

# Neotropical *Eois* (Lepidoptera: Geometridae): Checklist, Biogeography, Diversity, and Description Patterns

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**ABSTRACT** The moth genus *Eois* Hübner (Lepidoptera: Geometridae: Larentiinae) comprises 254 validly described species, 211 of them (83%) occurring in the Neotropical region, 12% in the Asian-Australian region, and 5% in Africa. A checklist of Neotropical *Eois* is provided and some taxonomic changes are made. *Aplogompha noctilaria* (Schaus) is excluded from the genus, and *Eois bermellada* (Dognin) and *Eois fragilis* (Warren) are transferred to the genus. Further changes include *Eois cellulata* (Prout) stat. rev., *Eois ambarilla* (Dognin) stat. rev., and *Eois telegraphica* Prout stat. rev. By far, the majority of *Eois* species (82%) were described between 1891 and 1920; approximately half of all species by just two authors. Within the Neotropical region, the majority of species (55%) were described from the tropical Andes (Colombia, Ecuador, Peru, and Bolivia), followed by Central America and the Caribbean (28%), and the rest of South America (17%). Large regions such as the Amazon basin, eastern South America, but also northern Peru are heavily underrepresented. Regional diversity studies provide evidence that the wet tropical Andes are the diversity hotspot of *Eois*. From a forested elevational gradient (1,020–2,670 m above sea level) in southeastern Ecuador, 154 morphospecies are currently known, with only ≈12% of them described. Regional species richness in Central America is lower (Costa Rica, 66 observed morphospecies along a gradient from 40 to 2,730 m; ≈29% described). Total richness of the genus is estimated to be >1,000 species in the Neotropical region. If the low proportions of described species only partly recur in other groups of Neotropical geometrid moths, their number may exceed 19,000 species. A taxonomic revision of *Eois* will be a prerequisite for comparison of ecological data from different regions.

**KEY WORDS** Larentiinae, diversity, Andes, species richness estimate

The diverse geometrid moth genus *Eois* Hübner has largely been ignored by researchers for many decades. The last Neotropical species was described by Fletcher in 1952. Since then, hardly any taxonomic or systematic work has been carried out on the genus—with the notable exceptions of the contribution of Holloway (1997) on Southeast Asian *Eois* species and the publication of a global catalog of geometrid moths by Parsons et al. (1999). The latter listed nearly all available taxonomic information, including a range of previously unpublished synonyms and subspecies. Only a decade ago, nearly nothing was known about species richness of Neotropical *Eois* at the regional scale and along environmental gradients. Host plant relationships were only known from a few New World species (Braga et al. 2001, Brehm 2002).

Within the past 10 yr, however, *Eois* became a focus of some ecology and evolutionary biology studies as a megadiverse model group of specialized tropical her-

bivores (Brehm et al. 2008). *Eois* species are a prominent component of tropical Andean moth diversity. Within the globally “hottest hotspot” for geometrid diversity, Brehm et al. (2005) reported 102 *Eois* species in an area of only ≈40 km<sup>2</sup>, accounting for 8.1% of all their collected geometrid moth species. Regional species richness was also high along the Barva transect in Costa Rica (60 species, 8.1% of the sampled geometrid fauna, Brehm et al. 2007). *Eois* also has attracted evolutionary biologists interested in host specificity of tropical herbivores (Connahs et al. 2009, Rodríguez-Castañeda 2009). It has become apparent that many (possibly most) of the Neotropical species are specialist feeders on *Piper* (Connahs et al. 2009, Dyer et al. 2010). The number of host plant records for *Eois* caterpillars increased substantially in the past few years, mostly through records from Costa Rica (Dyer et al. 2010, Janzen and Hallwachs 2010), and the Eastern Andes of Ecuador (Bodner et al. 2010, Dyer et al. 2010). Recently, major advances were made to resolve phylogenetic relationships in the genus (Strutzenberger et al. 2010). These data suggested that *Piper* is the ancestral host plant of Neotropical *Eois* and that it switches to other host plants occurred independently

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in several clades. Neotropical *Eois* diversity originated in the Miocene (Strutzenberger and Fiedler 2011).

Although substantial progress has been made in the knowledge of species richness patterns, host plant ecology, and phylogeny, other research areas have remained largely untouched—in particular, morphology, taxonomy, and biogeography of the group. Ecological data of *Eois* species are being gathered at an increasing pace, but scientific names are not available for most species. Without a solid taxonomic framework, however, the exchange and reliability of data are substantially hampered. Here, we address some basic questions in morphology, taxonomy, and biogeography. Given the enormous richness of the group (239 described taxa in the New World; see Results), our article is intended as a starting point for further investigations in systematics and biogeography of Neotropical *Eois*. The goals of our article are the following: 1) provide baseline morphological information of Neotropical *Eois* species, 2) provide an updated checklist of Neotropical *Eois* species, 3) present historical species description patterns of *Eois*, 4) provide baseline biogeographic information of *Eois*, 5) compare *Eois* richness and proportions of described species from two regions in Ecuador and Costa Rica, and 6) estimate Neotropical *Eois* and Geometridae species richness.

The taxonomic work described here uses the information provided by Parsons et al. (1999) as the basis for a new checklist. Only a few corrections were necessary in some taxa, including the addition and exclusion of species, the correction of a spelling error, as well as the revision of several synonyms and subspecies. However, we restricted taxonomic changes to cases where external morphology provided sufficient characters. It is far beyond the scope of this article to revise the genus—such work is certainly required and should be performed in future work, clade by clade.

## Materials and Methods

Species description data for *Eois* were extracted from Parsons et al. (1999) and cross-checked with selected original descriptions and all available type photographs (98% of the Neotropical types). The only type specimens that could not be checked are *E. russearia* Hübner (type specimen probably lost), *Eois cassandra* (Druce), *Eois tegularia* (Guenée), and *Eois nucula* (Druce).

Digital photographs of type specimens were kindly provided by colleagues in various museums, mostly in the United States Museum of Natural History, Washington, D.C., USA (USNM) (see Acknowledgments) and were taken by G.B. in the Natural History Museum (NHM), London, United Kingdom.

Data of type localities were taken from Parsons et al. (1999) and from original descriptions. Localities were searched using topographical maps as well as the program GoogleEarth (version 5.0.11733.9347 from 2009). For mapping and geographical analyses, all available geographical information was used, including all species, subspecies, and synonyms, from holotypes as well as from paratypes and syntypes. Geographical coordinates were assigned for 235 of 263 type localities (see Fig. 8). Geographical information

was insufficient in the remaining cases (e.g., specimens labeled “Amazon” or “Bolivia”). Because label data of old museum specimen are sometimes incorrect or doubtful, some errors might occur. A distribution map of type localities was produced with the program ArcGis, version 9 (ArcMap 9.2, ESRI, Redlands, CA), by using the model Gtopo30.

The data for regional species richness of *Eois* in southern Ecuador were compiled from collections carried out between 1999 and 2008 in the Reserva Biológica San Francisco and surroundings (Strutzenberger et al. 2011). Sorting of this material was based on external morphology criteria (i.e., predominantly wing patterns). The data for regional species richness from Costa Rica were taken from Brehm et al. (2007) (60 species from the Barva transect, Heredia Province) and supplemented by six additional records from La Selva Biological station. Species richness along the Barva transect was calculated using data from Brehm et al. (2007), with the program RangeModelMac5 (Colwell 2006).

For the preparation of the genitalia, the abdomens were macerated in 10% KOH at room temperature overnight and dissected in purified water. The ever-sible part of the aedeagus (vesica) was pushed out and immediately inflated with pure ethanol, by using a glass capillary held in a micromanipulator system. The valve complex and the integument were cleaned and dehydrated (alcohol sequence, 50, 70, 90, 100%). The preparations were stained with Chlorazol Black (solution in pure ethanol) and embedded in Euparal 3C 239 (Waldeck, Division Chroma, Münster, Germany) on microscope slides (Roth, Karlsruhe, Germany).

## Results

### Neotropical *Eois* Systematics and Morphology

*Eois* is assigned to the geometrid subfamily Larentiinae (Holloway 1997, Parsons et al. 1999). It still seems uncertain what true apomorphies for this subfamily are; the fasciae on the forewing tend to be multiple rather than single (Holloway 1997); the males usually lack a hair pencil on the hindtibia (Holloway 1997); in the hindwing, vein Sc+R usually fuses with Rs for at least half of the length of the cell (Minet and Scoble 1999). The monophyly of the Larentiinae is well supported by molecular data (e.g., Yamamoto and Sota 2007). *Eois* moths seem to share all of the mentioned potential Larentiinae apomorphies, particularly the wing venation (Fig. 1). Holloway (1997) assigned the genus *Eois* to the tribe Eupitheciini because *Eois* have large valves and lack an uncus. However, *Eois* males lack dorsal arms (labides), which are typically present in eupitheciines. Nielsen et al. (1996) assigned *Eois* to the tribe Asthenini, a placement that is supported by molecular data (Sihvonon et al. 2011). Molecular phylogenetic studies show that Neotropical *Eois* can be subdivided into at least nine clades that usually share a common wing-pattern type (Strutzenberger et al. 2010). It would be desirable to complement the existing molecular data with morphological and ecological data in future phylogenetic research.

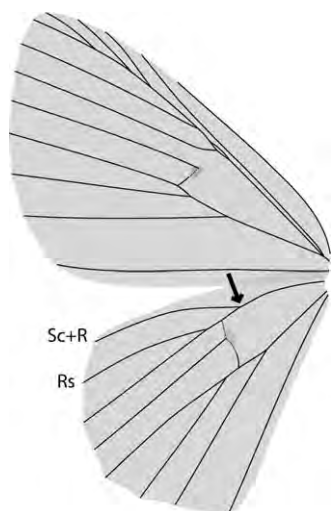


Fig. 1. Wing venation of *Eois* sp. near *basaliata* (Warren) (Ecuador). The arrow indicates the fusion of the veins Sc+R and Rs, a diagnostic feature of the Larentiinae.

**External Characters.** *Eois* moths possess numerous external and internal morphological characters (Figs. 2–5). They are rather small-sized (forewing length,  $\approx 8$ –18 mm). Wing patterns are highly diverse (Figs. 2 and 3). In most species, yellowish to brownish wing colors with brown or red-brown bands and spots dominate. Some species have metallic spots or bands, particularly in the *Eois adimaria* (Snellen) clade. Patterns generally follow symmetry systems as usual in the Larentiinae (Nijhout 1991). Species belonging in the *Eois olivacea* (Felder & Rogenhofer) clade have a green ground color and yellowish fringes (Fig. 3a–d). Another pattern (brown wings with yellow margins) can be observed in different *Eois* clades, e.g., the *Eois catana* (Druce) clade (Fig. 2a–c) and the *Eois xanthoperata* (Warren) clade (Fig. 2d and h). These two clades are not closely related (Strutzenberger et al. 2010). A similar pattern also occurs in Costa Rican *Eois* species (Fig. 2i), and in certain Asian species such as *E. grataria* (Walker) and unrelated Asian and Neotropical Sterrhinae geometrids (e.g., *Chrysocraspedata* Swinhoe). The evolutionary mechanisms underlying the existence of the brown-yellow wing pattern in various clades are still unexplored.

A few species, such as *Eois inflammata* (Dognin), have pinkish bands, whereas species related to *Eois pallidicosta* (Warren) (Fig. 3q) or *Eois nigriceps* (Warren) (Fig. 3u) are dull brownish. The wings are held outstretched at rest (Fig. 6t and w–y). Wing undersides usually show few deviations from the forewings; their colors are generally less bright and patterns are less pronounced than on the upper side (on the contrary, other larentiine moths such as *Hagnagora* Druce and *Callipia* Guenée rest with folded wings and their undersides exhibit accentuated patterns).

The legs are long and slender, and densely covered with scales. These scales are usually light yellowish on

the mid- and hindleg but of a darker coloration on the foreleg. The tibia of the foreleg bears a pair of spines near the femur-tibial joint, which is covered with long scales. The tibiae of the mid- and hindlegs display prominent spines: the midtibia bears one subapical pair, and the hindtibia bears two pairs near the apex.

Regarding the head morphology, the antennae of the males are bipectinate in the species examined so far, whereas those of the females are filiform. Filiform antennae in the male sex or bipectinate antennae in the female sex have not yet been found in the Neotropical taxa (see Holloway 1997). A distinct patch of white or yellowish scales between the antennae is found in many clades, but a considerable number of species lack this feature. The proboscis is well developed.

**Genitalia Characters.** Female: In the bursa copulatrix a robust, multispined signum is found (Fig. 5i). Structural similarities with the signa of *Eois* species from Borneo are obvious (Holloway 1997), and perhaps this special type of signum indeed represents an autapomorphy for the genus. However, the female genitalia morphology has to be examined in many more of the Neotropical *Eois* species, covering representatives of all clades.

The male genitalia, in particular the valves and the eversible vesica of the aedeagus, display such a high degree of variation throughout the genus that it is difficult to identify general characteristics, apart from the few mentioned by Holloway (1997) for the Bornean species (e.g., uncus absent, scaphium well developed, lack of labides). A sampling of male genitalia variation among Neotropical representatives of *Eois* is given in Figs. 4 and 5.

Species in the *E. catana* clade, the *E. xanthoperata* clade, and undescribed species (Fig. 2a–d, h, i) superficially resemble each other in their wing patterns (see above), but the morphology of the male genitalia differs widely (Fig. 4a–c). In the *E. catana* clade, valves are large and the aedeagus is short and massive. The vesica bears three large, heavily sclerotized cornuti, arising from three distinct areas of the membrane (Fig. 4a). In the *E. xanthoperata*-clade, the valves are comparatively smaller, with a well-developed tooth-like pollex and a different arrangement of hair-like setae. The aedeagus is slender and elongate, and the vesica bears a group of approximately a dozen small cornuti, all arising from a single area near the apex (Fig. 4b). A species of the third clade (no molecular data available so far), has abruptly narrowed valvae, and the vesica bears a few medium-sized cornuti (Fig. 4c). In a Bornean species with a similar wing pattern and coloration (*E. grataria*), the configuration of the male genitalia again differs strikingly (Holloway 1997: Fig. 565).

Pronounced morphological differences also can be found among more closely related species, such as members of the “green group” related to *E. olivacea* (Fig. 3c) and *E. goodmanii* (Fig. 3h): the vesica lacks cornuti in *E. sp.* near *olivacea* (Fig. 5a), whereas it shows a rich coverage with cornuti arising from several areas in *E. sp.* near *goodmanii* (Fig. 5b). In certain cases, the male genitalia can provide important morphological data for the delimitation of cryptic species, which were so far revealed exclusively by the cytochrome oxidase subunit I analysis



Fig. 2. Twenty-eight *Eois* adult moths. HT, holotype; ST, syntype; and nr, near. Genitalia of nine species are shown in Fig. 4. Specimens not labeled as type material are from two study areas in southern Ecuador and Costa Rica (see Table 2). (Online figure in color.)

(Strutzenberger et al. 2011). For example, the genitalia depicted in Fig. 4d and e are from two undescribed species that cannot be distinguished by external characters such as wing patterns (Fig. 2m and n). The male genitalia have a similar appearance, but pronounced differences are found in the valves (absence versus presence of a pollex; contour of the valve margins is different) and the vesicae (location of the cornuti-bearing areas).

**Early Stages.** Caterpillars (Fig. 6a–r) are typical geometrid larvae with mostly slender bodies and prolegs only on abdominal segments A6 and A10. They are rather variable in shape and coloration. In members of the *adimaria* clade, the larvae tend to be elongated and transparently greenish (Fig. 6b and c), but in other species they are stouter. Most caterpillars are green, and many have brownish, reddish, or black spots or bands

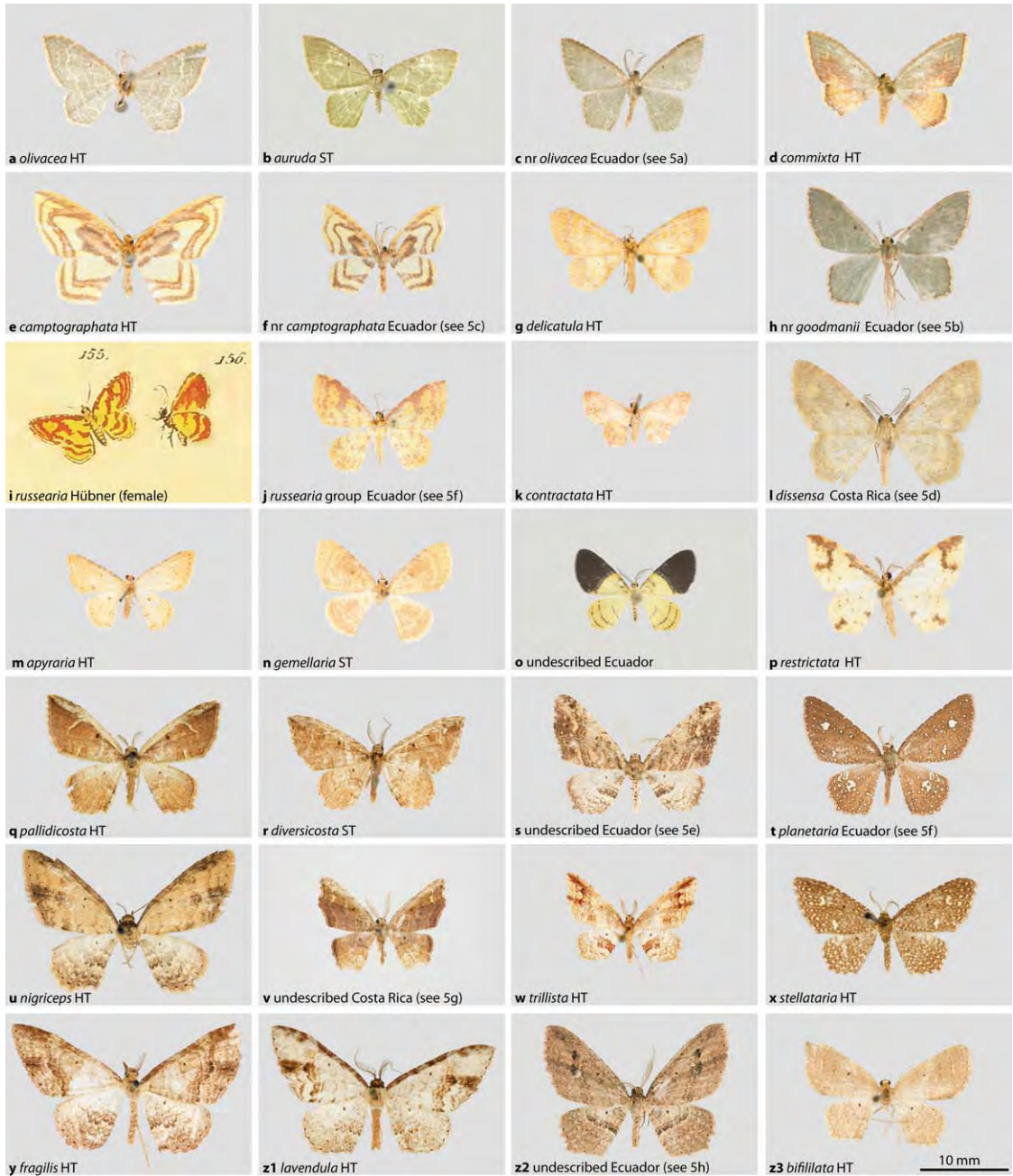


Fig. 3. Twenty-eight *Eois* adult moths. HT, holotype; ST, syntype; and nr, near. Genitalia of nine species are shown in Fig. 5. Specimens not labeled as type material are from two study areas in southern Ecuador and Costa Rica (see Table 2). (Online figure in color.)

(Fig. 6k–p), or they exhibit completely dark patterns (Fig. 6i and r). Species related to *E. olivacea* and *E. olivaria* show particularly contrasting patterns, including bright and dark spots dorsally (Fig. 6m and n), and pink spots laterally (Fig. 6m) in some species, whereas others exhibit merely some pale patches (not shown). *Eois* sp. near *catana* seems to mimic bird droppings (Fig. 6a) and is the only species illustrated with short but pronounced

cone-shaped paired dorsal appendages. Rather than feeding on whole leaves (which are often tough and hard), *Eois* caterpillars tend to scrape the lower epidermis and mesophyll from the leaf undersurface while leaving the epidermis of the leaf upperside intact (Fig. 6b and c, g, k, l, n–r). Only older larvae of particular *Eois* species eat whole parts of *Piper* leaves, but only when feeding on *Piper* species with thin, soft leaves. Other

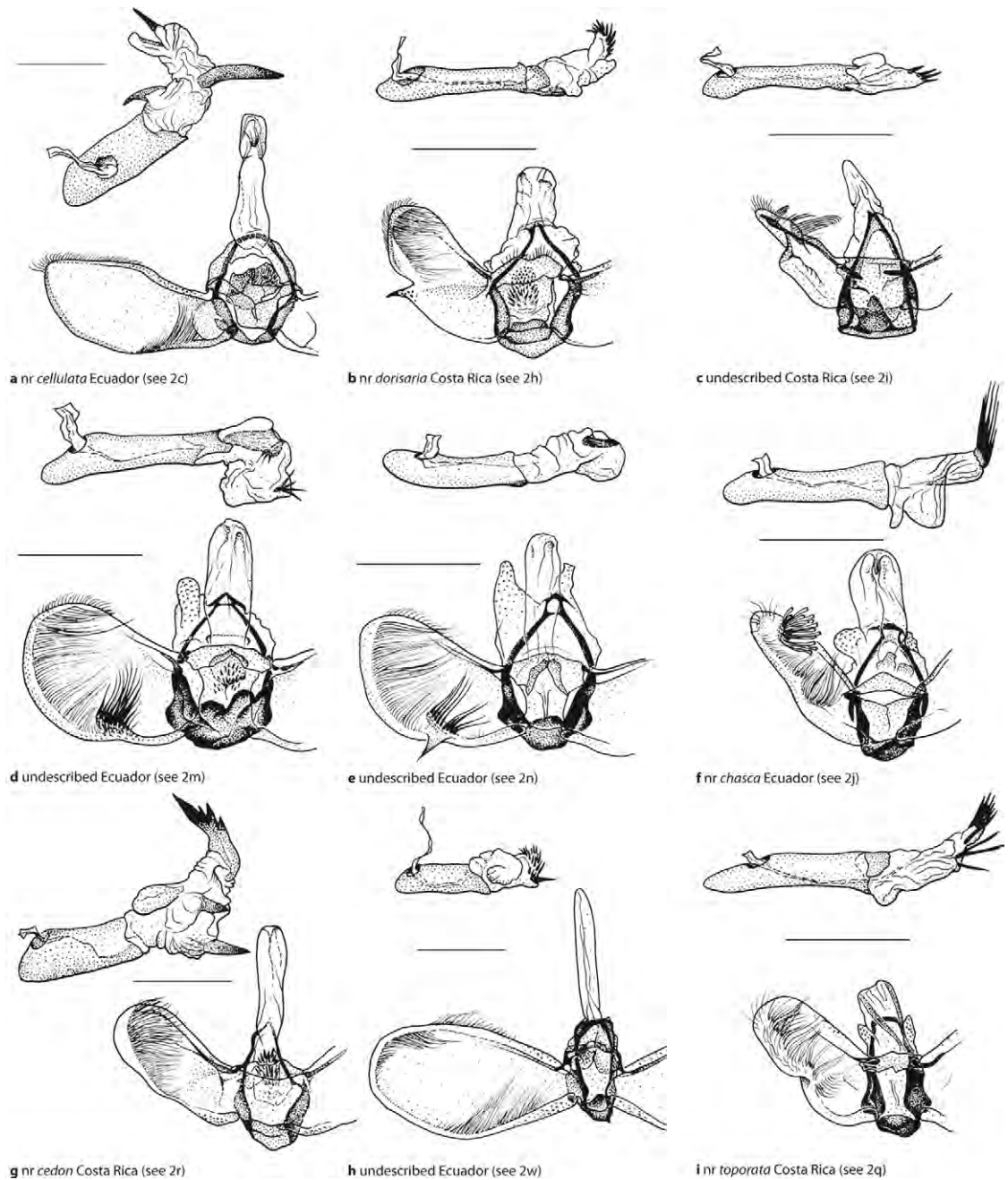


Fig. 4. Male genitalia of nine *Eois* species. The corresponding specimens are shown in Fig. 2. Scale bar = 1 mm.

caterpillars create holes which often leave a typical pattern of damage, e.g., in *Piper perareolatum* C.DC. (Fig. 6u). Most *Eois* caterpillars live solitarily, but some species (e.g., *Eois* sp. near *olivaria*, Fig. 6n) are gregarious or semigregarious. Morphology of Neotropical geometrid pupae needs to be studied in more detail. *Eois* pupae (Fig. 6z) vary in coloration from dark brown to ochre. They do not provide conspicuous characters, except for a relatively large frons. *Eois* eggs are undescribed.

**Behavior.** Little is known about adult behavior. All *Eois* species seem to be strictly nocturnal as adults. They are attracted to UV light (Brehm et al. 2005, 2007), and they are more frequently found in the forest understory (where most of the host plants grow) than in tree canopies (Brehm 2007). It is unknown whether the moths visit sources of nectar. Adults have sometimes been observed taking up fluid from the ground (Fig. 6s).

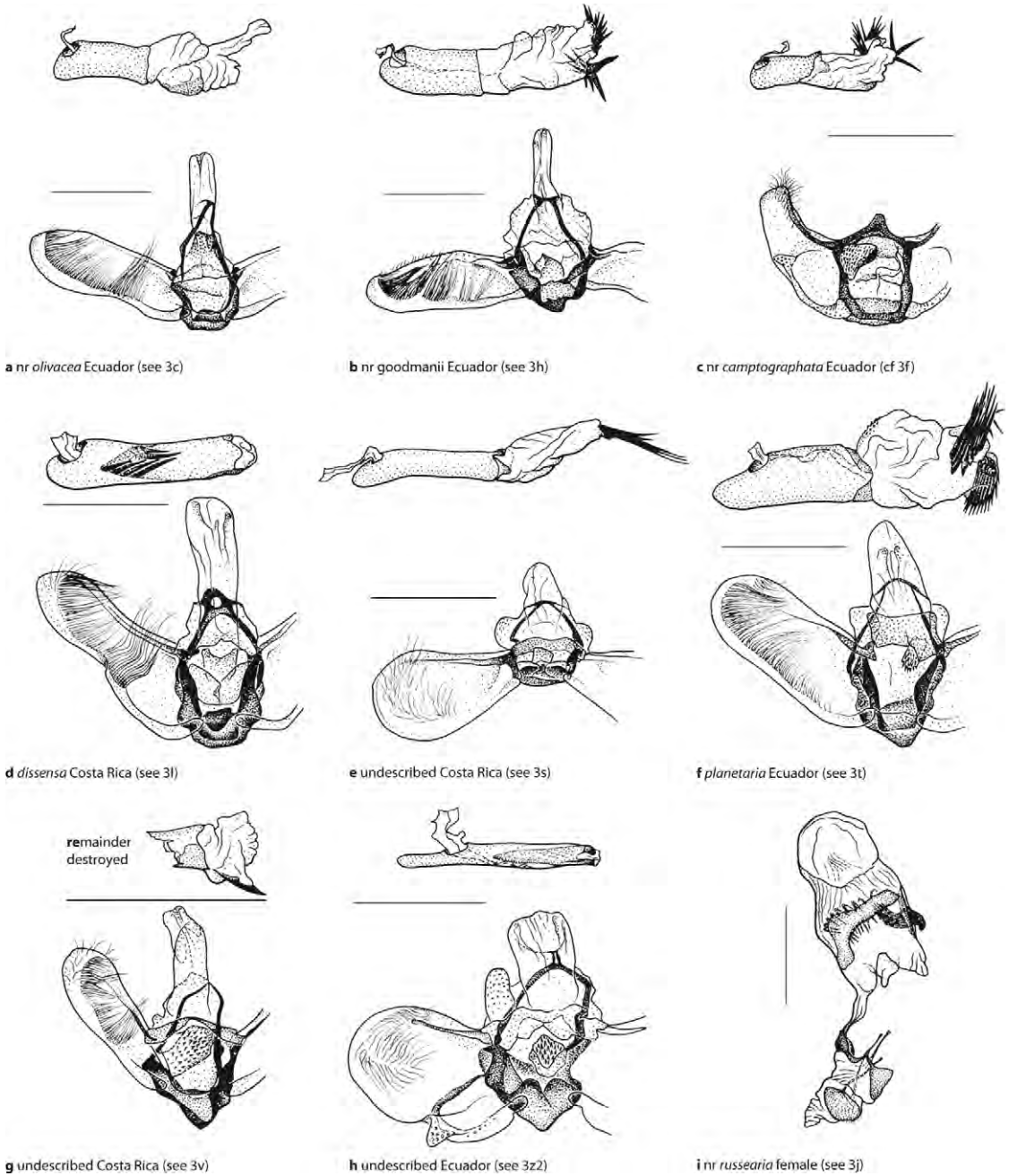


Fig. 5. Genitalia of eight male and one female *Eois* species. The corresponding specimens are shown in Fig. 3. Scale bar = 1 mm.

**Neotropical *Eois* Taxonomy and Checklist**

In total, 239 Neotropical species-level names are recognized here, among them 211 valid species, seven subspecies, and 21 synonyms (Table 1). Neotropical *Eois* represent 82% of all described species in the genus. A checklist of the Neotropical *Eois* species is provided in Appendix 1.

***Eois* Hübner, 1818, Zuträge zur Sammlung exotischer Schmetterlinge 1: 27**

**Type Species.** *Eois russearia* Hübner, 1818 (see fig. 3i). Type specimen probably lost. Synonyms: as listed by Holloway (1997) and Parsons et al. (1999).

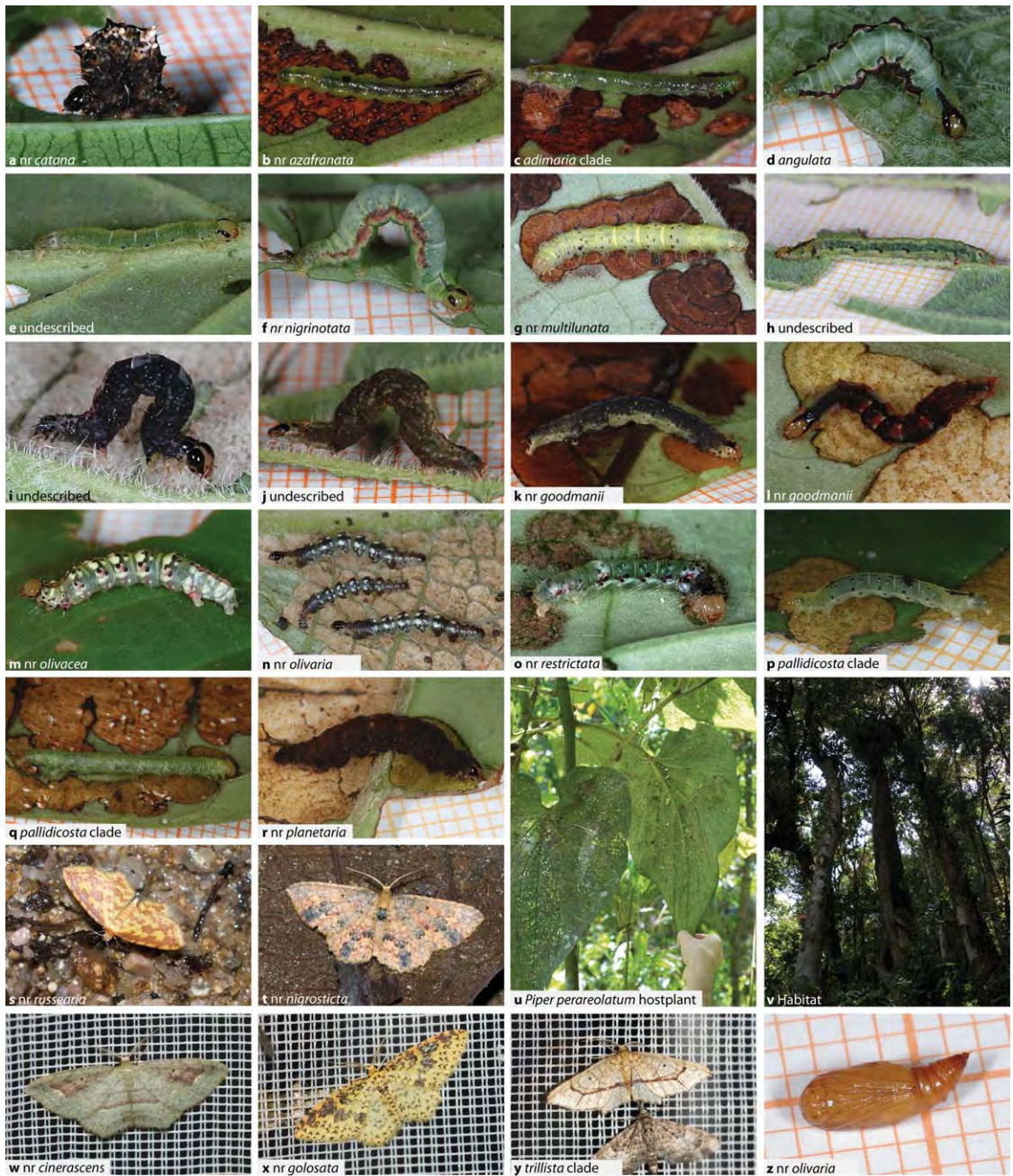


Fig. 6. Live *Eois* and habitats. a–t, caterpillars of 18 *Eois* species collected in southern Ecuador (Reserva Biológica San Francisco and surroundings), reared by F. Bodner between 2007 and 2009. u and v, host plant and habitat photographs taken in the study area. s, *Eois* sp. nr. *russearia* taking up fluid from the ground. t, *Eois* sp. nr. *nigrinotata* sitting on a dead leaf (both images from Parque Nacional Podocarpus entrance at Rio Bombuscaro, ≈1,000 masl, 2000–2200 hours, 24–27-XI-2008). w–z, *Eois* moths attracted to UV light at 3,000 masl (Parque Nacional Podocarpus, Cajanuma, ≈2000 hours, 20-XI-2008). (Online figure in color.)

Taxonomic Changes

*Aplogompha noctilaria* (Schaus 1901)

The taxon *noctilaria* (Schaus) is listed twice in the geometrid catalog (Parsons et al. 1999); once in *Eois*

(p. 279), and once in *Aplogompha* (subfamily Ennominae) (p. 55). It seems certain that they are one and the same because the cited references are identical, and only one *noctilaria* type specimen seems to exist in the USNM. In her revision of Neotropical ennomine moths, Pitkin (2002) listed *noctilaria* in the genus



**Table 1.** Available *Eois* names, sorted by world region

Region	Names	Valid species	Subspecies	Synonyms
Neotropical	239 (82%)	211 (83%)	7	21
Africa and Madagascar	13	13		
Asia	27	21	1	5
Australia	12	9	1	2
Total	291	254	9	28

Data were extracted from Parsons et al. (1999), with two recent species descriptions added (Herbulot 2000).

*Aplogompha*. As judged from digital photographs taken in the USNM, this species clearly does not belong to *Eois* because of a different wing shape, coloration, and pattern. The taxonomic placement in *Aplogompha* remains uncertain and needs to be confirmed by closer examination, but is beyond the scope of this article.

#### *Eois bermellada* (Dognin, 1893)

(Fig. 2e)

This species was overlooked by Parsons et al. (1999) but is present as *Eois* species in the online Global Lepidoptera Names Index (<http://www.nhm.ac.uk/jdsml/research-curation/research/projects/lepindex/index.dsm1>). It was described by Dognin (1890) (p. 85) as *Cambogia bermellada*. The species has a brownish ground color and broad yellow margins on both forewings and hindwings.

#### *Eois fragilis* (Warren 1900)

(Fig. 3y)

*E. fragilis* was not listed by Parsons et al. (1999) in *Eois*, but it is present in the online Global Lepidoptera Names Index (<http://www.nhm.ac.uk/jdsml/research-curation/research/projects/lepindex/index.dsm1>). Warren described the species as *Xanthorhoe fragilis*. Seven years later, he described a closely related species as *Cambogia lavendula* (Fig. 3z<sub>1</sub>) but did not revise his assignment of *fragilis*. The clade including *fragilis* (Warren), *lavendula* (Warren), *neclas* (Druce), *quadrilatera* (Dognin), and other species differs from “typical” *Eois* (with mostly yellow wing ground color) in their monochrome and grayish-brownish appearance. The assignment of the clade to *Eois* is supported by a general similarity of the habitus of the adults as well as caterpillar morphology and larval records from *Piper* (Dyer et al. 2010)—the plant genus used by most Neotropical *Eois* species (see Introduction). However, the clade around *E. fragilis* is in particular need of revisionary study.

#### *Eois cellulata* (Prout 1910), stat. rev

(Fig. 2b)

The species was described as *Amaurinia cellulata* (from central Peru) and later placed in synonymy with *Eois catana* (Druce) (from Guatemala) by Par-

sons et al. (1999) (Fig. 2a), based on the card index in the NHM. The two taxa are certainly closely related and belong to a clade relatively basal within *Eois* (Strutzenberger et al. 2010). The holotypes of the species (*cellulata*: female; *catana*: male) have a generally similar appearance with regard to size and wing shape. However, *cellulata* is darker than *catana*; the cell of the forewing is fulvous in *cellulata*, but not so in *catana*. Lines in *catana* are more pronounced, especially on the forewing, and thickness and distance between terminal and subterminal lines on the hindwings differ considerably between the species. Moreover, taking general biogeographical considerations into account, conspecificity of both taxa seems very unlikely because the species inhabit montane habitats whereas their type localities lie some 3,000 km apart (Guatemala and central Peru).

#### *Eois ambarilla* (Dognin, 1893), stat. rev

(Fig. 2l)

*Eois ambarilla* (Dognin), described from two male syntypes from southern Ecuador, was placed in synonymy with *Eois adimaria* (Snellen) (Parsons et al. 1999) (Fig. 2k, described with a male holotype from Colombia). Both species are closely related and belong to the *adimaria* clade sensu Strutzenberger et al. (2010). Although the coloration and pattern of the lines on fore- and hindwings are similar (but not the same), the lines are much broadened in *E. ambarilla*, which leads to an almost inverse proportion between lines and the pale yellow ground color in the two species.

#### *Eois telegraphica* Prout, 1933, stat. rev

(Fig. 2g)

The species was originally described as a subspecies of *Eois lilacea* (Dognin) (Fig. 2f). We regard *E. telegraphica* and *E. lilacea* as related, but not conspecific. Both probably belong to the same clade (*chasca* clade sensu Strutzenberger et al. 2010). However, *E. telegraphica* more closely resembles *Eois antiopata* (Warren) (not shown), especially with regard to the shape of the yellow margin on the forewing. The taxa differ considerably with regard to the pattern of the hindwings; *telegraphica* has an additional broad marginal yellow band that is absent in *antiopata*.

#### Further Taxonomic Remarks

At least three *Eois* species need closer inspection because their overall appearance differs considerably from other *Eois* species. Warren (1895) already stated in his description of *E. bifilata* (Fig. 3z<sub>3</sub>) that it was “very different in outward appearance from the rest of the genus: the hindwings have a distinct angulation in the middle of the hindmargin.” Likewise, *Eois haltima* (Schaus) and *Eois insolita* (Dognin) (not shown) need closer examination to confirm their assignment to *Eois*.

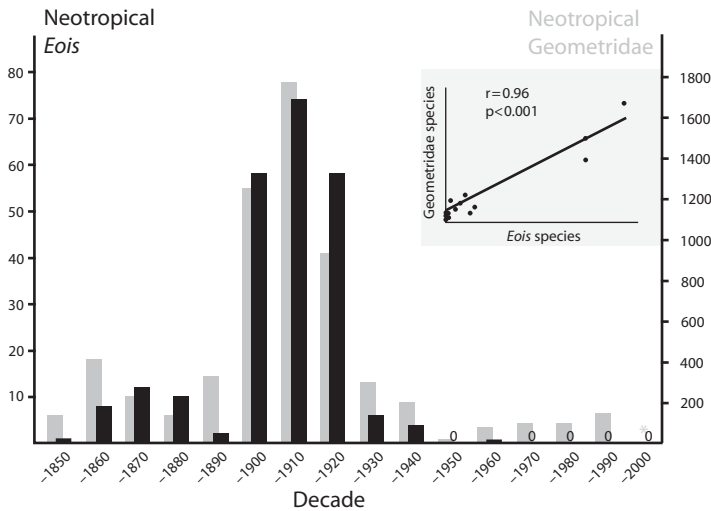


Fig. 7. Numbers of Neotropical *Eois* species described per decade (black bars) versus numbers of all Neotropical geometrid species (gray bars). Geometridae description data were extracted from Gaston et al. (1995) (p. 230; fig. 3-2).

In their catalog of the geometrid moths of the world, Parsons et al. (1999) list *Eois necula* (Druce). However, the taxon *necula* is a Sterrhinae species belonging to the genus *Tricentra* Warren. The species name was apparently mixed up with the taxon *nucula*, described by Druce on the same page and depicted on the same plate as *necula*. The male holotype of *nucula* has so far not been labeled in the collection of the NHM and needs to be identified in future revisionary work. As judged from Druce's plate, the species belongs to the *odatis* (Druce) clade sensu Strutzenberger et al. (2010).

Future work will almost certainly revive more species from synonymy. For example, two taxa currently treated as junior synonyms of *Eois azafanata* (Dognin) (Fig. 2o): *Eois denlerata* (Warren) (not shown), and *Eois anguinata* (Warren) (Fig. 2p), seem not to be conspecific with each other. Moreover, Dognin included a series of six syntypes for the description of *E. azafanata* from the Loja region (Ecuador), which partly seem not to be conspecific either. We also suspect that *Eois veniliata* (Walker) and its currently accepted junior synonym *E. leprosa* (Felder & Rogenhofer) are not conspecific and that *E. olivacea* (Felder & Rogenhofer) (Fig. 3a) and its junior synonym *Eois auruda* (Dognin) (Fig. 3b) are both good species. However, these cases need closer inspection not only of external morphology but also of genitalia morphology and DNA sequence data before a formal change of their taxonomic status can be made. Conversely, future revisionary work will probably also reveal a few species that need to be put into synonymy.

A remarkable and somewhat mysterious case is the description of two taxa (the largest known *Eois* species) with the same name in the same year by two authors. Dognin and Schaus independently described a taxon *multilunata* in 1912 (Fig. 2y and z<sub>1</sub>). Dognin's description preceded Schaus', and 3 yr later, Schaus

invented the replacement name *lunatissima* for his *multilunata*. The strange coincidence is the use of an identical name that is otherwise uncommon—*multilunata* has not been used for any other of >21,000 described geometrid species (Parsons et al. 1999). Moreover, both taxa closely resemble each other and might even be conspecific. Although type specimens of *multilunata* (Dognin) are from Colombia, Schaus' type specimen is from Costa Rica.

### Species Description Patterns

The known type specimens of the 239 recognized Neotropical *Eois* taxa are deposited in six museums with the majority being in only two institutions, i.e., the USNM (112 taxa), followed by the NHM (109), Naturalis, Leiden (five), the Oxford University Museum of Natural History (five), the Naturkundemuseum Berlin (two), and the Muséum d'Histoire Naturelle, Paris (two). The depository for types of four taxa is currently unknown (see Materials and Methods).

*Eois* species were described by 23 authors or author teams (i.e., Felder & Rogenhofer), and Neotropical *Eois* species by only 13 authors/teams. Most Neotropical taxa were described by Dognin during 1893–1918 (67), followed by Warren between 1894 and 1908 (63), Schaus (38), Prout (17), Druce (15), Walker (12), Guenée (eight), Snellen (five), Dyar (four), Möschler (two), and Fletcher and Hübner (one each).

After the description of *Eois russearia* by Hübner (1818), 40 yr passed until the next eight species were described by Guenée in 1858. A moderate number of 24 new *Eois* species was described before 1890 when a rush of descriptions started: 194 species (81.5%) were described in only three decades between 1890 and 1920 (Fig. 7), followed by a rapid decrease in the

1920s and 1930s. The most recent Neotropical *Eois* to be described was named by Fletcher in 1952.

The description patterns observed in *Eois* are not exceptional in the Geometridae, and they are probably similar in many other Lepidoptera groups. Numbers of Neotropical *Eois* described per decade are significantly correlated with numbers of all Neotropical Geometridae described (Fig. 7). The most obvious difference is, however, that still a smaller number of geometrid moths (100–200 per decade) were described in the decades after 1960, whereas the number of new Neotropical *Eois* taxa dropped to zero.

### Biogeography

As distribution data are currently unavailable for the majority of *Eois* species, type localities provide almost the only published source of information on the distribution of this group. By far most type specimens were collected in the Neotropical region (239 taxa, 82.1%), followed by Asia (27 taxa, 9.3%), Africa (13 taxa, 4.5%), and Australia/Oceania (12 taxa, 4.1%). The latitudinal distribution globally reaches 27° N [*Eois plicata* (Moore), Darjeeling region, India] and for the Neotropical species 19° N [*Eois carmenta* (Druce) and *Eois odatis* (Druce)] in the Coatepec region, Mexico. The southernmost type locality is Tucuman, Argentina, at 27° S [*Eois coerulea* (Warren)]. Altogether, only ≈20 taxa were described from locations outside the inner tropics (i.e., ≥23° N or S).

Within the Neotropical region, the majority of the type specimens (55%) were collected in and around the tropical Andes (the countries of Colombia, Ecuador, Peru, and Bolivia), 17% in the rest of the South American continent, 25% in Central America, and 4% in the Caribbean (Fig. 8). Only very few species have been described from vast regions in the Amazon basin (including the eastern lowland parts of the tropical Andean countries) and from the eastern part of the continent. Larger gaps also exist in southern Bolivia, northern Peru, northern Ecuador, Nicaragua, and Honduras, where *Eois* certainly occur. The histogram in Fig. 8 shows that most type specimens were collected between 0 and 10° N, the number decreasing both southward and northward. The majority (≈60%) of type specimens were collected in the Northern Hemisphere.

*Eois* richness along an elevational gradient in Costa Rica shows a peak ≈1,700 m above sea level (masl) (34 observed/interpolated species) and declines both with increasing and decreasing elevation (Fig. 9).

### Regional Diversity and Richness Estimations

Sampling of geometrid moths in two regions in Costa Rica and Ecuador allows a comparison of regional species richness of *Eois*. While a complete elevational gradient was sampled in Costa Rica, a truncated gradient was sampled in Ecuador (Table 2). However, sampling was more intensive and occurred over a longer period in Ecuador. Species richness in Ecuador was considerably higher than in Costa Rica.

Only 19 species in each of the study areas could be assigned to described species. Notably, none of the identified species occurred in both areas (Appendix 1). The proportion of taxonomically described species is considerably lower in Ecuador (12.3%) compared with Costa Rica (29%; Table 2). Simple richness estimations based on the ratio of described versus undescribed species lead to values between 733 and 1,710 Neotropical *Eois* species in total (Table 2).

### Discussion

**Biogeography.** The distribution of type localities (Fig. 8) provides a coarse image of distribution of *Eois* in the New World. Although it is unknown how appropriately the type localities reflect true distribution patterns of *Eois*, the data clearly suggest that the group has a predominantly montane distribution with a hot-spot of diversity in the tropical Andes, particularly along the eastern slope (Fig. 8). Along an elevational gradient in Costa Rica, most species were found at medium to higher elevations (>25 observed and interpolated species between 1,100 and 2,100 masl; Fig. 8). However, *Eois* is also present in lowlands (e.g., Costa Rica: nine observed species at 40 masl). Qualitatively similar patterns were observed by Rodríguez-Castañeda (2009) along an elevational gradient in northern Ecuador. She found that *Eois* species richness was best explained by increased host plant biomass and relaxation of predation pressure from natural enemies such as ants.

The distribution map also reflects strong sampling biases in museum collections. Although some regions are relatively well sampled, especially between 5 and 10° N (Colombia, Panama, and Costa Rica), others have been visited by collectors less frequently. Such biases have commonly been observed across a wide spectrum of Lepidoptera (e.g., Miller 2009). For example, very few specimens in the NHM are from Ecuador, whereas many are from Colombia and, particularly, from southeastern Peru. This is somewhat counterbalanced by the USNM holdings with more material from Ecuador and Central America. However, sampling from the Amazon region is generally “extremely inadequate,” as expressed by Miller (2009) for the Dioprinae. The statement is certainly true for many other groups of the Lepidoptera.

It is well known that species richness of organisms generally increases toward the equator. Because of general biogeographical considerations and explanations such as the mid domain effect, e.g., Colwell and Lees (2000), highest *Eois* species richness would be expected around the equator, decreasing toward the poles. Indeed, the available regional diversity studies from Ecuador and Costa Rica support such a pattern (lower diversity at higher latitudes). However, the histogram of type localities (Fig. 8) shows a bias toward the Northern Hemisphere. The Southern Hemisphere seems to be strongly undersampled (only 40% of type locations), particularly between 5 and 10° S, and 15 and 20° S, despite its larger tropical land area and its significant part of the tropical Andes.

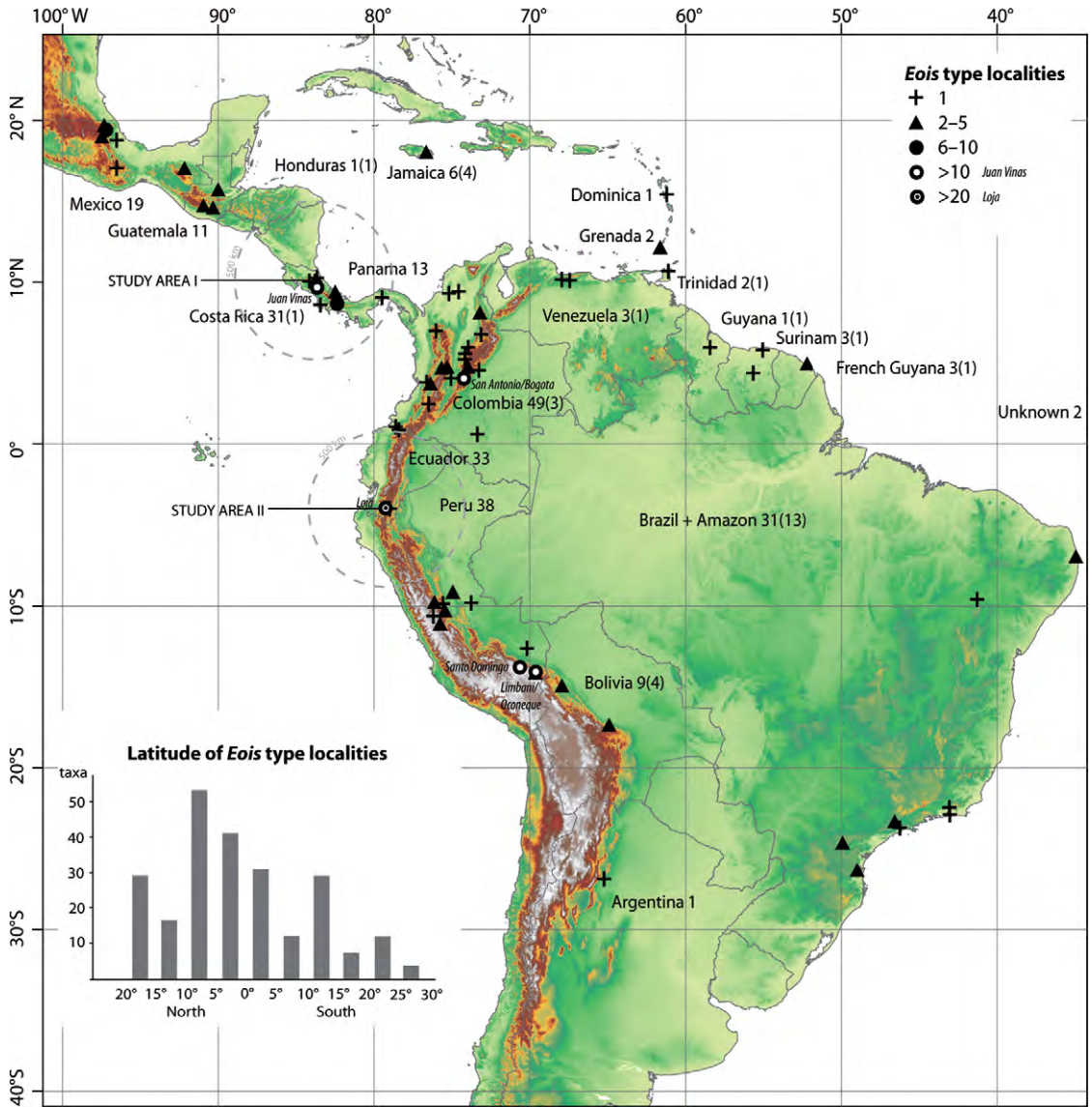


Fig. 8. Localities of *Eois* type specimens in the New World, including holotypes, paratypes, and syntypes (sum: 263), providing basic information on the distribution of Neotropical *Eois*. The numbers behind each country indicate the total number of its associated taxa. The number in brackets indicates how many of the type specimens are only labeled with the country's name. For example, nine types are associated with Bolivia, and among these, four are only labeled "Bolivia," whereas labels of the remainder provide more precise locations. The inserted histogram shows type localities according to latitude where geographical information was available (235 of 263 localities). Study area I, Barva transect, Costa Rica; study area II, Reserva Biológica San Francisco and surroundings, southern Ecuador. (Online figure in color.)

**How Many Species?** The proportion of taxonomically described *Eois* species in regional quantitative samples was previously estimated to be higher in both study areas, particularly in Ecuador (Brehm 2002; Brehm et al. 2005, 2007). Photographs of type specimens have eased the identification of sampled material, and species previously assigned to described species are now regarded as new. Moreover, new barcoding data (Strutzenberger 2011) stimulated the discovery of small but distinct morphological differences within complexes of closely related species.

The fraction of described species must still be regarded as a preliminary estimate. In many cases, it is impossible to judge whether a species is truly conspecific with a type specimen unless more data are available for identification (i.e., genitalia morphology, DNA sequence data, host and distribution data). Much revisionary work remains to be done.

The proportion of described *Eois* species is considerably lower in the study area in Ecuador than in Costa Rica. This can be explained by a higher species richness accompanied by a worse taxonomic coverage in

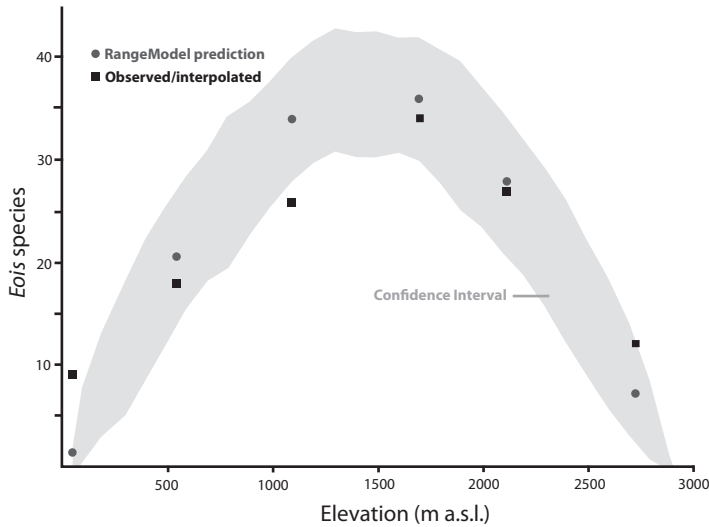


Fig. 9. Species richness of *Eois* along an elevational gradient in Costa Rica (40–2,730 masl). Black boxes: observed/interpolated richness. Gray circles, RangeModel predictions; light gray, confidence interval area.

Ecuador. Within a radius of 500 km (Fig. 8), fewer species were described around the study area in Ecuador (33 species) than around the study area in Costa Rica/Panama (44 species). Such regional pools of named species are most important in both areas and account for 58% of the currently identified species (Table 2).

It is possible that the rate of described species is somewhat higher than 19 of 154 (12.3%) in Ecuador because some species might be conspecific with type specimens despite slight morphological differences, and a few identifiable species might be hidden in species complexes found in the area [e.g., *Eois paraviolascens* (Dognin) and *Eois violada* (Dognin)]. However, the Costa Rica material might include a couple of previously unrecognized (and probably undescribed) species.

By multiplying the ratio of undescribed versus described species (Costa Rica, 3.47; Ecuador, 8.11) with the number of valid *Eois* species (211), we estimated a potential total number of Neotropical *Eois* between ≈730 (Costa Rica estimate) and 1,700 (Ecuador estimate). Although this a very coarse approach, the estimate has a similar order of magnitude as another

recent estimate based on host specificity of *Eois* (Rodríguez-Castañeda et al. 2010). Given that the tropical Andes are the bioregion with higher diversity than Central America (with subsequently higher importance), a conservative assumption would be 1,000 existing species of Neotropical *Eois*. A few more studies of regional *Eois* richness from other sites in the Neotropical region could quickly substantiate our estimate.

Are *Eois* representative of higher taxa of the Lepidoptera? Scoble et al. (1995) counted 6,433 described species of Neotropical Geometridae, accounting for 31% of the world fauna of the family. Description patterns have been largely identical in *Eois* and the Geometridae as a whole (Fig. 7). It is well known that large and colorful organisms (including Lepidoptera) have a higher probability of being described (Gaston et al. 1995). *Eois* indeed tend to be a little smaller than an average geometrid moth, but the wing patterns are more conspicuous and colorful than in many geometrids. Recent revisions of eight clades of the Geometridae (worldwide) produced up to 2.8 times more species than were known previously (Kristensen et al. 2007). Our data suggest a net change between

Table 2. Comparison of *Eois* species richness between Costa Rica and Ecuador

Study area and period of fieldwork	Elevational range (masl)	Observed morphospecies	Identified at species level	Neotropical <i>Eois</i> richness extrapolation (211 valid names)	Type locality countries
Costa Rica: Barva transect (2003–2004)	40–2,730	66	19 (29%)	(factor 3.47) 733	Costa Rica (11) Panama (4) Colombia (2) Brazil (1) Mexico (1)
Ecuador: Reserva Biológica San Francisco and surroundings (1999–2008)	1,020–2,670	154	19 (12.3%)	(factor 8.11) 1,710	Ecuador, Loja (11) Peru (6) Bolivia (1) Colombia (1)

3.47- (Costa Rica) and 8.11-fold (Ecuador) (see above). However, revisions can only include material already represented in museum collections. Many moth species have not been sampled and deposited in a museum yet. The true number of Neotropical geometrid moth species is unknown, but our data suggest that this number could easily triple the number of currently described species (6,433). Such a high number ( $\approx 19,000$ ) would be close to the total of all currently described geometrid species in the world.

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#### Appendix 1. Checklist of Neotropical *Eois*

Species	Author	Yr	Southern Ecuador	Costa Rica
<i>abbreviata</i>	(Dognin)	1906		
<i>acerba</i>	(Dognin)	1900		
<i>adimaria</i>	(Snellen)	1874	3 nr	
<i>argentifilata</i>	(Felder & Rogenhofer)	1875		
<i>agroica</i>	(Dyar)	1913		
<i>albigrisea</i>	(Dognin)	1913		
<i>albosignata</i>	(Dognin)	1911		
<i>amarillada</i>	(Dognin)	1893	x	
<i>amaryllaria</i>	(Schaus)	1901		
<i>ambarilla</i>	(Dognin)	1893		
<i>angulata</i>	(Warren)	1904	x	
<i>antiopata</i>	(Warren)	1904	x	1 nr
<i>apryaria</i>	(Guenee)	1858	1 nr	1 nr
<i>arenacea</i>	(Dognin)	1912		
<i>aurata</i>	(Warren)	1897		
<i>azafranata</i>	(Dognin)	1893	x, 2 nr	1 nr
<i>anguinata</i>	(Warren)	1904		
<i>denlerata</i>	(Schaus)	1901		
<i>basaliata</i>	(Warren)	1907	x	1 nr
<i>batea</i>	Druce	1892		
<i>bellissima</i>	(Warren)	1904		
<i>bermellada</i>	(Dognin)	1893		
<i>bifilata</i>	(Warren)	1895		
<i>binaria</i>	(Guenee)	1858		
<i>hyriaria</i>	(Snellen)	1874		
<i>vitellaria</i>	(Felder & Rogenhofer)	1875		
<i>biradiata</i>	(Dognin)	1911	x	
<i>bitaeniata</i>	(Prout)	1910		
<i>bolana</i>	(Dognin)	1899		
<i>boliviensis</i>	(Dognin)	1900		
<i>borrata</i>	(Dognin)	1893	x, 3 nr	
<i>borratoides</i>	(Prout)	1910		
<i>brasiliensis</i>	Prout	1933		1 nr
<i>brunnea</i>	(Warren)	1904		
<i>brunneicosta</i>	(Dognin)	1916		
<i>burla</i>	(Dognin)	1899		
<i>camptographata</i>	Prout	1922	2 nr	
<i>canariata</i>	(Dognin)	1903	1 nr	
<i>cancellata</i>	(Warren)	1906	1 nr	1 nr
<i>carmenta</i>	(Druce)	1892		
<i>carnana carnana</i>	(Druce)	1892		1 nr
<i>carnana aberrans</i>	(Prout)	1922		
<i>carrasca</i>	(Dognin)	1899	1 nr	
<i>cassandra</i>	(Druce)	1892		

#### Appendix 1. Continued

Species	Author	Yr	Southern Ecuador	Costa Rica
<i>catana</i>	(Druce)	1892	1 nr	1 nr
<i>cedon</i>	(Druce)	1892		
<i>particolor</i>	(Warren)	1895		
<i>cellulata</i>	(Prout)	1910		
<i>cervina</i>	(Warren)	1901		
<i>chasca chasca</i>	(Dognin)	1899	x, 1 nr	
<i>chasca oculata</i>	(Dognin)	1916		
<i>chione</i>	Prout	1933		
<i>chrysocraspedata</i>	(Warren)	1897	1 nr	
<i>cinerascens</i>	(Warren)	1907		
<i>ciocolatina</i>	(Warren)	1907		
<i>citriaria</i>	(Schaus)	1912		x, 1 nr
<i>cobardata</i>	(Dognin)	1893	x, 2 nr	
<i>coerulea</i>	(Warren)	1905		
<i>cogitata</i>	(Dognin)	1918		
<i>coloraria</i>	(Schaus)	1901		
<i>commixta</i>	(Warren)	1904	1 nr	
<i>concatenata</i>	(Prout)	1910	4 nr	1 nr
<i>consocia</i>	(Warren)	1897		
<i>contractata</i>	(Walker)	1861		1 nr
<i>hyriaria</i>	(Warren)	1894		
<i>contraversa</i>	(Warren)	1907	x	
<i>costalaria</i>	(Schaus)	1901		
<i>crocina</i>	(Schaus)	1912		
<i>decursaria</i>	(Mschler)	1886		
<i>ferruginata</i>	(Warren)	1897		
<i>deleta</i>	(Schaus)	1912	1 nr	
<i>delicatula</i>	(Warren)	1904	2 nr	
<i>dibapha</i>	(Schaus)	1912		x
<i>dione</i>	(Schaus)	1912		
<i>dissensa</i>	(Schaus)	1912		x
<i>diversicosta</i>	(Prout)	1911		
<i>dorisaria</i>	(Schaus)	1913		
<i>dryantis</i>	(Schaus)	1912		
<i>dryope</i>	(Schaus)	1912		x
<i>elongata</i>	(Schaus)	1912	1 nr	
<i>encina</i>	(Dognin)	1899	2 nr	
<i>escamata</i>	(Dognin)	1893	x	
<i>expressaria</i>	(Walker)	1861		
<i>fasciata</i>	(Warren)	1901	1 nr	
<i>filiferata</i>	(Dognin)	1912		
<i>flavifulva</i>	(Warren)	1904		
<i>flavotaeniata</i>	(Warren)	1895		
<i>fragilis</i>	(Warren)	1900		
<i>fuscata</i>	(Dognin)	1912	1 nr	
<i>fulva</i>	(Prout)	1910		

## Appendix 1. Continued

Species	Author	Yr	Southern Ecuador	Costa Rica
<i>fulvicosta</i>	(Dognin)	1912	1 nr	
<i>funiculata</i>	(Warren)	1904		
<i>furvibasis</i>	(Dognin)	1914		
<i>fuscicosta</i>	(Dognin)	1912		
<i>gemellaria</i>	(Guenee)	1858		
<i>multiplicata</i>	(Walker)	1861		
<i>pyraliata</i>	(Warren)	1895		
<i>glauculata</i>	(Walker)	1863		
<i>golosata</i>	(Dognin)	1893	1 nr	1 nr
<i>goodmani</i>	(Schaus)	1913	8 nr	x
<i>viridiflava</i>	(Dognin)	1918		
<i>griseicosta</i>	(Warren)	1904		
<i>guapa</i>	(Schaus)	1912	1 nr	1 nr
<i>haematodes</i>	(Warren)	1907		
<i>haltima</i>	(Schaus)	1901		
<i>heliadaria</i>	(Guenee)	1858		
<i>hermosaria</i>	(Schaus)	1901	1 nr	
<i>heza</i>	(Dognin)	1899	x, 1 nr	
<i>hocica</i>	(Dognin)	1899		
<i>hulaquina</i>	(Dyar)	1914		
<i>hyperythraria</i>	(Guenee)	1858		
<i>ignefumata</i>	(Dognin)	1910	2 nr	
<i>imitata</i>	(Warren)	1907		
<i>inconspicua</i>	(Warren)	1907		
<i>inflammata</i>	(Dognin)	1911	2 nr	
<i>insignata</i>	(Walker)	1861	1 nr	1 nr
<i>insoleus</i>	(Warren)	1905		
<i>insolita</i>	(Dognin)	1913		
<i>insueta</i>	(Schaus)	1912		x
<i>intacta</i>	(Warren)	1904		
<i>internexa</i>	Dognin	1911		
<i>isabella</i>	(Schaus)	1901		1 nr
<i>isographata</i>	(Walker)	1863		1 nr
<i>jifa</i>	(Dognin)	1899	x	
<i>lavendula</i>	(Warren)	1907	1 nr	
<i>lavinia</i>	(Schaus)	1912		x
<i>lilacea</i>	(Dognin)	1909		1 nr
<i>lilacina lilacina</i>	(Warren)	1904		
<i>lilacina condensata</i>	(Warren)	1907		
<i>lilacina inviolata</i>	(Prout)	1910		
<i>lineolata</i>	(Warren)	1897		
<i>lucivittata lucivittata</i>	(Warren)	1907	1 nr	
<i>lucivittata expurgata</i>	Prout	1922		
<i>lunatissima</i>	(Schaus)	1915		
<i>multilunata</i> (junior homonym, unavailable)	(Schaus)	1912		
<i>lunifera</i>	(Dognin)	1912	2 nr	
<i>marcearia</i>	(Guenee)	1858		x
<i>expallidata</i>	(Warren)	1904		
<i>indignaria</i>	(Walker)	1863		
<i>simplicearia</i>	(Walker)	1861		
<i>margarita</i>	(Dognin)	1911	1 nr	1 nr
<i>mediogrisea</i>	(Dognin)	1914		x
<i>mediostrigata</i>	(Warren)	1907	x	
<i>mexicaria</i>	(Walker)	1866		
<i>mictographa</i>	Prout	1933		
<i>multilunata</i>	(Dognin)	1912	1 nr	x
<i>multistrigaria</i>	(Warren)	1901		x, 1 nr
<i>muscosa</i>	(Dognin)	1910	1 nr	
<i>muscularia</i>	(Dognin)	1900		
<i>myrrha</i>	(Schaus)	1912		x
<i>nacara</i>	(Schaus)	1901		
<i>naias</i>	(Schaus)	1912		x

## Appendix 1. Continued

Species	Author	Yr	Southern Ecuador	Costa Rica
<i>neclas</i>	(Druce)	1892		
<i>neutraria</i>	(Guenee)	1858		
<i>nigriceps</i>	(Warren)	1907	1 nr	
<i>nigricosta</i>	Prout	1926	1 nr	
<i>nigrinotata</i>	(Warren)	1907	4 nr	
<i>nigriplaga</i>	(Warren)	1897		
<i>nigrosticta</i>	(Warren)	1901	1 nr	1 nr
<i>nucula</i>	(Druce)	1892		
<i>numeria</i>	(Druce)	1892		
<i>numida</i>	(Druce)	1892		x
<i>nundina</i>	Druce	1892		
<i>nympha</i>	(Schaus)	1912		
<i>obada obada</i>	(Druce)	1892		
<i>obada transsecta</i>	(Warren)	1901		1 nr
<i>obscura</i>	(Dognin)	1909		
<i>occia</i>	(Druce)	1892		
<i>odatis</i>	(Druce)	1892	1 nr	
<i>olivacea</i>	(Felder & Rogenhofer)	1875	6 nr	
<i>auruda</i>	(Dognin)	1900		
<i>beebei</i>	(Fletcher)	1952		
<i>olivaria</i>	(Schaus)	1901		
<i>operbula</i>	(Dyar)	1913		
<i>ops</i>	Druce	1892		1 nr
<i>pallidicosta</i>	(Warren)	1907	3 nr	
<i>pararussearia</i>	Dognin	1901	2 nr	
<i>paraviolascens</i>	(Dognin)	1900	5 nr	
<i>parva</i>	(Dognin)	1918		x
<i>paulona</i>	(Schaus)	1927		
<i>percisa</i>	(Warren)	1907		
<i>perstrigata</i>	(Warren)	1907		
<i>peruviensis</i>	(Schaus)	1901		
<i>plana</i>	(Dognin)	1918		
<i>planetaria planetaria</i>	(Warren)	1907	x	
<i>planetaria albimaculata</i>	(Dognin)	1911		
<i>platearia</i>	(Schaus)	1901		
<i>plumbeofusa</i>	(Warren)	1901		x
<i>primularis</i>	Prout	1922		1 nr
<i>pseudobada</i>	(Dognin)	1918		
<i>punctata</i>	(Dognin)	1913		
<i>punctifera</i>	(Dognin)	1911		
<i>quadrilatera</i>	(Dognin)	1895	1 nr	
<i>relaxaria</i>	(Snellen)	1874		
<i>restrictata</i>	(Warren)	1901	1 nr	x
<i>cinyras</i>	(Schaus)	1912		
<i>reticulata</i>	(Schaus)	1901		
<i>roseocincta</i>	(Warren)	1908		
<i>rubiada</i>	(Dognin)	1893	x	
<i>rubicunda</i>	(Dognin)	1912		
<i>russearia</i>	Hübner	1818		
<i>sagittaria</i>	(Snellen)	1874	1 nr	
<i>sanguilinea</i>	(Warren)	1895		
<i>saria</i>	(Dyar)	1913		2 nr
<i>scama</i>	(Dognin)	1899	x	
<i>semipicta</i>	(Warren)	1897		
<i>semirosea</i>	(Dognin)	1913		
<i>seria</i>	(Dognin)	1900		
<i>serrilineata</i>	(Prout)	1910	1 nr	
<i>signaria</i>	(Schaus)	1901		
<i>silla</i>	(Dognin)	1899		
<i>simulata</i>	(Dognin)	1911		
<i>singularia</i>	(Schaus)	1901		
<i>snellenaria</i>	(Möschler)	1882		
<i>unilineata</i>	(Warren)	1895		



## Appendix 1. Continued

Species	Author	Yr	Southern Ecuador	Costa Rica
<i>stellataria</i>	(Warren)	1907		
<i>subangulata</i>	(Walker)	1861		
<i>subcrocearia</i>	(Snellen)	1874		
<i>subpallida</i>	(Dognin)	1913	1 nr	
<i>subtectata</i>	(Walker)	1861		
<i>tegularia</i>	(Guenee)	1858		
<b><i>lurida</i></b>	<b>(Felder &amp; Rogenhofer)</b>	<b>1875</b>		
<i>telegraphica</i>	Prout	1933	1 nr	
<i>tertulia</i>	(Dognin)	1893		
<i>tessellata</i>	(Warren)	1897		
<i>thetisaria</i>	(Schaus)	1913		
<i>toporata</i>	(Schaus)	1901		1 nr
<i>trillista</i>	(Warren)	1905	2 nr	
<i>trinotata</i>	(Warren)	1895		
<i>undulosata</i>	(Warren)	1901		x
<i>veniliata</i>	(Walker)	1861		1 nr
<b><i>leprosa</i></b>	<b>(Felder &amp; Rogenhofer)</b>	<b>1875</b>		
<i>vinosata</i>	(Warren)	1907	x	
<i>violada</i>	(Dognin)	1899	3 nr	
<i>warreni</i>	(Dognin)	1914		1 nr
<i>xanthoperata</i>	(Warren)	1897		
<i>ycata</i>	(Dognin)	1893		1 nr
<i>zenobia</i>	(Schaus)	1912		x
<i>zorra</i>	(Dognin)	1896	x	1 nr
		<b>Total</b>	<b>19/154</b>	<b>19/66</b>

The last two columns provide information on the presence of species in two study areas in Costa Rica and Ecuador. (nr, undescribed species near; **bold**, synonyms; gray shade, subspecies.)