansson & Mikolajewski 2008, Hettyey et al. 2014). More research is needed that integrates different antipredator defenses and their relative costs in the evolution of antipredator defenses (Vencl & Srygley 2013).

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First record of *Cydia tonosticha* (Meyrick) (Tortricidae) from Chile and a new host plant

Additional key words: *Cydia largo*, Fabaceae, Neotropical, *Prosopis alba*

Cydia Hübner, 1825 is a cosmopolitan and highly diverse genus of Tortricidae (Gilligan et al. 2014) that is currently represented in Chile by two species (Vargas & Parra 2006, Razowski & Pelz 2010): *C. pomonella* (Linnaeus, 1758) and *C. largo* Heppner, 1981. *Cydia pomonella*, commonly known as the codling moth, is a widely distributed pest of apple, pear, and walnut (Gilligan & Epstein 2012); in Chile it is a primary pest of apple (Razowski & Pelz 2010). *Cydia largo*, whose larvae are associated with Fabaceae, was described from southern Florida and was also recorded from Cuba (Heppner 1981); later it was reported from the coastal valleys of the Atacama Desert of Chile (Vargas & Parra 2006), where its larvae are florivorous on *Acacia macracantha* (Fabaceae) (Vargas & Parra 2006, 2009).

As part of a survey of Lepidoptera associated with native plants in the coastal valleys of the Atacama Desert of northern Chile, some seed-feeding larvae were detected in pods of *Prosopis alba* (Fabaceae) in October 2014 in the Lluta Valley, Arica Province. Infested pods were collected and brought to the laboratory in plastic vials and were kept at room temperature to obtain adults. Five adults were reared, and they were identified as *Cydia tonosticha* (Meyrick, 1922) based on morphology of the male and female genitalia (Lima 1952, Heppner et al. 2009, Razowski 2011) (Fig. 1–3).

Cydia tonosticha was described from Amazonas, Brazil, and apparently it is widely distributed in the Neotropics; it has been reported from Panama, Peru, and Venezuela (Heppner et al. 2009, Razowski 2011). Its synonym (*Laspeyresia cassiana* Lima, 1952) also has a Brazilian type locality in Rio de Janeiro State. Larvae of *C. tonosticha* have been recorded as seed-feeders in pods of four species of Fabaceae belonging to the genera *Cassia* and *Stryphnodendron*, based on sampling performed in Brazil and Panama (Lima 1952, Becker 1971, Nomura et al. 1976, Penteado-Dias et al. 2008, Razowski 2011). In the collection of the National Museum of Natural History, Washington, DC, USA (USNM), there are specimens of *C. tonosticha* reared from *Acacia farnesiana* (Panama), *Cassia fistula* (Brazil), *Cassia moschata* (Panama), *Cassia grandis* (Panama), *Senna bacillaris* (Brazil), and *Senna rugosa* (Brazil). Surprisingly, *Punica granatum* (Punicaceae) was recently recorded as a host for *C. tonosticha* in Peru (Heppner et al. 2009). In addition, the wasp *Pseudophanerotoma* (Pseudophanerotoma) *alvarengai* Zettel, 1990 (Hymenoptera: Braconidae: Cheloninae) was recorded parasitizing larvae of *C. tonosticha* in Brazil (Penteado-Dias et al. 2008).

This is the first record of *C. tonosticha* from Chile, adding one more country to the distribution range of this widespread Neotropical species. The southern limit previously reported in Peru is in Omate, Departamento de Moquegua, about 200 km north of the Lluta Valley (Heppner et al. 2009). It remains unknown whether the presence of *C. tonosticha* in Chile is a result of a recent range expansion or the species is native to the coastal valleys of the Atacama Desert. Although the original description of *C. tonosticha* was based on Brazilian specimens, its wide distribution raises the question about its evolutionary origin, as the type locality does not necessarily represent the geographic origin of the species (Gonçalves et al. 2015); molecular studies at the population level are required in order to explore this scenario (Valade et al. 2009).

This is the first record of a species of *Prosopis* as a host plant for larvae of *C. tonosticha*, adding one more genus to the family most commonly recorded for this species (Lima 1952, Becker 1971, Penteado-Dias et al. 2008, Razowski 2011). Apparently, Fabaceae is an important host plant family for Tortricidae in northern Chile (Clarke 1987, Vargas & Parra 2006, Vargas 2011).

Finally, the discovery of *C. tonosticha* in northern Chile, together with other recent additions to the Chilean Tortricidae (Vargas & Parra 2006, Vargas 2011, 2012,
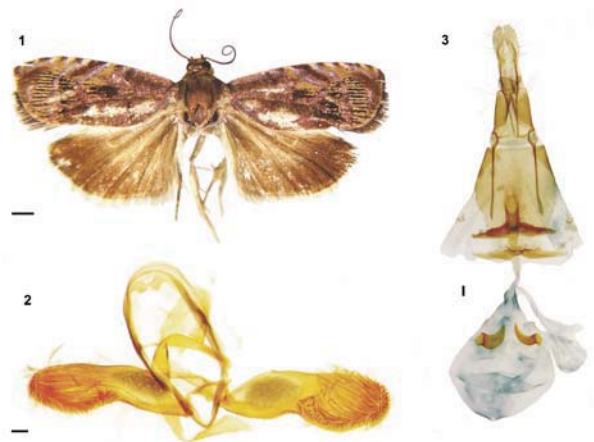

Fig. 1–3. *Cydia tonosticha* (Meyrick, 1922). **1**. Female adult in dorsal view; scale bar = 1 mm. **2**. Male genitalia in ventral view; scale bar = 0.1 mm. **3**. Female genitalia in ventral view; scale bar = 0.1 mm.

Vargas et al. 2015), highlight the importance of surveys to understand the diversity of this family throughout these arid landscapes.

Material examined. Chile, Arica. Three males, two females: Lluta, Arica, Chile, November 2014, D. Bobadilla coll., seed-feeder larvae in pods of *Prosopis alba*, October 2014 (IDEA). Vouchers will be deposited in the Colección Entomológica de la Universidad de Tarapacá (IDEA), Arica, Chile.

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