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A REVISION OF THE GENUS *APHRISSA*

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The genus *Aphrissa* Butler, along with *Phæbis* Hübner, is usually found classified as *Callidryas* Boisduval.¹ *Aphrissa* was erected in 1873 to contain *statira* and its allies with that species as the genotype. It is clean-cut and related more closely to *Phæbis* than to any other known genus, and together with *Phæbis* forms a group among the rhodocerid pierids rather distantly related to the present existing genera, as has been indicated by Klots in his recent studies of the phylogeny of the Pieridæ. As surmised by Klots in his study of the male genitalia, the origin of *Aphrissa* is probably from a common ancestral form of the present *Phæbis agarithe* and *Aphrissa orbis*. This indication is further strengthened by the color pattern of the females, *orbis* approaching *agarithe* more closely than it does any other species of *Phæbis*. Since the pattern of *orbis* females is the most complete in the genus, we may take it as another indication of the primitive position of *orbis* in the genus.

In this study, I have relied upon the structure of the secondary male and female genitalic organs to a great degree, but have not neglected the usual characters of wing-shape and color pattern. Dr. August Busck of the National Museum suggested to me a method of dissecting and studying the softer parts of the female system and I present it here with his permission. After saponification of fats and the destruction of muscular tissues either by boiling gently for a minute or so in ten per cent caustic potash or by allowing the specimen to soak in such a solution at room temperature for twenty-four hours, it is washed free of excess caustic and the abdomen cleaned of soaps, scales, and the tracheal system by means of a camel's hair brush and very fine dissecting needles. The specimen is then soaked in water containing a few drops of aqueous "mercurochrome" (di-sodium hydro-oxymercury dibromo-fluorescein) until it is intensely dyed. From this solution the specimen is transferred to a slip of glass, a cut is made the full length of the dorsal surface and any residual tracheal material is removed; then the specimen is placed in a small quantity of full-strength glycerin until thoroughly impreg-

¹For a discussion of the generic names that have been used with this group of pierids and their availability, see Brown, F. M., 1929, 'A Revision of the Genus *Phæbis*,' Amer. Mus. Novit., No. 368, pp. 1-3, and Klots, A. B., 1929, Bull. Brooklyn Ent. Soc., XXIV, No. 4, pp. 203-214.

nated. Now, upon placing the dissection in a few drops of clear water upon a slide, the internal organs may easily be studied. The transfer from glycerin to water causes even the finest structures to swell and become fully distended. With a little practice and care excellent preparations may be made. If it is desirable, they can be washed free of glycerin, dehydrated in ethyl alcohol, cleared in xylol, and mounted in balsam. However, in mounts, only the "chitinous" parts will be well preserved. For study, I usually prepare several slides by this method and several to be mounted in lateral aspect in order that fuller knowledge of the structures and their relations may be gained.

The names used in connection with the male organs are according to the diagram on page two of my 'Revision of the Genus *Phæbis*.' The names of the organs of the female are strictly in accord with those used by Dr. Busck and Dr. Heinrich in their publications, in fact, were supplied by Dr. Busck.

The salient characters of the male armature may be briefly set forth as follows:

Valvæ roughly triangular; harpes insignificant; marginal process greatly modified and strongly chitinated; distal process prolonged; annellus rudimentary; juxtæ large and leaf-like. Uncus and tegumen simple; saccus simple and about as long as the combined uncus and tegumen; no dorsal lobe on the tegumen; scaphium absent; vinculum slender. *Ædœagus* stocky; two sharp, reversed bends toward the distal end which is bifurcate; cornuti² absent.

Species of the genus *Aphrissa* differ in the leaf-like structure of the juxtæ when compared with *Phæbis* in which they are filamentous.

KEY TO MALES BASED ON GENITALIA

1. Marginal process³ blade-like, serrate-edged. 2.
Marginal process not blade-like. 3.
2. Uncus trifurcate at tip. *hartonia*.
Uncus simple at tip. *statura* and varieties.
3. Marginal process a single bent rod. *orbis*.
Marginal process biramous, fluke-like. *godartiana*.

COLOR KEY TO IDENTIFICATION OF MALES⁴

1. Ground color of forewing slightly darker than that of hind wing. 2.
Ground color of forewing markedly darker than that of hind wing. 3.

¹In a letter dated March, 6, 1930, Dr. August Busck says: "I hope you will adhere to the nomenclature as given; this has not been published in full in English, so far as I know, but was adopted in translation, from continental workers."

²The cornuti described by me on the *ædœagus* of *Phæbis* are not true cornuti but merely thorns on the *ædœagus*. True cornuti are found on the penis proper.

³In my revision of *Phæbis* I erroneously called this harpes; Klots calls it a dorsal spine.

⁴For complete key to males of *Phæbis* and *Aphrissa*, see Brown, 1929, Amer. Mus. Novit., No. 368, p. 4.

2. Outer margin of forewing markedly concave, white chalky marginal area extending well into cell.....*hartonia*.
Outer margin of forewing straight or only very slightly concave, white chalky marginal area barely reaching cell.....*statira* and varieties, 4.
3. Forewing with orange spot on disc.....*orbis*.
Forewing with yellow spot on disc; hind wings pale tea-color.....*godartiana*.
4. Marginal and discal areas markedly differently color.....6.
Marginal and discal areas about the same color.....5.
5. General ground color white.....*schausi*, *etiolata*.
General ground color chrome-yellow.....*neleis* varieties.
General ground color tea-color.....*boisdewali* varieties.
6. Discal area greenish yellow.....*statira*.
Discal area orange.....*jada*.

The females of *Aphrissa* differ from those of *Phæbis* in having the terminal joint of the palpi long and well exposed.

KEY TO THE IDENTIFICATION OF THE FEMALES

1. External margin of forewing straight or nearly so.....*statira* and varieties.
External margin of forewing markedly concave.....2.
2. Dark marginal spots of hind wing above well developed.....3.
Dark marginal spots of hind wing small, not conspicuous.....*hartonia*.
3. Post-medial row of spots of forewing prominent, dark margin of apex ending abruptly.....*orbis*.
Post-medial row of spots of forewing lacking, dark margin of apex running well down the costa.....*godartiana*.

This key is not particularly good, its weakness being primarily in section 1. However, accurate locality data will practically fix the species name of any specimen, since the ranges of all except *statira* are quite restricted. The plates in Butler's monograph are good, but care must be taken to bear in mind that the orange color is exceedingly intense in many figures.

Unfortunately, I have been unable to make a dissection of the female of *hartonia* because my single specimen had its body destroyed by ants; so, since not all full species have been examined, I can not give a genitalic key for them.

The salient characters of the female genitalia are:

Ovipositor prominent, bi-lobed, ventral lobe twisted and the larger, clothed with spines of varying length; apophyses slender, of moderate length, two in number.

Ninth segment arched, reduced to a narrow bridge across the dorsal area expanding ventrally; the anterior margin curved around the anterior margin of the genital plate.

Genital plate robust, yoke-shaped, broad across the ventral region, tapering and open dorsally; the anterior margin folded back inwardly.

Ostium cover crudely circular, attached to the posterior margin of the ninth segment.

Ducta bursæ chitinized at least two-thirds of its length, a ribbon bent into a trough and connected with the bursæ by a membranous tubular portion. The ducta bullæ originates at the termination of the chitinous portion.

Bursa copulatrix large, ovoid and completely stippled with small chitinous (?) papulæ; a small spheric secondary bursa attached to the anterior end by a slender ducta; signum large and prominent, situated directly at the mouth of the bursa, heavily spined and slightly produced in the middle posteriorly and slightly concave anteriorly.

Ducta bullæ long, gradually expanding into bulla seminalis which enters the oviduct well back and just anterior to the duct leading to the pyriform receptaculum seminis. Cement glands similar, tapering, joined to and dorsal to oviduct about half-way between opening and junction with seminal ducts. The cement glands and receptaculum seminis terminate in long slender filaments. The egg-stocks extend anteriorly and practically fill the body-cavity.

Scent pouch large, ovoid, lying and opening ventral and anterior to the genital plate.

Aphrissa orbis Poey

MALE GENITALIA

Valvæ roughly triangular, the distal process stubby and not hooked; corona bulging, surmounted by a long sharply flexed chitinous rod of uniform diameter tapering abruptly to a point; harpes represented merely by a long thickened fold of chitin, slightly curved and with few spines; annellus and juxtæ longer than in *statura*, juxtæ less distinctly separated at their junction with the annellus. Uncus, vinculum, etc., much as in *statura*. *Ædœagus*¹ slender, slightly tapering distally with an almost imperceptible reversed curve at that end and terminating in a slender but blunt spur.

FEMALE GENITALIA

It is far more difficult to express verbally the subtle forms and differences found in the female armature than those found in the males. The differences are just as marked but the complexity of the organs almost defies expression. I shall confine myself merely to indicating the outstanding features that may assist in identification; the figures tell the story completely and clearly.

Apophyses short and stubby, about two-thirds as long as the ovipositor. Ventral lobe of the ovipositor much larger than the dorsal lobe. Ninth segment simple and sturdy. The folded anterior margin of the genital plate is rather complexly ridged. There is a marked acute ridge paralleling the margin in its entirety with a spur originating at the angular break in the mid-region that sweeps backward and upward. A less prominent ridge parallels the dorsal portion of the marginal ridge. Two parallel ridges originating on the external portion of the fold of the plate curve on to the interior of the fold and run toward the scar which is in the form of a truncate cone. This scar may possibly be the vestige of a spiracle on the eighth segment. The ostium cover is more or less quadrate in shape, not subcordate as in *statura*. The

¹Description of *ædœagus* from a dissection by Mr. A. B. Klots.

lunulate, pouch-like folds on the seventh abdominal segment, to receive the antero-ventral corners of the genital plate, are narrow, long, and slightly curved.

Of all the strictly Antillean species this insect has the widest range. It is found on Cuba, Isle of Pines, and Hispaniola. The male is the most easily distinguished of any in this genus, the bright orange orb on the disk of the forewings giving the species its name. The females are marked like any other female *Aphrissa* but are vivid orange.

***Aphrissa godartiana* Swainson**

MALE GENITALIA

Valvæ roughly triangular with the distal process greatly extended, straight and slender, with a slightly hooked tip; corona broken at its mid-point by a deep cleft and the chitinous marginal process characteristic of the genus, the marginal process resembling the flukes of a whale's tail, the tip of the anterior division occasionally toothed; harpes obscure much as in *statira*; annellus and juxtæ as in *statira* but more delicate. Uncus simple and moderately heavy in structure, the tip not blade-like but trifurcate, tegumen quite setous. *Ædœagus* heavy and curved as in *statira* but less sharply so; the distal spur is very large and heavy.

FEMALE GENITALIA¹

Apophyses long and slender, one and one-half to twice as long as ovipositor, lobes of ovipositor about the same size. Ninth segment simple and broad, differing from all other members of the genus and approaching the *Phæbis* type. Genital plate simple as in *statira*, the scar a truncate cone. Ostium cover more or less cordate as in *statira*. The lunulate, pouch-like folds on the seventh segment narrow, short and slightly curved. The chitinous portion of the ducta bursæ is about one-half the total length, less than in any other species in the genus.

A. godartiana is another strictly Antillean species of this genus and is found only on the islands of Hispaniola and Porto Rico. It is fairly common but by no means as abundant as *A. statira neleis*. The male resembles *orbis* in color-distribution but the area so vividly orange in *orbis* is lemon-yellow in *godartiana*.

***Aphrissa hartonia* Butler**

MALE GENITALIA

Valvæ subtriangular; dorsal margin irregular and adorned with a spiny, chitinous, foot-shaped marginal process; outer margin smoothly undulating, terminating in a slender prolonged distal process; annellus short, terminating in two leaf-like juxtæ; harpes an inconspicuous lunulate fold. Uncus slender, sharply curved, almost as long as vinculum. *Ædœagus* moderately stout with a slight reversed curve toward the distal end which is armed with a short blunt spur.

¹A single female specimen of this species was received and dissected too late to include a drawing of the dissection.

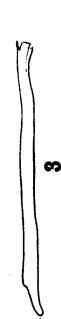
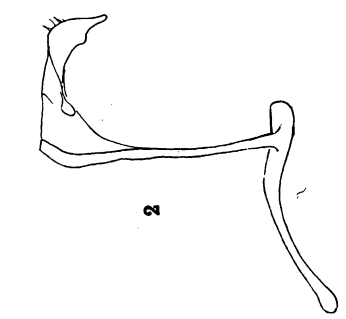
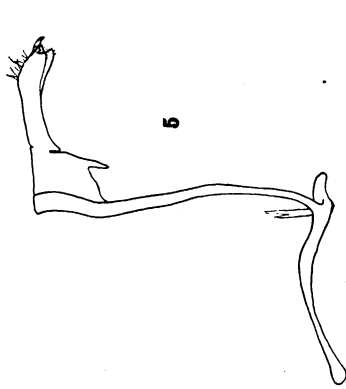
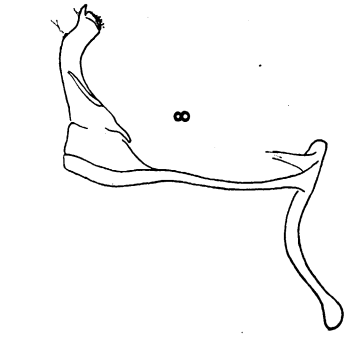
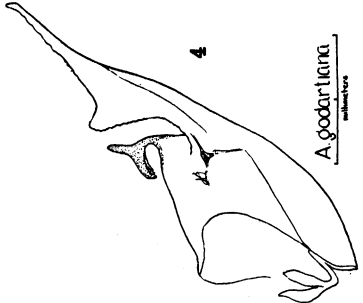
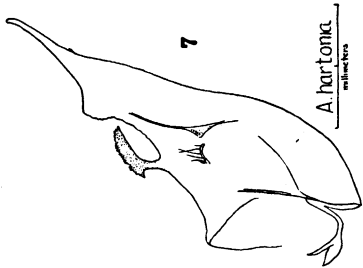


Fig. 1. Valva of *Amphrissa orbis*.
 Fig. 2. Valva of *A. godartiana*.
 Fig. 3. Valva of *A. hartonia*.
 Fig. 4. Uncus, etc., of *Amphrissa orbis*.
 Fig. 5. Uncus, etc., of *A. godartiana*.
 Fig. 6. Uncus, etc., of *A. hartonia*.
 Fig. 7. Edeagus of *A. orbis*.
 Fig. 8. Edeagus of *A. godartiana*.
 Fig. 9. Edeagus of *A. hartonia*.

This species superficially resembles *statira* which it approaches structurally more closely than any other. It is confined to the island of Jamaica where it is apparently local in distribution. The only specimens of which I actually know are in the British Museum and in my own collection.¹ Both Dr. Schaus, of the National Museum, and Mr. Watson, of The American Museum of Natural History, failed to get it when collecting there. Mr. N. D. Riley has told me that Butler's type material is the only lot in the British Museum. The "*statira*" of Kaye's Jamaican list is *hartonia*.

***Aphrissa statira* Cramer and forms**

MALE GENITALIA

Valvæ roughly triangular, dorsal margin irregular and adorned with a subtriangular chitinous comb-like marginal process, usually with a small secondary process situated slightly anterior to it, both originating from the inner surface of the valvæ; the outer margin of the valvæ terminating dorsally in an incurved spur heavily chitinized at the tip, the inner margin of this process is very irregular; the top of the comb either convex or concave, irregularly toothed. Annellus very short, juxtæ broad, long and leaf-like; surface of the valvæ covered with long bristly hairs, shortest on the caudal margin. Uncus simple, lightly chitinized, terminating in a single incurved blade-like tip, armed with a few delicate hair-like spines. Vinculum moderately long and slender. Saccus about as long as vinculum, slender. *Ædoeagus* heavy, with a reverse curve at the distal end; tip armed with a very short spur directed parallel to the length.

A series of about thirty dissections shows no consistent variation among the following named forms: *statira*, *neleis*, *wallacei*, *boisduwali*, *etiolata*, *jada*, *felderi*, *butleri*. The marginal process shows the most variation but this is not consistent for any form.

FEMALE GENITALIA

The apophyses in all forms of *statira* are long and slender, about as long as the ovipositor itself. The ninth segment and the genital plate are both simple. The anterior margin of the genital plate usually shows dorsally a slight twist and fold. The scar on the plate is rather simple and in the form of a hollow truncate cone and medially situated. The lunulate folds on the seventh abdominal segment are small and sharply curved.

The specimen figured is form *neleis* from Cuba. There is some variation, as might be expected, but it is not consistent for any form or geographic range.

An analysis of approximately three hundred and fifty specimens from over the entire range in the collections of The American Museum of Natural History, the Museum of Comparative Zoölogy, the National

¹One male now deposited at the National Museum and several males and a female at the American Museum.

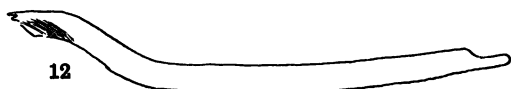
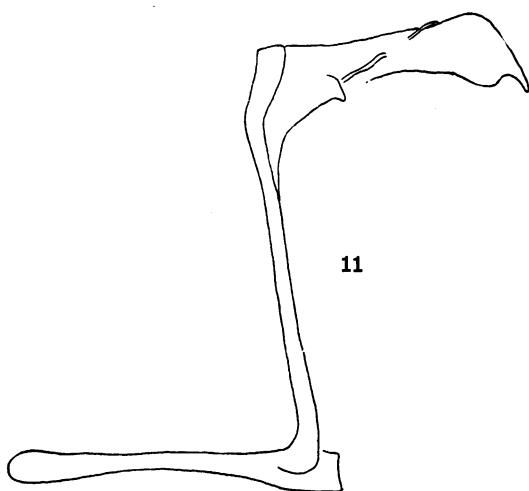
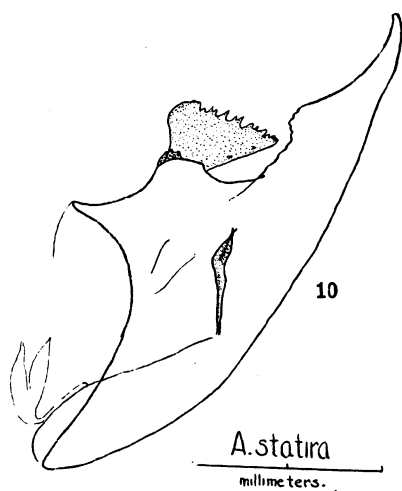


Fig. 10. Valva of *Amphrissa statira*.

Fig. 11. Uncus, etc., of *A. statira*.

Fig. 12. Ædœagus of *A. statira*.

Museum, Cornell University, and the author, encompassing all of the named forms and varieties, is here summarized.

A. statira and its forms are found throughout the American tropics and the bordering temperate regions, the nymotypical form is common in northern South America completely across the continent and everywhere except in the decidedly temperate and colder mountain ranges; of this form, *evadne* Godart and female form *pseudomas* Giacomelli, of which I have a metatype, are synonyms. As in most yellow pierids, there are albinic female forms, *fabia* Fabricius (*hyperici* Sepp) may be applied to the white females from this region. Recently Forbes and Avinoff have named white males. Forbes' specimens are from South America and Avinoff's from Guatemala. It is of interest that in these forms the patches of sex-scales in the overlapping areas of the wings are reduced to a few scales or are totally absent. This absence of scales is found, but very rarely, in otherwise normal *statira* and in the totally yellow form *wallacei* Felder from South America. I cannot agree with Forbes in believing that it is a distinct species; everything points otherwise. I have seen a complete series showing every intergrade from normal scale-patches to none, and the genitalia of the males, which differ markedly in the species of this genus, are identical in the case of *etiolata* Forbes¹ and *statira*. Forbes' specimens show considerable yellow-green coloring at the base of the wings, and, since he emphasized the lack of sex-patches in his description, his name should be applied to those specimens that totally lack the sex-scales, regardless of coloration. The name *schausi* Avinoff I apply to the pure white males. Poey has named the *statira*-like specimens from Cuba *zulema*.

There occurs an interesting variation in each of the three color forms found with the typical form. Specimens taken in the northern or Gulf region either lack or have only a few black scales representing the apical margin of the forewing, while those from southern Central America and South America have marked black apical margins. The name *boisduvali* Felder applies to the tea-colored form from South America with the black marginal marking. The specimens of this color from the northern part of the range have not been named.

The form in which the yellow extends to the margin has been usually called *neleis* Boisduval; this name must be restricted to the West Indian race as it was described from Cuban specimens which in the female differ markedly from the mainland specimens. The typical *neleis* females have

¹Four specimens totally lacking the sex-patches have been examined: one of these was marked by Forbes as *etiolata* and is mentioned in the original description; two others are identical with it; the fourth is typically *statira* as to color but totally lacks the patches.

the black apical margin broken into patches and have a marked sub-marginal row of spots extending from the apex about half-way down the wings; beneath, the markings are more intense than in the mainland form. However, males from Cuba are colored more like those from the mainland, with the underside of the hind wings tea-color, while in the Haitian males it is bright yellow. The name *wallacei* Felder is reserved for the South American yellow form which differs from the Gulf region form, *butleri* Scudder, in the manner noted above. Neumoegen described a form of the *neleis* type from Florida and called it *floridensis*. Whether this name should stand or sink to *butleri* Scudder or *neleis* Boisduval, I am not sure, but I feel that it may stand for a Florida race. It is materially larger and much less intensely marked than any other form. I have seen some twelve or fifteen specimens and they are consistent in this respect. The females that I have seen correspond with the female type and are albinic. I know it from only two localities in Florida; Indian River (the type material), and a small lot from Fort Worth in the A. T. Slosson collection at The American Museum of Natural History.

The third color form is much more rare in collections. In it the predominating color of the wings is decidedly orange, though not so vivid as both Butler's and Sietz' figures would indicate. The margined South American form is *jaresia* Butler and the marginless northern race is *jada* Butler, of which I have seen and dissected but a single male from the National Museum collection.

I have come to the conclusion that all of the varieties are valid and that the names listed below are necessary to recognize properly the facts as they appear to be. It is to be expected that this most recent development of these very recently evolved genera (*Phæbis* and *Aphrissa*) of rhodocerotid pierids should show much diversification under varying environmental conditions. Doubtless, as time passes, many of these will ultimately develop into full-fledged species.

***Aphrissa statira neleis* female form *poeysæ*, new form**

ABOVE.—Pure white with a very faint flush of pale yellow at the base of the hind wings. Marginal brown markings of the forewings reduced to a minimum. Discal spot on the forewings of normal size and color. Hind wings immaculate.

BELOW.—Faintly flushed with pale lemon-yellow. Maculation of both wings faint and of pink-brown scales; discal spots without any silver scaling.

EXPANSE.—53 mm.

HOLOTYPE.—Female; Cuba (Wm. Schaus); in United States National Museum, Washington, D. C.

TABLE OF DESCRIBED FORMS OF *Aphrissa statira*

Race	<i>A. s. statira</i>	<i>A. s. jada</i>	<i>A. s. floridensis</i>	<i>A. s. neleis</i>
Range	S. and C. America	North America	Florida	West Indies
Typical white and lemon-yellow form	<i>statira</i> Cramer	(nameless)		f. <i>zuelma</i> Poey
	f ♀ . <i>fabia</i> Fabricius	f ♀ . <i>stalba</i> Brown		f ♀ . <i>poeyæ</i> Brown
	ab ♂ . <i>etiolata</i> Forbes	ab ♂ <i>schausi</i> Avinoff		
Yellow form	f. <i>wallacei</i> Felder	f. <i>butleri</i> Scudder	<i>floridensis</i> Neumoegen	<i>neleis</i> Boisduval
Buff form	f. <i>boisduvali</i> Felder	(nameless)		
Orange form	f. <i>jaresia</i> Butler	<i>jada</i> Butler		

***Aphrissa statira jada* female form *stalba*, new form**

ABOVE.—White, sometimes with a slight greenish cast; some buff at the base of the hind wings. Forewings with a black-brown margin at the apex and continuing along the outer margin as a row of spots at the terminal of the nervures; these spots may be contiguous toward the apex, occasionally represented by only a few scales. Discal spot on the veins between M and M₂. Hind wings immaculate.

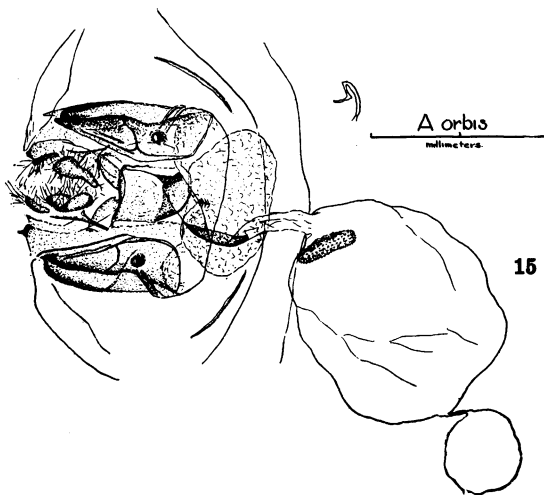
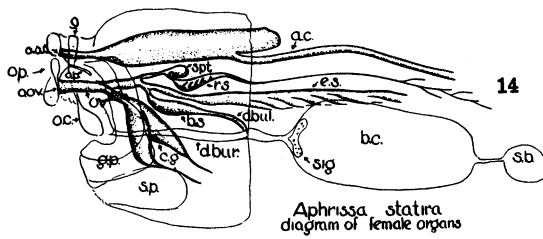
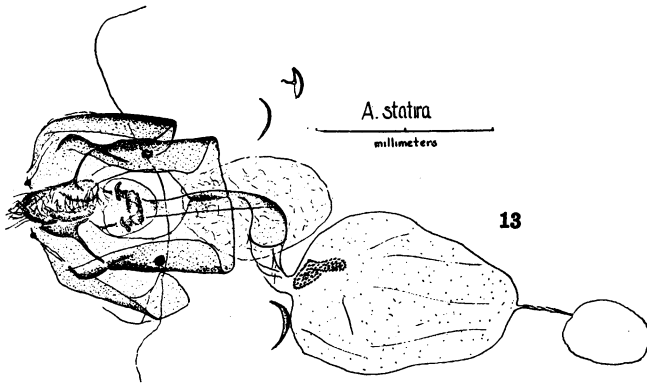
BELOW.—Pearly white in anal area of forewings and buff to light cadmium-yellow at the base of both wings. Normal maculation but reduced to a few scales in each spot. Discal spot and maculation of apex of forewing prominent.

HOLOTYPE.—Female; Truxillo district, Honduras; collected by F. C. Nicholas; No. 18314, in collection of American Museum of Natural History.

The major portion of the material used for this revision is in The American Museum of Natural History and with my own collection [now deposited there] constitutes about nine-tenths of all the specimens examined. I wish to express my thanks to Mr. Frank E. Watson of that institution for many hours of his time and kind counsel.

ABBREVIATIONS USED IN DIAGRAM OF FEMALE ORGANS

a.c.	—alimentary canal	o.a.c.	—opening of alimentary canal
ap	—apophysis	o.c.	—ostium cover
b.c.	—bursa copulatrix	o.ov.	—opening of oviduct
b.s.	—bulla seminalis	op.	—ovipositor
c.g.	—cement glands ("glandulæ sebaceæ") (actually dorsal to oviduct)	ov.	—oviduct
d.bul.	—ducta bullæ	r.s.	—receptaculum seminis
d.bur.	—ducta bursæ	s.b.	—secondary bursa ("accessory organ")
e.s.	—egg-stocks	s.p.	—scent pouch
g.p.	—genital plate	spt.	—lobe near the mouth of the receptaculum
		9	—ninth segment ("collar")



- Fig. 13. Genital armature of female *Amphrissa statira* (dissected dorsal view).
- Fig. 14. Genital armature of female *A. statira* (diagrammatic lateral view).
- Fig. 15. Genital armature of female *A. orbis* (dissected dorsal view).

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- bulleri* (*statira*) SCUDDER, 1874, Proc. Bost. Soc. Nat. Hist., XVII, p. 208.
- etiolata* (*statira*) FORBES, 1927, Ann. Ent. Soc. Amer., XX, p. 479.
- evadne* (*statira*) GODART, 1819,² 'Enc. Méth.,' IX, p. 98, No. 28.
- fabia* (*statira*) FABRICIUS, 1798, 'Ent. Syst.,' Suppl., p. 426.
- floridensis* (*statira*) NEUMOEGEN, 1891, Can. Ent., XXIII, p. 122.
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- hartonia* BUTLER, 1870, Trans. Ent. Soc. Lond., part 1, p. 10.
- hyperici* (*statira*) SEPP, 1848, 'Surinam. Vlinders,' I, p. 45, Pl. xix.
- jada* (*statira*) BUTLER, 1870, Trans. Ent. Soc. Lond., p. 11.
- jaresia* (*statira*) BUTLER, 1871, Trans. Ent. Soc. Lond., p. 171.
- neleis* (*statira*) BOISDUVAL, 1836, 'Spec. Gen.,' p. 630.
- orbis* POEY, 1832, 'Cent. Léop. Cuba,' Dec. 1, p. [1], Pl. [1].
- poeyæ* (*statira*), new form.
- pseudomas* (*statira*) GIACOMELLI, 1911, An. Soc. Cien. Argentina, LXXII, p. 21.
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- stalba* (*statira*), new form.
- statira* CRAMER, 1779, 'Pap. Exot.,' II, Pl. cxx, figs. C, D.
- wallacei* (*statira*) FELDER, 1862, Wein. Ent. Mon., VI, p. 6.
- zulema* (*statira*) POEY, 1851, 'Mem. Sobr. Hist. Nat. Cuba,' I, p. 198.

¹The names in brackets refer to the species under which the form is discussed.

²This is the usual date given for the 'Enc. Méth.,' IX, and is probably satisfactory for this page reference. See Riley, N. D., Trans. Ent. Soc. Lond., 1926, p. 231.