

TAXONOMIC NOTES ON THE GENUS *ZARETIS*, WITH THE DESCRIPTION OF A NEW SPECIES (LEPIDOPTERA: NYMPHALIDAE: CHARAXINAE)

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ABSTRACT.— We review the taxonomy of the genus *Zaretis* Hübner, [1819], restoring *Zaretis isidora* Cramer to specific status (stat. rev.) and describing a new species, *Zaretis pythagoras* n. sp., from the Chocó region of western Colombia and western Ecuador. We also provide a key to identification of adult *Zaretis* and a synonymic checklist of all described names.

KEY WORDS: *Anaea*, *Anaeni*, Antioquia, Chocó, Colombia, *Consul*, Ecuador, endemism, Esmeraldas, *Memphis*, Neotropical, Pichincha, premontane, rainforest, Risaralda, *Siderone*, South America, taxonomy, *Zaretis pythagoras* n. sp.

The genus *Zaretis* Hübner, [1819], is an exclusively Neotropical member of the subfamily Charaxinae, whose species range from Mexico to southern Brazil and Paraguay (Comstock, 1961). All species are canopy insects confined to forest habitats, ranging from sea-level to over 2000m (Willmott and Hall, unpubl. data). Males are strongly attracted to a wide variety of baits, particularly rotting carrion, and certain species are among the most commonly seen members of the canopy fauna (DeVries, 1987, 1988; Neild, 1996; DeVries *et al.*, 1999; Willmott and Hall, unpubl. data).

Adults of all members of the genus have a predominantly orange to cream dorsal surface with variable dark brown shading in the forewing apex and traces of a dark brown submarginal line on both wings (see Comstock, 1961; d'Abrera, 1988). The ventral surface is mottled brown with a prominent line running from the hindwing costa to the tornus, frequently extending on the forewing to the apex, producing a strong resemblance to a dead and dry leaf. Most species possess, in at least some individuals, translucent spots near the base of cells Cu2-Cu1 and Cu1-M3 on the forewing. All species have a tornal lobe on the hindwing at vein 2A, an emarginate forewing tornus and hindwing apex and falcate forewing apex.

Zaretis appears to be the sister genus to *Siderone* Hübner, [1823], and indeed several earlier authors treated all *Zaretis* species under the latter name (e.g., Westwood, 1850; Kirby, 1871; Godman and Salvin, 1884; Staudinger, 1887). Both *Zaretis* and *Siderone* share a similar wing shape, both possessing a hindwing tornal lobe, a continuous dark postdiscal line on the ventral hindwing (though this is less pronounced in *Siderone*), cream scaling on the ventral surface of the thorax between the forelegs, in contrast to the otherwise dark thorax, porrect labial palpi and distinctive and similar immature stages. The larvae of both *Siderone* and *Zaretis* differ from other members of the *Anaeni* (*sensu* Ackery, 1988), including *Consul* Hübner, [1807], which is otherwise similar in several wing shape and pattern characters, in having pronounced head horns and a dark dorsal "saddle" on the first abdominal segment, which is also expanded slightly dorsolaterally (Rydon, 1971; Muyschondt, 1973, 1974a,b, 1975a,b, 1976; DeVries, 1987). Despite these notable features of the immature stages, Comstock (1961) placed the species from both genera under the name *Anaea* Hübner, [1819], but Rydon (1971) again resurrected both genera and separated *Zaretis* from *Siderone* on the basis of several slight wing pattern and venation characters. None of the latter characters inspire confidence in the monophyly of *Zaretis*, but one character not mentioned by Rydon

(1971), the strongly emarginate hindwing apex, may prove to be a synapomorphy for the genus. However, given the apparently highly derived wing shape and pattern of *Siderone*, and the fact that some female specimens have a slightly emarginate hindwing apex, a cladistic analysis of the tribe would be desirable to examine the phylogenetic validity of both genera, and indeed many other currently recognised anacine genera (Rydon, 1971; DeVries, 1987; d'Abrera, 1988; Neild, 1996).

Zaretis species exhibit only subtle variation on the same basic wing pattern, which may be intraspecifically very variable, and often lack any interspecific genitalic differences. Thus, much as in the more speciose but closely related genus *Memphis* Hübner, [1819] (Comstock, 1961; Neild, 1996; Willmott and Hall, in prep.), it has been similarly plagued by taxonomic problems. Principal contributors to the species-level taxonomy of the genus include Cramer (1777, 1779), Westwood (1850), Godman and Salvin (1884), Fruhstorfer (1909), and Comstock (1961), although no valid new species have been described for over a century (Felder, 1869). The discovery of a distinctive *Zaretis* phenotype in western Ecuador, apparently belonging to an undescribed species, and the realisation that a common sibling species has escaped recognition by almost all authors, including all modern workers, has prompted us to make a preliminary review of the genus to clarify several taxonomic problems. However, certain parts of the taxonomic arrangement proposed here must be considered tentative and subject to testing by workers in the field in relevant areas of the Neotropics.

We have examined the original descriptions and attempted to locate type material for all names applicable to the genus. As this is not intended to be a revision, we do not designate lectotypes, though this would be desirable when an in-depth study is made. A number of syntypes for various *Zaretis* names are listed by Vane-Wright (1975), but there are certainly others unlabelled in the main collection of The Natural History Museum, London, UK. We have also collected *Zaretis* specimens in Ecuador over the last eight years as part of a long term study on the butterfly fauna of Ecuador, and examined additional *Zaretis* material in many of the major public and private European, North and South American collections, to determine ranges and investigate wing pattern variation (in part listed by Willmott, in press). The following collection acronyms are used throughout the text:

BMNH The Natural History Museum, London, UK [(R)=Rothschild coll.; (M)=Main coll.]

JS	Julián Salazar collection, Manizales, Colombia
KWJH	Keith R. Willmott & Jason P. W. Hall collection, London, UK
MECN	Museo Ecuatoriano de Ciencias Naturales, Quito, Ecuador
MHNUC	Museo de Historia Natural, Universidad de Caldas, Manizales, Colombia
NMI	National Museum of Ireland, Dublin, Ireland
USNM	National Museum of Natural History, Smithsonian Institution, Washington, DC, USA
ZMHU	Zoologisches Museum für Naturkunde, Humboldt Universität, Berlin, Germany

TAXONOMIC REVIEW OF *ZARETIS*

Two *Zaretis* species, *Z. callidryas* (R. Felder, 1869) and *Z. syene* (Hewitson, 1856), are very distinctive and have caused few taxonomic problems, except for a couple of synonyms inadvertently described by independent authors at the time of the discovery of the former species. Several early authors placed *Z. callidryas* in the genus *Anaea* (s. l.) (Godman & Salvin, 1884; Röber, 1916), and Rydon (1971) questioned Comstock's (1961) placement of both these species in *Zaretis* (as a subgenus). However, both possess an emarginate hindwing apex in addition to many other characters typical of *Zaretis*, including those of the early stages for *Z. callidryas* (Muyschondt, 1976), suggesting they belong in the latter genus. The taxonomy of these two species is discussed by Comstock (1961) and will not be considered further here. Both species are clearly figured by d'Abrera (1988).

The remainder of the genus has been regarded as constituting either two species, *Z. itys* and *Z. ellops* (Godman & Salvin, 1884; DeVries, 1987; Neild, 1996), or only a single species, *Z. itys* (Staudinger, 1887; Röber, 1916; Comstock, 1961; Vane-Wright, 1975; d'Abrera, 1988). The great intraspecific wing pattern variation in the genus has generated numerous names, but there has been little consensus on how to apply them.

Cramer (1777:34) described the first name, *Papilio itys*, in what is now *Zaretis*, figuring both wing surfaces on Plate 119, as Fig. F and G. The figures show a female specimen, reputedly from Surinam, with a dark reddish orange dorsal surface, dark brown dorsal forewing apices and a dark ventral surface with the ground color strongly contrasting in the basal and distal halves. These figures correspond well with the lectotype female in the BMNH(R) designated by Vane-Wright (1975). A few years later, in the same work, Cramer (1779:72) introduced the name *isidora* for male and female specimens, also from Surinam, illustrating both wing surfaces on Plate 235, as Fig. A, B, E, and F. Single male and female specimens in the BMNH(R) closely match the original figures in having medium orange dorsal coloration, with strongly contrasting dark brown forewing apices, and a pale, uniform orange-brown ventral ground color, and both very probably represent syntypes (Vane-Wright, 1975). Although Westwood (1850) retained the two names, Kirby (1871) synonymized them and was followed by most subsequent authors (e.g., Godman and Salvin, 1884; Staudinger, 1887; Röber, 1916), including Comstock (1961) in his revision of the genus. However, examination of extensive series of specimens in collections shows the two female phenotypes represented by *Z. isidora* and *Z. itys* to be consistently distinct throughout the Neotropics and, furthermore, each matches a distinct male phenotype. Both sexes of *Z. itys* are distinguished from those of *Z. isidora* (correctly associated by Cramer (1779) in his original description) by having a smaller emargination at the forewing tornus, a longer tornal lobe at hindwing vein 2A, and more sharply contrasted basal and postdiscal areas on both ventral wings (see Figs. 1,2).

Of the names described in *Zaretis* by subsequent authors, only two, *Z. itylus* Westwood, 1850, and *Z. pseuditys* Fruhstorfer, 1909,

apply to *Z. itys*, which appears to be less common than *Z. isidora* throughout its range. Westwood (1850) described *Z. itylus* from a single, supposedly female specimen, but the description clearly applies to a male, as confirmed by examination of the holotype in the BMNH. This specimen is typical of a phenotype occurring in southeastern Brazil, which we regard as a subspecies of *Z. itys* (*stat. rev.*). Although this taxon does not have the small forewing tornal "hook" typical of nominate *Z. itys*, it shares the long hindwing "tail", contrasting ventral coloration, and the matching female phenotype scarcely differs from that of nominate *Z. itys*. Since no specimens referable to nominate *Z. itys* are known to be sympatric with *Z. itylus*, it seems most parsimonious to regard the two taxa as conspecific. Fruhstorfer (1909) also regarded *Z. itys* and *Z. isidora* as distinct species, but presumably because he was unable to examine the type of *Z. itylus* he placed that name as a subspecies of *Z. isidora* and redescribed the southeastern Brazilian population under the name *Z. itys pseuditys*. The latter name is therefore a synonym of *Z. itylus*, as confirmed by examination of all four syntypes of *Z. pseuditys* in the BMNH.

The correct taxonomic association of the remaining described names in the genus is somewhat less certain. The name *ellops* was described by Ménétrières (1855) based on an unspecified number of males from Nicaragua, and both wing surfaces were figured in color on Plate 3, as Fig. 1. The figured specimen is typical of a male phenotype common throughout Central America. It is characterized by the dorsal surface being almost uniformly pale orange, with a narrow and only slightly darker area in the forewing apex, and a broad forewing shape with the apex hooked only near the tip, with the distal margin being almost straight between the tornus and vein M1 (Fig. 3a,b). Male specimens are matched by pale yellow female specimens (Fig. 3c,d) with similar wing pattern and shape characters, in contrast to the darker orange females of typical *Z. isidora* (Fig. 2c,d). The male and female syntypes of *Z. anzuletta* Fruhstorfer, 1909, from Mexico, in the BMNH, do not differ significantly from typical *Z. ellops* and we regard the two names as synonymous. Most authors working on faunistic studies (Godman and Salvin, 1884; DeVries, 1987; Neild, 1996) have treated *Z. ellops* as a species distinct from *Z. isidora*, while those who have reviewed the entire genus have tended to regard *Z. ellops* as a form or subspecies of *Z. isidora* (Staudinger, 1887; Röber, 1916; Comstock 1961; d'Abrera, 1988). The relatively consistent consilience of characters in the two phenotypes in series of specimens from single localities throughout Central America (see Fig. 2-3) has convinced us to follow faunistic workers, who typically also have access to better quality information on sympatry and synchrony of phenotypes, in treating *Z. ellops* and *Z. isidora* as distinct species. Nevertheless, the variability exhibited by each wing character, and the fact that forewing apex shape and dorsal color are characters believed to be subject to seasonal or individual variation within the Charaxinae (Comstock, 1961; Caldas, 1996; Neild, 1996), suggests that further collecting throughout the year and, if possible, rearing experiments conducted under different artificial climatic regimes, could greatly improve our understanding of the true taxonomic status of *Z. ellops*. DeVries (1987) stated that there were differences in the early stages between *Z. ellops* and *Z. itys*, but it is not clear whether he was using the latter name to refer to true *Z. itys*, which is clearly distinct from *Z. ellops*, or to *Z. isidora*, since he was apparently unaware of the existence of the latter species in Costa Rica.

Throughout the remainder of its range, *Z. isidora* exhibits substantial variation in wing pattern and shape. Specimens from higher elevations in both the eastern and western Andes are often larger and paler than typical *Z. isidora*, and Staudinger (1887) introduced the name *cacica* for such specimens from eastern Peru

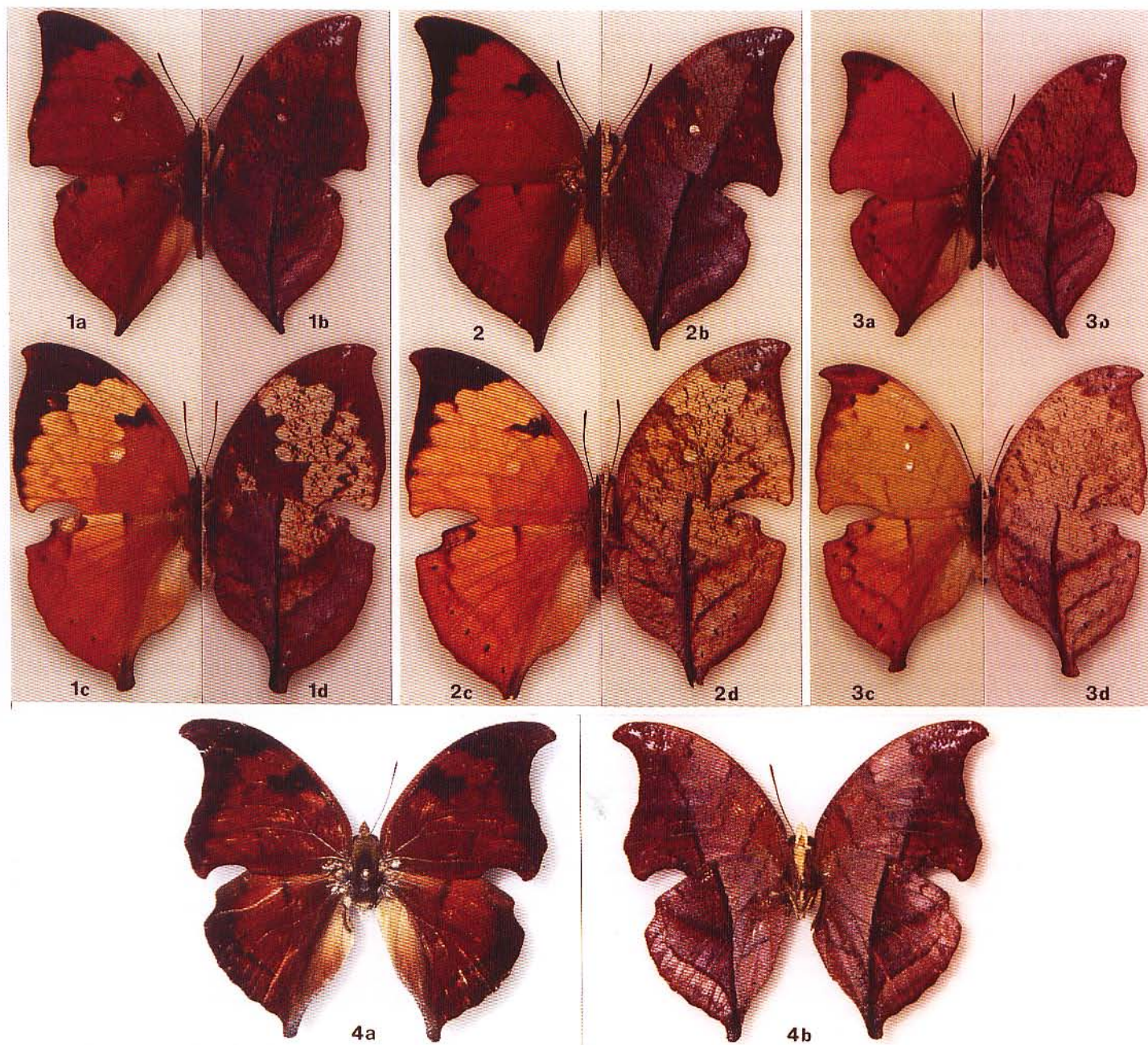


Fig. 1-4. Adults of *Zaretis* (a,c, dorsal surface; b,d, ventral surface; a,b, male; c,d, female; all in the USNM except HT *Z. pythagoras*): 1. *Zaretis itys*: a,b) Gatún, Canal Zone, Panama; c,d) Gatún, Canal Zone, Panama. 2. *Zaretis isidora*: a,b) Cerro Jefe, Panamá, Panama; c,d) 6 miles NW Gamboa, Canal Zone, Panama. 3. *Zaretis ellops*: a,b) Summit, Canal Zone, Panama; c,d) Farfán, Canal Zone, Panama. 4a,b. *Zaretis pythagoras* n. sp., holotype male.

(TL: Chanchamayo; ST, ZMHU). While east Andean specimens lack other characters typical of *Z. ellops*, suggesting that they represent variation in *Z. isidora*, specimens from middle elevation sites in western Ecuador have a similar wing shape to *Z. ellops*, and may represent that species. Many specimens with pale dorsal coloration from coastal areas of South America inland through southeastern Brazil to northern Paraguay are also phenotypically similar to, and may indeed be, *Z. ellops*. We have insufficient data to determine the exact taxonomic status of such specimens, and for the present treat the names *vulpina* Fruhstorfer, 1909 (TL: Paraguay; ST, BMNH) and *vulpecula* Fruhstorfer, 1909 (TL: Bahia, Brazil; ST, BMNH), both representing this pale phenotype, as synonymous with *Z. isidora*. The names *zethus* Westwood, 1850 (TL: Pará, Brazil; HT, BMNH), *russeus* Fruhstorfer, 1909 (TL: Colombia; ST,

BMNH) and *leopoldina* Fruhstorfer, 1909 (TL: Espírito Santo, Brazil; ST, BMNH) all apply to specimens phenotypically similar to typical *Z. isidora* and are considered synonymous with the latter name (Comstock, 1961; Vane-Wright, 1975). The female lectotype of the name *strigosus* Gmelin, 1790 (TL: unknown ["extra Europam"]; LT, NMI) probably originated from the Guianas (Vane-Wright, 1975), and we are grateful to Jim O'Connor (NMI) for confirming that it also represents *Z. isidora*.

***Zaretis pythagoras* Willmott & Hall, new sp.**

Fig. 4a,b; 5

Description.— MALE: forewing length 30mm. Forewing with falcate, rounded apex, distal margin slightly scalloped, tornal "hook" approximately

one third length of anal margin; hindwing "tail" at vein 2A short. **Dorsal surface:** forewing ground color dark red-brown overlaid with a dark purple sheen visible in oblique view; dark blackish brown postdiscal bar, concave at distal edge, extending from costal vein to vein M3; apical quarter dark brown, extending as slightly thinner, even dark border along distal margin, with basal edge slightly scalloped at each vein; very faint, jagged, dark brown postdiscal line basal of dark apical area from cell M3-M2 to anal margin. Hindwing ground color and purple sheen as on forewing; area posterior of vein Cu2, where wings fold against abdomen, very pale brown; sparse whitish scaling along distal half of anal margin to tip of tornal lobe; dark blackish brown postdiscal line extending in from costa to vein M2; apex dark blackish brown, extending indistinctly along distal margin and thinning towards tornus; dark blackish brown postdiscal line extending from vein 2A to merge with dark apical area at vein M2. **Ventral surface:** forewing ground color matt dark reddish brown, mottled with minute, sparse blackish dots; darker brown discal line extending through base of vein Cu2 from costa to anal margin; dark brown postdiscal line extending from middle of anal margin towards wing apex to vein M1, then displaced basally to form indistinct line perpendicular to costa in cells M2-M1 and M1-R5; area between latter postdiscal line and discal line shining purplish brown; distal of latter postdiscal line an indistinct, jagged dark brown line faintly visible in cells 2A-Cu2 and Cu2-Cu1; submarginal row of minute white dots, single in each cell except double in cell 2A-Cu2; sparse purplish brown scaling in submarginal area; mottled white scaling in apical area in cells M1-R5 and R5-R4. Hindwing ground color matt dark reddish brown mottled with minute sparse blackish dots; indistinct dark brown line over humeral vein extending into base of cell Rs-Sc+R1; prominent, very slightly concave, dark brown postdiscal line extending from middle of costa to tornus, with area basal of this line shining purplish brown; indistinct dark brown postdiscal line perpendicular to vein 3A and former postdiscal line in cells 3A-2A and 2A-Cu2; base of cell Cu1-M3 with dark blackish scaling extending in an indistinct dark line to apex, with area basal of this line shining purplish brown towards apex; concave, dark brown subapical line in cell Rs-Sc+R1; dark brown, slightly sigmoidal submarginal line extending from apex to tornus, with area between line and distal margin shining purplish brown, and area immediately basal with sparse, shining purplish brown scales; "tail" at tornus dark blackish brown with sparse pale scales; submarginal row of minute black dots with white scales at basal edge, single in each cell except double in cell 2A-Cu2. **Head:** ventral surface of labial palpi cream, dorsal surface dark reddish brown; eyes brown and bare; frons dark reddish brown; antennae brown with sparse white scales ventrally at base of each segment. **Body:** thorax and abdomen dark brown, except cream on ventral surface of thorax from head to base of hindlegs; forelegs dark brown; mid and hindlegs cream, except dorsal surface of femur dark brown. **Genitalia** (Fig. 5): typical of genus, with slight hooked point at tip of uncus, valvae with small dorsal projection.

FEMALE: unknown.

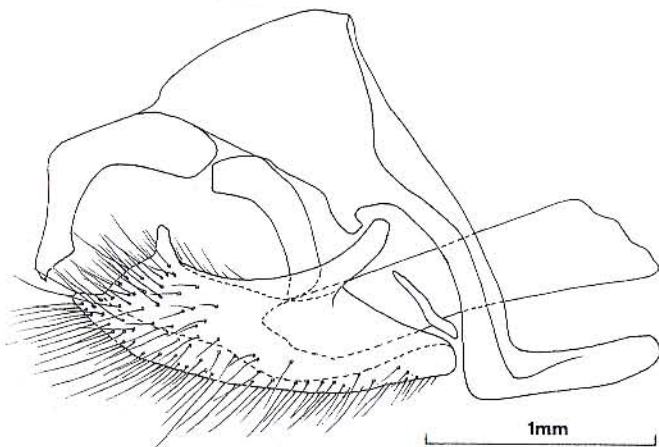


Fig. 5. *Zaretis pythagoras*, holotype male, genitalia (lateral view).

Types.—*Holotype* male: ECUADOR.—*Pichincha*: Tatuaza, Santo Domingo, 23 Aug 1973; in the BMNH(M).

Paratypes: ECUADOR.—*Pichincha*: 1 male: Río Tanti, Tinalandia, 750m, 2-3 Aug 1993 (K. Willmott & J. Hall); in the KWJH; 2 males: same data as preceding except 1 Jul 1993; in the KWJH; *Esmeraldas*: 1 male: Reserva

Biológica de Bilsa, nr. Quinindé, 600m, Jul 1999 (A. Young); to be deposited in the MECN; 1 male: Salidero, Feb-Mar 1901 (Fleming & Miketta); in the BMNH(R). COLOMBIA.—*Antioquia*: Valdivia, 1897 (Pratt); in the BMNH(M); *Risaralda*: 1 male: Santa Cecilia, 12 Oct 1981 (J. Salazar); in the JS; 1 male: Hcda. Bacori, Mpio. Pueblo Rico; in the MHNUC; *Chocó*: 1 male: Guarato, Dec 1980 (J. Salazar); in the JS.

Etymology.—Pythagoras, the renowned Greek mathematician and philosopher, was a student of Zaretis. The name is treated as a noun in apposition.

Diagnosis.—*Zaretis pythagoras* is most similar in wing pattern to *Z. isidora*, from which it differs in having a more falcate forewing apex, darker dorsal surface coloration with a purplish sheen when viewed obliquely and heavier black markings in the wing apices. These characters also distinguish it from *Z. ellops* and *Z. itys*, while the latter also has a less pronounced emargination at the forewing tornus and a longer hindwing tornal lobe. The male genitalia of the four species do not show any consistent differences.

Discussion.—*Zaretis pythagoras* n. sp. was figured by d'Abrera (1988:720) as a form of *Zaretis "itys itys"* (= *isidora*), but it is sympatric and synchronic with *Z. isidora* (we have collected series of males of each species in the same traps in western Ecuador) and the species is phenotypically very stable throughout its known range. Although *Z. pythagoras* has not yet been recorded flying at the same locality as *Z. itys*, the ranges of the two species do appear to overlap at the northern tip of the Cordillera Central in Colombia; there are specimens of typical *Z. itys* in the USNM from Victoria, Caldas, a locality on the eastern slope of the Cordillera Central that lies to the south of Valdivia, a locality for one of the paratypes of *Z. pythagoras*. Regardless of sympatry, the stability of the diagnostic characters of *Z. itys* (with the exception of the emargination of the forewing tornus) throughout its range from Mexico to Brazil, suggests that *Z. itys* and *Z. pythagoras* are not conspecific. *Zaretis itys* seems to be significantly rarer than *Z. isidora*, and this surely explains it being unknown from most of the range of *Z. pythagoras* to date.

Zaretis pythagoras is known only from wet rainforest habitats from 300-900m in western Colombia and northwestern Ecuador, the Chocó biogeographic region. A single male specimen in the BMNH from Río Topo (1300m) in eastern Ecuador was collected by a commercial dealer and is certainly mislabelled. All the specimens we have seen in western Ecuador were collected towards the end of the wet season, along forested rivers, where males were locally common in traps baited with rotting fish.

KEYS TO THE SPECIES OF ZARETIS

MALES

(some South American specimens of *Z. isidora* may key out to *Z. ellops* - see taxonomic review):

1. Basal area of dorsal forewing orange to reddish brown, hindwing distal margin smoothly rounded 2
 - Basal area of dorsal forewing pale silvery white/cream, hindwing distal margin produced slightly at vein M3 *callidryas*
- 2(1). Forewing apex slightly falcate; forewing distal margin very slightly scalloped between tornus and vein M3; dorsal forewing with trace of or no dark brown postdiscal line in cell 2A-Cu2; dorsal hindwing with dark brown submarginal line fading towards tornus and not extending to tornal lobe 3
 - Forewing apex strongly falcate; forewing distal margin heavily scalloped between tornus and vein M3; dorsal forewing with prominent dark brown postdiscal line in cell 2A-Cu2; dorsal hindwing with continuous, well-marked dark brown submarginal line extending to tornal lobe *syene*
- 3(2). Dorsal forewing predominantly orange 4
 - Dorsal forewing predominantly dark reddish brown 5

- 4(3). Forewing tornal emargination relatively pronounced (approximately 33% length of anal margin); hindwing tornal lobe at vein 2A relatively short 6
 - Forewing tornal emargination relatively small (less than 25% length of anal margin); hindwing tornal lobe at vein 2A relatively long *itys itys* (Fig. 1a,b)
- 5(3). Hindwing tornal lobe relatively long; forewing apex only slightly hooked at tip; dark apical and marginal markings on dorsal forewing blend into ground color; S.E. Brazil-Paraguay *itys itylus*
 - Hindwing tornal lobe relatively short; forewing apex strongly falcate; dark apical and marginal markings on dorsal forewing sharply defined from ground color; W. Colombia-W. Ecuador *pythagoras* (Fig. 4a,b)
- 6(4). Forewing apex orange or orange brown, slightly darker than remainder of wing; width along costa of darker apical area on dorsal forewing less than costal width of orange area between dark postdiscal bar and apical area; forewing distal margin relatively straight, apex beginning to curve above vein M1 *ellops* (Fig. 3a,b)
 - Forewing apex dark brown, strongly contrasting with remainder of wing; width along costa of darker apical area on dorsal forewing approximately equal to costal width of orange area between dark postdiscal bar and apical area; forewing distal margin smoothly concave, apex beginning to curve above vein M3 *isidora* (Fig. 2a,b)

FEMALES

(some South American specimens of *Z. isidora* may key out to *Z. ellops* - see taxonomic review; female of *Z. pythagoras* is unknown):

1. Hindwing with distal margin smoothly rounded 2
 - Hindwing with "tail" at vein M3 *callidryas*
- 2(1). Forewing apex slightly falcate; forewing distal margin very slightly scalloped between tornus and vein M3; dorsal forewing with trace or no dark brown postdiscal line in cell 2A-Cu2; dorsal hindwing with dark brown submarginal line fading towards tornus and not extending to tornal lobe 3
 - Forewing apex strongly falcate; forewing distal margin heavily scalloped between tornus and vein M3; dorsal forewing with prominent dark brown postdiscal line in cell 2A-Cu2; dorsal hindwing with continuous, well-marked dark brown submarginal line extending to tornal lobe *syene*
- 3(2). Ventral surface of forewing pale yellowish mottled with dark brown, except for apical third darker brown; ventral surface of hindwing anterior of discal cell with area basal of dark postdiscal line of similar color to area distal of line 4
 - Ventral surface of forewing with prominent, well-defined pale yellowish discal band, mottled with dark brown, apical and basal thirds almost uniform dark brown; ventral surface of hindwing anterior of discal cell with area basal of dark postdiscal line uniform dark brown, area distal of line pale yellowish mottled with dark brown *itys* (Fig. 1c,d)
- 4(3). Dorsal forewing basal area darker orange compared to yellowish postdiscal area; dorsal forewing apical area uniform dark blackish brown, width along costa of darker apical area greater than costal width of yellowish area between dark postdiscal bar and apical area; forewing apex relatively blunt *isidora* (Fig. 2c,d)
 - Dorsal forewing basal area of similar color compared to postdiscal area; dorsal forewing apical area brown, darker brown at basal edge, width along costa of darker apical area less than costal width of yellowish area between dark postdiscal bar and apical area; forewing apex relatively pointed *ellops* (Fig. 3c,d)

SYNONYMIC CHECKLIST

Zaretis Hübner, [1819]. *Verz. Bekannt. Schmett.* (4): 49. Type species by selection by Scudder (*Proc. Amer. Acad. Arts Sci.* 10: 289): *Papilio isidora* Cramer, 1779, *Util. Kapellen* 3(20): 72, pl. 235, figs. A, B.

NOTE: "-" denotes a subspecies, "--" a synonym, and "---" an unavailable name; "*" denotes a name for which we have not examined type material.

callidryas (R. Felder, 1869)* [Mexico-Panama]

--*opalina* (Godman & Salvin, 1884)

--*clara* (Staudinger, 1886)

ellops (Ménétrières, 1855)* [Mexico-N. W. Venezuela, Trinidad?; to W. Ecuador?]

--*anzuleta* Fruhstorfer, 1909

itys (Cramer, 1777) [Mexico-C. Colombia, Venezuela-Bolivia, Amazon basin, Guianas]

--*itylus* (Westwood, 1850) **stat. rev.** [S.E. Brazil, N. Paraguay]

--*pseuditylus* Fruhstorfer, 1909

isidora (Cramer, 1779) **stat. rev.** [Mexico-W. Ecuador, Venezuela-N. Argentina, Brazil, Guianas]

--*strigosus* (Gmelin, 1790)*

--*zethus* (Westwood, 1850)

--*cacica* (Staudinger, 1887)

--*leopoldina* Fruhstorfer, 1909

--*vulpina* Fruhstorfer, 1909

--*vulpecula* Fruhstorfer, 1909

--*russeus* Fruhstorfer, 1909

---*bisaltina* Fruhstorfer, 1909

---*foliacea* Fruhstorfer, 1909

---*strigosa* (Staudinger, 1887)* (preoccupied, Gmelin, 1790)

---*monops* Bryk, 1953

syene (Hewitson, 1856) [Colombia-Bolivia]

pythagoras Willmott & Hall, **n. sp.** [W. Colombia-W. Ecuador]

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LITERATURE CITED

- Ackery, P. R.
 1988. Host plants and classification: A review of nymphalid butterflies. *Biol. J. Linn. Soc.* (London), 33:95-203.
- Caldas, A.
 1996. Intraspecific variation in *Anaea ryphea* Cramer and *Anaea euryppyle* C. and R. Felder (Nymphalidae). *J. Res. Lepid.* (Beverly Hills), 32: 37-44.
- Comstock, W. P.
 1961. *Butterflies of the American Tropics. The Genus Anaea. Lepidoptera*

- Nymphalidae. A Study of the Species Heretofore Included in the Genera Anaea, Coenophlebia, Hypna, Polygrapha, Protogonius, Siderone and Zaretis.* New York: Amer. Mus. Nat. Hist. 214pp.
- Cramer, P.**
1777. *De Uitlandische Kapellen Voorkomende in de Drie Waereld-Deelen Asia, Africa en America. Papillons Exotiques des Trois Parties du Monde l'Asie, l'Afrique, et l'Amerique.* Amsterdam: S. J. Baalde; Utrecht: Barthelemy Wild and J. van Schoonhoven & Comp. 2(9/16): 1-151, pls. 97-192.
1779. *Ibid.* 3(17/22): 1-128, pls. 193-264.
- d'Abbrera, B. L.**
1988. *Butterflies of the Neotropical Region. Part V. Nymphalidae (Conc.) & Satyridae.* Victoria: Black Rock, Hill House. pp. 679-877.
- DeVries, P. J.**
1987. *The Butterflies of Costa Rica and their Natural History. Papilionidae, Pieridae, Nymphalidae.* Princeton: Princeton Univ. Pr. 327pp.
1988. Stratification of fruit-feeding nymphalid butterflies in a Costa Rican rainforest. *J. Res. Lepid.* (Beverly Hills), 26:98-108.
- DeVries, P. J., T. R. Walla, and H. F. Greene**
1999. Species diversity in spatial and temporal dimensions of fruit-feeding butterflies from two Ecuadorian rainforests. *Biol. J. Linn. Soc.* (London), 68:333-353.
- Felder, R.**
1869. Diagnosen neuer von dem k. k. Oberlieutenant H. v. Hedemann in Mexico in den Jahren 1865-1867 gesammelter Lepidopteren. *Verh. Kais.-König. Zool.-Bot. Ges. Wien*, 19:465-580.
- Fruhstorfer, H.**
1909. Neue *Zaretis*-Formen und Uebersicht der bekannten Rassen. *Ent. Zeit.* (Frankfurt), 23:166-168.
- Gmelin, P. F.**
1790. *Caroli a Linné. Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis. Editio Decima Tertia, Aucta, Reformata.* Lipsiae: Georg Emanuel Beer. 1(5):2225-3020.
- Godman, F. D., and O. S. Salvin**
1884. *Biologia Centrali-Americana. Insecta. Lepidoptera-Rhopalocera*, 1: 313-344. London: Dulau & Co., Bernard Quaritch.
- Kirby, W. F.**
1871. *A Synonymic Catalogue of Diurnal Lepidoptera.* London: John Van Voorst. 690pp.
- Ménétrières, E.**
1855. *Enumeratio Corporum Animalium Musei Imperialis Academiae Scientiarum Petropolitanae. Classis Insectorum. Ordo Lepidopterorum.* Petropoli, Eggers et Soc.; Lipsiae, Leop. Voss. 1:1-97+[2]pp.
- Muyshondt, A.**
1973. Notes on the life cycle and natural history of butterflies of El Salvador. II. *Anaea (Zaretis) itys* (Nymphalidae). *J. Lepid. Soc.* (Los Angeles), 27:294-302.
1974a. Notes on the life cycle and natural history of butterflies of El Salvador. III. *Anaea (Consul) fabius* (Nymphalidae). *J. Lepid. Soc.* (Los Angeles), 28:81-89.
1974b. Notes on the life cycle and natural history of butterflies of El Salvador. IV. *Anaea (Memphis) euryptyle confusa* (Nymphalidae). *J. Lepid. Soc.* (Los Angeles), 28:306-314.
1975a. Notes on the life cycle and natural history of butterflies of El Salvador. V. *Anaea (Memphis) morvus boisduvali* (Nymphalidae). *J. Lepid. Soc.* (Los Angeles), 29:32-39.
1975b. Notes on the life cycle and natural history of butterflies of El Salvador. VI. *Anaea (Memphis) pithyusa* (Nymphalidae). *J. Lepid. Soc.* (Los Angeles), 29:168-176.
1976. Notes on the life cycle and natural history of butterflies of El Salvador. VIII. *Archaeoprepona antimache gulina*, *Siderone marthesia*, *Zaretis callidryas* and *Consul electra* (Nymphalidae). *J. Lepid. Soc.* (Los Angeles), 30:159-168.
- Neild, A. F. E. N.**
1996. *The Butterflies of Venezuela. Part 1: Nymphalidae I (Limenitidinae, Apaturinae, Charaxinae). A Comprehensive Guide to the Identification of Adult Nymphalidae, Papilionidae and Pieridae.* London: Meridian Publ. 144pp.
- Röber, J. K. M.**
1916. 59. Gattung *Coenophlebia* Fldr. - 65. Gattung *Anaea* Hbn. In A. Seitz (ed.), *Der Gross-Schmetterlinge der Erde*, 5:577-592. Stuttgart: A. Kernen.
- Rydon, A. H. B.**
1971. The systematics of the Charaxidae (Lepidoptera, Nymphaloidea). *Ent. Rec. J. Var.* (London), 83:219-233, 283-287, 310-316, 336-341, 384-388.
- Staudinger, O.**
1887. I. Theil. *Exotische Tagfalter in Systematischer Reihenfolge mit Berücksichtigung neuer Art.* In O. Staudinger and E. Schatz, *Exotische Schmetterlinge*, 15:175-194. Fürth: G. Löwensohn.
- Vane-Wright, R. I.**
1975. The butterflies named by J. F. Gmelin (Lepidoptera: Rhopalocera). *Bull. Br. Mus. Nat. Hist. (Ent.)* (London), 32:17-64.
- Westwood, J. O.**
1850. In E. Doubleday, *The Genera of Diurnal Lepidoptera, Comprising their Generic Characters, a Notice of their Habits and Transformations, and a Catalogue of the Species of Each Genus*, 2:315-326. London: Longman, Brown, Green & Longmans.
- Willmott, K. R.**
in press. *Systematics, Biology and Biogeography of the genus Adelpha (Lepidoptera: Nymphalidae: Limenitidinae).* Gainesville: Scientific Publ.