

W. A. Lamborn's Breeding Experiments upon *Acræa encedon* (Linn.), in the Lagos District of West Africa, 1910-1912. By EDWARD B. POULTON, D.Sc., F.R.S., Pres.L.S.

[Read 2nd April, 1914.]

THE typical form of *Acræa encedon* is a tawny butterfly with a black, white-barred tip to the fore wing. The pattern thus closely resembles that of the type form of *Danaïda chrysippus*, Linn. *A. encedon* is polymorphic in both sexes, and the following forms are referred to in the present memoir :—

Infuscata, Staud., "the tawny areas of the typical forms are replaced by smoky brown" (p. 112*). This form is transitional in one direction into dark-grey butterflies without any tawny tint, and in the other into dark forms of *encedon*.

Alcippina, Auriv. "The h.-w. has a white central suffusion of varying extent" (p. 212), thus reproducing the pattern of the *alcippus*, Cram., form of *chrysippus* and of transitional varieties between *alcippus* and *chrysippus*.

Daira, Godm. & Salv., "the black of apical half of f.-w. and the white subapical band are absent. In some cases the subapical band may be traced as a slightly paler area on the ground-colour. All the black markings much reduced" (p. 212).

Commixta, Poulton †. This form is a combination of the two preceding, having the central white patch on the hind wing of *alcippina*, and a fore wing approaching that of *daira* in the tint of the subapical bar, which is tawny like the ground-colour. The pattern thus resembles the *albinus*, Lanz, form of *chrysippus*, but the mimetic relationship is not suggested because of the rarity of the model and its restriction to the parts of Africa where *dorippus* is abundant.

Lycia, Fabr. "The ground-colour of both wings is white, the black markings being as in the typical form" (p. 112). "Examples of the *lycia* form may have the ground-colour pale creamy yellow" (p. 213), and are thus transitional towards the *sganzini* form.

Sganzini, Boisd. "The tawny areas of the typical form are replaced by a dusky yellowish colour" (p. 212).

* This description and those of the other forms except *commixta* are quoted from H. Eltringham's great work, "Monograph of the African Species of the Genus *Acræa*," Trans. Ent. Soc. Lond. 1912, pt. i.

† Trans. Ent. Soc. Lond. 1913, p. 409.

*The Geographical Distribution and Mimetic Associations of the forms of *Acræa encedon*.*

The account contained in the following four paragraphs was drawn up by the present writer in 1907 but has not hitherto been published.

Acræa encedon, like the female of *Hypolimnasia misippus* (Linn.), presents three forms mimicking the three forms of *Danaida chrysippus* (Linn.), but, being without the extraordinary powers of flight possessed by the Nymphaline co-mimic, their geographical coincidence with the forms of the model is closer. This superiority is particularly interesting in relation to Müllerian mimicry when we remember that the *Acræinæ* are a highly protected group.

In South Africa the predominant form is *encedon*, resembling the predominant *chrysippus*. Dr. Dixey and Dr. Longstaff, from their experience of it in this part of the Region, state that *encedon* was "so successful in its mimicry of *L. chrysippus* as at first to make one of us believe it to be that species".* There is also a black and white form, *lycia*, F., and, even more commonly, a black and yellowish form (*sganzini*, Boisd.) which occur not only here but throughout the East Coast range of *encedon*. Mr. Marshall has recorded that *lycia*, when upon the wing, shows a decided resemblance to the whiter forms of *Acræa esebria*, Hew.†

As we pass northwards, forms with white hind wings (*alcippina*, Auriv.) and forms in which the black and white tip to the fore wing is evanescent (*daira*, Godm. & Salv.), both rare in the South, begin to increase in numbers, intermixed with the type *encedon*. Finally, in British East Africa, all three forms occur commonly, *daira* and *encedon* being most abundant, just as are the corresponding models—the *dorippus*, Klug, and type forms of *D. chrysippus*.

In the West, all forms except *sganzini* occur, but the late Mr. Herbert Druce, F.L.S., received ‡ from a locality in Sierra Leone several specimens of *alcippina*, which seem to show that the *alcippus* form of *D. chrysippus* has here at least produced some effect as a model. The specimens in Mr. Druce's series are not only all *alcippina* but unusually pronounced examples of this form, and beautiful mimics of the tropical West African form of *D. chrysippus*.

H. Eltringham remarks of the distribution of *encedon*: "None of the forms seems to be specially characteristic of any particular locality, though the *alcippina* form seems to attain its maximum development in West Africa" (*l. c.* p. 213). "The *lycia*, *alcippina*, and *infuscata* forms are more numerous in West African localities than elsewhere, though they seem liable to occur elsewhere" (p. 211).

* Trans. Ent. Soc. Lond. 1907, p. 318; also p. 328. See also p. 321 for the converse mistake, viz. of model for mimic.

† Trans. Ent. Soc. Lond. 1902, p. 479.

‡ Trans. Ent. Soc. Lond. 1902, p. 480. The *daira* form is *extremely* rare in the West.

Since the appearance of Eltringham's monograph much evidence has accumulated proving beyond doubt the strong development of the white-hind-winged *alcippina* form in the interior of Sierra Leone, from which area it is probably continuous into N. Nigeria. The following list of examples of *alcippina* and its model *alcippus*, recently received by the British Museum of Natural History, has been kindly prepared by Mr. N. D. Riley, F.E.S. The extraordinary predominance of the female *alcippina* over the male—50 to 5—strongly suggests the prevalence of all-female families such as Mr. W. A. Lamborn finds in the Lagos district.

Dated examples of Danaida chrysippus, f. alcippus, and Acræa encedon, f. alcippina in the British Museum, from Sierra Leone and N. Nigeria.

I.—SIERRA LEONE. Collected by J. J. Simpson.

		<i>D. chrysippus,</i> <i>f. alcippus.</i>		<i>A. encedon,</i> <i>f. alcippina.</i>	
Kambia.	24. iii. 1912.	14 ♂	—	—	—
Bassia.	25. iii. „	5 ♂	—	—	—
Kokona.	26. iii. „	5 ♂	—	—	—
Yana.	30. iii. „	1 ♂	—	—	—
Laminaia	23-25. iv. „	1 ♂	—	—	—
Port Lokko.	9-11. v. „	1 ♂	1 ♀	—	—
Batkam.	15-18. v. „	8 ♂	5 ♀	—	—
Kafogo.	23. v. „	5 ♂	2 ♀	—	1 ♀
Kaballa.	27. v. „	4 ♂	—	—	1 ♀
Benikoro.	30. v. „	—	—	—	1 ♀
Falaba.	1. vi. „	—	1 ♀	—	1 ♀
Tirikoro.	15-17. vi. „	—	—	1 ♂	1 ♀
Keneura.	20. vi. „	—	—	—	1 ♀
Bumbanya.	22. vi. „	1 ♂	—	—	—
Johanna.	28. vi. „	1 ♂	—	—	—
Giema.	6. viii. „	—	—	1 ♂	—
Jowati.	19. viii. „	—	—	—	1 ♀
Gigbema.	22. viii. „	—	—	1 ♂	38 ♀
Bo.	1. ix. „	4 ♂	3 ♀	—	—
Mafwe.	7. x. „	5 ♂	—	—	2 ♀

II.—N. NIGERIA. Collected by G. T. Fox.

Panyam.	2. vi. 1910.	—	2 ♀	—	—
(Banchi Prov.).	3. vi. „	—	—	1 ♂	1 ♀
	4. vi. „	—	1 ♀	1 ♂	1 ♀
	31. vii. „	—	—	—	1 ♀
	13. viii. „	1 ♂	—	—	—
Totals		56 ♂	15 ♀	5 ♂	50 ♀

In addition to the above, the British Museum Collection contains a single undated female *alcippina* from Panguma, N. Nigeria, another undated female from 70 miles up the river from Freetown, Sierra Leone, and an undated male from Liberia.

The predominant development of *alcippina* in Sierra Leone will be rendered evident by the following list of the other West African forms of *encedon* in the British Museum, also prepared by Mr. N. D. Riley, together with all West African forms, including *alcippina*, in the Hope Department, Oxford, and the Tring Zoological Museum :—

LOCALITIES AND MUSEUMS.									
I. British Museum. II. Hope Department. ¹ III. Tring Museum.		<i>encedon.</i>	<i>encedon infuscata.</i>	<i>infuscata.</i>	<i>alcippina.</i>	<i>daira.</i>	<i>commieta.</i>	<i>lycia.</i>	
Gambia River ...	III.							1 ♂	2 ♀
Sierra Leone	I.			1 ♂ ²			2 ♂ 2 ♀	4 ♀	
	II.				1 ♀ ³			1 ♂	1 ♀
	III.				1 ♀			3 ♀	
Gold Coast	I.							1 ♂	
Nigeria, N. & S....	I.			2 ♂ 20 ♀		1 ♂ ⁴	3 ♂ 1 ♀	5 ♂	17 ♀
	II ⁵ .		1 ♂	7 ♂ 2 ♀ ⁶	1 ♂ ⁷		1 ♂ 1 ♀	7 ♂ ⁸	5 ♀
	III.							2 ♀	
Cameroons	I.	1 ♂		1 ♀					
	III.				1 ♀				
Congo State	I.	2 ♀ ⁹							
	II.		2 ♀	2 ♂ ¹⁰				2 ♂	
	III.		2 ♂ 7 ♀		1 ♀			1 ♂	1 ♀
Angola	I.	1 ♀						1 ♀	
	II.		1 ♀						
	III.		21 ♂ ¹¹ 6 ♀					7 ♂	3 ♀
Totals		1 ♂ 3 ♀	24 ♂ 16 ♀	12 ♂ 23 ♀	1 ♂ 4 ♀	1 ♂	6 ♂ 4 ♀	25 ♂	39 ♀

¹ Including a few specimens from the collections of M. Charles Oberthür and of the Luxembourg Museum, which I have had the opportunity of studying at Oxford.

² Transitional towards *lycia*.

³ Port Lokkoh: 1912: Mrs. Addison.

⁴ The type of the form, from Lower Niger.

⁵ Not including the captured parents of any of the families tabulated on pp. 407, 409–414.

⁶ The ♀ ♀ very dark: one ♂ with a fulvous f.-w. bar.

⁷ Ibadan, S. Nigeria: May 1910: Rev. Lake S. Noble.

⁸ Included in the 7 ♂ ♂ is an injured specimen of which the sex is not quite certain.

⁹ One ♀ is the type of "*fulva*," Doubl., Westw., and Hew.

¹⁰ Very dark specimens

¹¹ One ♂ transitional towards *alcippina*.

The relative proportion of males and females suggests the prevalence of all-female families, especially in Nigeria. The figures from Old Calabar, included in the Nigerian totals from the British Museum (I.), are remarkable :—18 ♀ *infuscata*, 1 ♀ *commixta*, 14 ♀ *lycia*.

The two lists confirm Eltringham's conclusions as to the West African forms quoted on p. 392. The second list also shows the excessive rarity of *daira*, the predominance of *lycia*, and, next to it, *infuscata* and *infuscata-encedon*, followed by *commixta*. The two lists together show that *alcippina* is rare except in Sierra Leone.

The nearest approach to the proportion of the *encedon* forms on the West coast, S. of Sierra Leone, is to be found in Madagascar, where the pale form *sganzini* is predominant like the still paler *lycia*, and a dark dull form of *encedon* represents *infuscata*. The Madagascan *sganzini* are transitional into a cream-coloured *lycia*. I have not seen any form from Madagascar except those above-named and intermediates between them.

In the Hope Department there are 15 ♂ and 3 ♀ of *sganzini* (1 ♂ might be called a cream-coloured *lycia*), and 6 ♂ 1 ♀ of *encedon-infuscata* (1 ♂ showing transition towards *sganzini*); in the Tring Museum 9 ♂ and 1 ♀ of *sganzini*; in the British Museum 4 ♂ and 1 ♀ of *sganzini*; in the Luxembourg Museum 1 ♂ and 1 ♀ of *sganzini* and 1 ♂ transitional between *sganzini* and *infuscata*.

On the opposite East coast of the continent the pale forms are chiefly *sganzini*, like Madagascar, but their proportion is very different, being much less than that of *encedon*. Thus there are 15 *encedon* and 4 *sganzini* from Natal in the Hope Department. The *lycia* of the West is replaced by the yellower *sganzini*, somewhere about the Rift Valley, in British East Africa.

The much larger amount of material now available supports the conclusions, arrived at in 1907 (p. 392), as to the geographical relationship between certain forms of *encedon* and those of *D. chrysippus*. The form *daira* is common where *dorippus* is common, and becomes rare where *dorippus* is rare or wanting: the typical, brightly coloured *encedon* is predominant where the type form of *chrysippus* prevails: the only locality where *alcippina* is abundant is part of the area over which *alcippus* displaces every other form of *D. chrysippus*. Mimicry occurs in both sexes, although the female, at least in the *encedon* form, is a better mimic than the male, partly on account of its larger size but also because of the whiter subapical bar to the fore wing.

*The Forms of Acræa encedon in the Locality of the
Breeding Experiments.*

The following specimens, captured by Mr. W. A. Lamborn in the Oni district, about 70 miles east of Lagos, are included in the Table on p. 394. From Oni: 1 ♂ 2 ♀ *lycia*, 1 ♀ *infuscata*; from Idakun, 4 miles N.W. of Oni: 4 ♂ *infuscata*, 1 ♂ 1 ♀ *commixta*, 1 ♂ 1 ♀ *lycia*. To these must be added

the captured parents of Families 1, and 3-16, recorded on pp. 407, 409-414, viz. 2 ♂ 7 ♀ *lycia*, 1 ♂ 3 ♀ *infuscata*, 1 ♀ *commixta*, from Oni; 1 ♂ 1 ♀ *lycia*, 1 ♀ *infuscata*, from Idakun. The totals from the Oni district are therefore 16 *lycia* (5 ♂ 11 ♀), 10 *infuscata* (5 ♂ 5 ♀), and 3 *commixta* (1 ♂ 2 ♀).

The artificial conditions produced no apparent effect, the *lycia*, *infuscata*, and *commixta* of the breeding experiments being similar to the captured specimens of the same forms. The families were examined by Eltringham, who states that "the majority . . . consist of two forms, viz. *infuscata* and *lycia*. The latter are somewhat unusual in having broad suffused orange internervular markings on the hind margin of the secondaries on the under side, also some basal markings of the same colour" (*l. c.* p. 213). It is also noticeable that the males of these Southern Nigerian *lycia* are distinctly yellower than their females, and that the subapical bar of the fore wing in the *infuscata* forms is yellow in the male, white in the female. Lamborn concludes that *lycia* is certainly three and probably four times as numerous as *infuscata* in the neighbourhood of Oni, and his material shows that *commixta* is much rarer than *infuscata*. He did not meet with any other form except these three, nor did any other appear in his long series of breeding experiments.

Tabular Statement of W. A. Lamborn's Breeding Experiments (pp. 397-8).

It will be observed that Companies 5 and 7, together with Family 8, suggest that *lycia* and not *infuscata* is dominant, a conclusion rendered improbable by the rest of the figures. These 3 sets, together with Family 7, are probably to be explained by comparison with Families 4 and 13. The *lycia* ♀ parents of these two families laid eggs in two batches, which were kept distinct, and the larvæ reared separately. Both families as a whole yield approximate equality of *infuscata* and *lycia*, but the constituent batches depart widely from this ratio. The 4 irregular results referred to above are all manifest in relatively small numbers, and they may be fairly referred to the causes which produced the constituent batches of Families 4 and 13.

The inferences as to the Mendelian constitution of the parents were submitted to my friend Mr. L. Doncaster, who has had so wide an experience in this line of research. He kindly wrote, April 16, 1913:—

"I think *lycia* must be recessive in spite of the inverted 3 : 1 cases, because of Family 2. Both parents were from Company 4, and if *lycia* were dominant all the *lycia* individuals would presumably be heterozygous. I think all your inferences as to parentage are correct."

Mr. Doncaster also remarks:—"It is a pity there are no known cases of *infuscata* ♀ × *lycia* ♂ and *vice versa*, which would test whether the *infuscata* character is sex-limited in the ♀; but as none of the mixed families have all the ♂ ♂ *infuscata* and ♀ ♀ *lycia*, it does not seem likely."

The results of breeding the Wild Larvæ, the Companies, and Families 1-3 have been recorded in Proc. Ent. Soc. Lond. 1911, pp. liv-lvi, before the appearance of Eltringham's monograph, containing a thorough account of all the forms of *A. encedon*. The darker forms found and bred at Oni, named *encedon* in the 1911 publication, are now recognised as *infuscata*, and a few as *commixta*.

Source of the Broods, with the forms of the parents when known.	<i>INFUSCATA</i> , with a few <i>COMMIXTA</i> .		<i>LYCIA</i> .		Inferred Mendelian constitution of the Parents. Remarks.
	Male.	Female.	Male.	Female.	
Wild Larvæ (1)	6	8	5	26	Two ♂♂ & 1 ♀ <i>commixta</i> and 1 transitional ♂ are included among the <i>infuscata</i> . The 27 latest emergences were all ♀.
„ „ (2)	...	17	3	18	One ♀ <i>commixta</i> is included among the <i>infuscata</i> . The 3 ♂♂ appeared with 2 ♀♀ in the 5 latest emergences.
Company 1	...	...	46	32	Both parents recessive (<i>lycia</i>). Two ♂♂ approach <i>commixta</i> .
„ 2	...	24	...	23	One parent heterozygote (<i>infuscata</i>), the other recessive (<i>lycia</i>).
„ 3	...	35	...	...	One parent dominant (<i>infuscata</i>), the other either dominant, heterozygote (<i>infuscata</i>), or recessive (<i>lycia</i>).
„ 4	6	2	4	1	One parent heterozygote (<i>infuscata</i>), the other recessive (<i>lycia</i>).
„ 5	...	6	...	16	The proportions, suggesting heterozygote <i>lycia</i> for both parents, are more probably due to a special batch of ova. (See Fams. 4 & 13.)
„ 6	...	...	3	3	Both parents recessive (<i>lycia</i>).
„ 7	2	1	7	6	Inference as in Co. 5.
Fam. 1. ♂ ♀ <i>lycia</i>	...	...	...	48	Both parents recessive.
„ 2. ♂ ♀ <i>lycia</i> fr. Company 4...	...	...	19	13	Both parents recessive. One ♂ approaches <i>commixta</i> .
„ 3. ♀ <i>infuscata</i> ...	5	11	6	13	The ♀ parent heterozygote, the ♂ recessive (<i>lycia</i>).
„ 4. ♀ <i>lycia</i>	...	33	...	36	The ♀ parent recessive, the ♂ heterozygote (<i>infuscata</i>). Eggs in 2 batches, yielding very different proportions.
„ 5. ♂ ♀ <i>infuscata</i> ...	...	28	...	...	One parent dominant, the other dominant or heterozygote. ♀ parent with fulvous subapical bar inherited by 13 offspring, of which 2 approach <i>commixta</i> .

Source of the Broods, with the forms of the parents when known.	<i>INFUSCATA</i> , with a few <i>COMMIXTA</i> .		<i>LYCIA</i> .		Inferred Mendelian constitution of the Parents. Remarks
	Male.	Female.	Male.	Female.	
Fam. 6. ♀ <i>infuscata</i> ...	...	21	...	21	The ♀ parent heterozygote, the ♂ recessive (<i>lycia</i>). A single ♂ <i>lycia</i> , perhaps accidentally introduced, is not included.
„ 7. ♀ <i>commixta</i> ...	...	3	...	9	The 3 ♀ ♀ in 2nd column are <i>commixta</i> . Inference as in Co. 5: 2 heterozygote <i>lycia</i> parents are here excluded.
„ 8. ♀ <i>lycia</i>	...	7	...	21	Inference as in Co. 5.
„ 9. ♀ <i>lycia</i>	...	1	...	1	The ♀ parent recessive, the ♂ heterozygote (<i>infuscata</i>).
„ 10. ♀ <i>lycia</i>	...	...	...	12	Both parents recessive (<i>lycia</i>).
„ 11. ♀ <i>infuscata</i> ...	...	12	...	14	The ♀ parent heterozygote, the ♂ recessive (<i>lycia</i>).
„ 12. ♀ <i>lycia</i>	...	...	...	41	Both parents recessive (<i>lycia</i>).
„ 13. ♀ <i>lycia</i>	...	45	...	42	The ♀ parent recessive, the ♂ heterozygote (<i>infuscata</i>). Eggs in 2 batches, yielding different proportions.
„ 14. ♂ ♀ <i>lycia</i>	...	...	...	19	Both parents recessive.
„ 15. ♂ ♀ <i>lycia</i>	...	...	...	19	„ „ „
„ 16. ♂ ♀ <i>lycia</i>	...	...	12		„ „ „
„ 17. ♂ ♀ <i>lycia</i>	...	...	...	34	„ „ „
„ 18. ♂ ♀ <i>lycia</i>	...	...	...	11	„ „ „
„ 19. ♂ ♀ <i>lycia</i>	...	...	24	16	„ „ „
„ 20. Parents unknown	...	35	...	36	One parent heterozygote (<i>infuscata</i>), the other recessive (<i>lycia</i>).
„ 21. „ „	16	5	...	...	One parent dominant (<i>infuscata</i>), the other dominant, heterozygote (<i>infuscata</i>), or recessive (<i>lycia</i>).
TOTALS	35	294	129	539	

Segregation into infuscata, commixta, and lycia.

Looking at the 998 bred specimens* as a whole, it is remarkable how completely they segregate into *infuscata*, *commixta*, and *lycia*, and how few specimens can be considered as intermediate between these. Those that did

* Including the single ♂ which appeared in Family 6.

appear are transitional between *commixta* and *infuscata* on the one side, and *commixta* and *lycia* on the other, rather than directly between the two chief forms. Hence, by selecting the examples, a fair transition from *infuscata* to *lycia* may be constructed by way of *commixta*. This latter form is clearly hereditary. Thus the female parent of Family 7 is *commixta*, and all 3 of her non-*lycia* offspring are *commixta*. Particularly interesting in this respect is Family 5, of which the female parent possesses the fulvous bar but not the white hind wing of *commixta*. About half of the offspring, namely 13 out of 28, resemble the mother in this respect *, while 2 of them have also the white hind wing. Other evidence of the hereditary transmission of this combination of characters will be found under Family 2 (pp. 407-8).

Families of which the female parent only is known.

When the only known parent is a female *infuscata* (or *commixta*) the offspring show, in all four families, a mixture of *infuscata* (or *commixta*) and *lycia* with approximate equality three times. In the single exception, Family 7, the numbers are small. The inference is that one parent was recessive and the other heterozygote.

When the only known parent is a female *lycia*, the offspring are all *lycia* twice and mixed *lycia* and *infuscata* four times, with equality thrice (including the small Family 9) and irregularity once (Family 8).

In the absence of selective breeding, for which there is insufficient evidence, the great numerical superiority of *lycia* would result in the majority of the pairings being between males and females of this form, or between *lycia* and *infuscata*, the latter being far more commonly heterozygote than pure dominant. We can thus, on the hypothesis that *lycia* is recessive, understand why the families bred from a female of this form were either all *lycia* or mixed *lycia* and *infuscata*, but, owing to the relative rarity of the pure dominant, never, in the author's experience, entirely made up of heterozygotes bearing the appearance of the dominant (*infuscata*). It is unfortunate that the *infuscata* in the families with equal numbers of the two forms never happen to have been bred from, so that their heterozygote constitution could be tested.

Families of which both parents are known.

Both male and female are of the form *lycia* in 8 families ; both are of the form *infuscata* in only 1, namely Family 5. The 8 former produced only *lycia* offspring ; the latter only *infuscata*.

* The numbers suggest that, as regards this character, the parents were recessive and heterozygote respectively. If this be so, the female, belonging to the rarer form, was probably heterozygote, while *infuscata*, although dominant in relation to *lycia*, is recessive to the form with a fulvous bar.

The fact that 2 *lycia* parents should 8 times have produced offspring which were nothing but *lycia* strongly supports the view that this form is recessive. It is unfortunate that there was only a single family with *infuscata* parents, and that this one should have failed to afford evidence as to the dominance of the latter form.

Companies and Families with equality of infuscata and lycia.

The frequency with which there is exact or approximate equality between the two forms is striking. Omitting very small numbers, we notice conspicuous instances in Company 2, Families 3, 4, 6, 11, 13, & 20. It is to be observed that Family 3 is the only one of these that is not all-female.

The female parents of these groups, so far as they are known, are *infuscata* 3 times (Families 3, 6, & 11) and *lycia* twice (Families 4 & 13).

The Proportion of the all-female Companies and Families and of the Sexes in the mixed groups.

The two series bred from Wild Larvæ are omitted from these considerations because of the uncertainty which naturally attaches to them, although it must be remembered that there are good reasons for believing that the great majority of each set belonged to a single all-female family.

Three out of the 7 companies, and 16 out of the 21 families, are made up of all-female offspring. On the other hand, there are almost precisely 50 per cent. more males than females in the mixed sets. In 3 out of 4 companies with mixed sexes, the males are more numerous; in the 4th (the very small Company 6) the numbers are equal (3 of each sex). The totals in these mixed companies are 68 males and 45 females, and in the 5 mixed families 82 males and 56 females. In this latter series there is also one exception, and a very marked one, namely, Family 3 with 11 males and 24 females. The totals, in all mixed companies and families, are 150 males and 101 females.

Relationship between the all-female and the mixed Families.

It is important to notice that the male parents may produce very definite hereditary effects upon their female offspring in the all-female families. Thus the Mendelian relationship between the forms of parents and offspring appears to be the same in all-female families as in those with mixed sexes.

It is quite clear that the all-female families bear no special relation to one of the local forms of *Acræa encedon* rather than another. They may be all *infuscata* or they may be all *lycia*, or approximately half *infuscata* and half *lycia*.

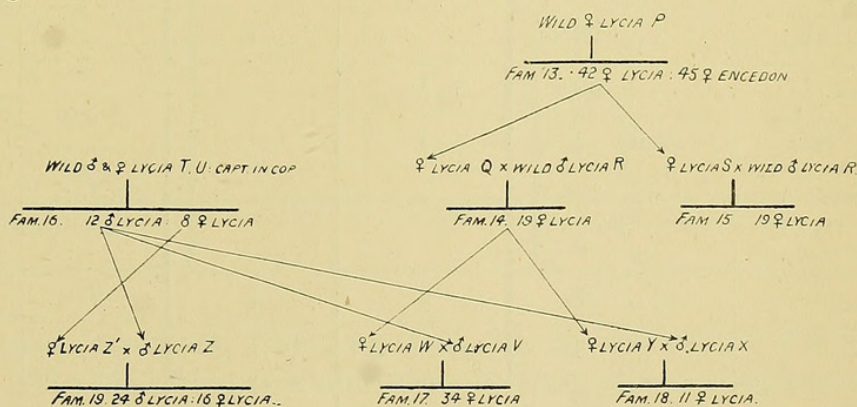
Considering the 19 all-female groups among the companies and families, 2 are all *infuscata* (the known parents of one being ♂ ♀ *infuscata*), 7 are all *lycia* (the known parents ♀ *lycia* twice, ♂ ♀ *lycia* five times), and 10 are mixed *infuscata* or *commixta* and *lycia* (the known parents ♀ *infuscata* twice, ♀ *commixta* once, and ♀ *lycia* four times).

Seven out of the 10 mixed groups are exactly or approximately half *infuscata* and half *lycia*. The remaining three are Company 5 with 6 *infuscata* to 16 *lycia*, Family 7 with 3 to 9, Family 8 with 7 to 21. It is rather curious that the proportions are here—exactly in the 2 families and approximately in Company 5—the Mendelian expectation if *lycia* were dominant and 2 heterozygotes had paired: an interpretation untenable for Family 7, of which the ♀ parent was not *lycia*. The probable explanation of these irregularities and that exhibited by Company 7 has been suggested on p. 396.

Among the 9 groups with mixed sexes, out of the 28 companies and families, 1 is all *infuscata* (parents unknown), 5 are all *lycia* (known parents ♂ ♀ *lycia* three times), and 3 are mixed *infuscata* and *lycia* (known parent ♀ *infuscata* once). Of these 3, Company 7 with 3 *infuscata* to 13 *lycia* is considered above, while the other two give approximate equality (Family 3) and probably rough equality (Company 4).

Probable existence of two strains of females, one producing all-female, and the other male and female families.

It will be observed in the Table on pp. 397–8 that Family 2 with mixed sexes was produced by a male and female *lycia* from Company 4 also made up of males and females. These facts favour the conclusion that the power of producing mixed sexes is hereditary. Confirmation is also provided by the offspring of Family 16, with mixed sexes, bred from a pair of *lycia* captured in the wild state. From two of these offspring sprang Family 19, also of mixed sexes. The relationship between Families 16 & 19 is shown in the following Table.



The existence of a strain producing nothing but females is supported by stronger evidence; for the breeding experiments extended over 3 generations, also set forth in the accompanying Table. In this we see that two males from the mixed Family 16, paired with females from the all-female Family 14, produced nothing but females in the resulting Families 17 and 18. Another male from Family 16, paired with a female from the same family, produced, as stated above, the mixed Family 19.

Although further evidence is desirable, the whole of Mr. Lamborn's experiments, so far as they bear on this subject, point in one direction. There are no grounds for the belief that parthenogenesis ever takes place in this species, but the determination whether the family is to be all-female or mixed rests solely with the female parent.

W. A. LAMBORN'S BREEDING EXPERIMENTS.

WILD LARVÆ.—Two sets of wild larvæ collected on *Commelina* were bred, and it will be seen that there are indications of an all-female company in the later emergences of the first set and in all except the very latest emergences of the second.

Wild Larvæ 1.

These larvæ were collected in Googa Creek, about five miles north of Oni. Their whole life-history fell well within the wet season, which lasted from about April 25 to Nov. 15, 1910. The dates of emergence and some of the dates of pupation are shown in the following Table :—

Dates of Pupation. 1910.	Dates of Emergence. 1910.	<i>infuscata</i> and <i>commixta</i> .		<i>lycia</i> .	
		Male.	Female.	Male.	Female.
June 19.	June 26.		1		
„ 21.	„ 27.		1		
„ 20.	„ 27.		1		
„ 22.	„ 28.		1		
—	„ 30.	1			
„ 28.	July 4.	1			
—	„ 5.			1	
—	„ 6.				1
—	„ 7.	4	1	4	1
—	„ 8.				2
—	„ 9.		1		5
—	„ 10.				3
—	„ 11.		2		4
—	„ 12.				7
—	„ 13.				3
—	Totals	6	8	5	26

Three *commixta* are included in the series of *infuscata*, namely, 2 males emerging July 7 and 1 female emerging July 9. *Commixta* possesses a fulvous fore-wing subapical bar with a white hind wing, approaching that of the form *alcippina*. One other male of July 7 has the former of these characters only, and is thus transitional. Some *lycia* of this series also exhibited a slight suffusion of the fore wing with a fulvous tint.

Wild Larvæ 2.

The larvæ were collected on the bank of Oni River, about two miles north-west of Oni. Their whole life-history fell within the dry season, which lasted from about mid-Nov. 1910 to mid-March 1911. The dates of emergence are shown in the following table.

Dates of Emergence. 1910.	<i>infuscata</i> and <i>commixta</i> .		<i>lycia</i> .	
	Male.	Female.	Male.	Female.
Dec. 10		3		4
„ 11				3
„ 14		4		1
„ 15		8		6
„ 16		1		1
„ 17				1
„ 21		1		
„ 23			1	2
„ 24			2	
Totals		17	3	18

One female *commixta*, emerging Dec. 10, is included in the series of *infuscata*. The hind wing is whiter than in most other examples—so much so, indeed, that the specimen might, except for the fulvous fore-wing bar, be fairly classed under the form *alcippina*.

COMPANIES :—The following 7 companies of larvæ were bred each from a batch of eggs laid on a single leaf of the food-plant *Commelina*, by the Oni River, about two miles north-west of Oni Camp. Great care was taken

to ensure that the larvæ of each company should be kept separate. The eggs themselves formed in each case a clump no larger than a threepenny-bit, and it may be assumed that each was laid by a single female. The dates at which some of the batches of ova were found were not preserved, but all of them fell into Dec. 1910 or Jan. 1911, and therefore well within the dry season, which extended from about mid-Nov. 1910 to mid-March 1911.

Company 1.

The eggs hatched Dec. 24, 1910. The 2 imagines which emerged on Jan. 21 pupated on Jan. 16. The other dates of pupation were not preserved.

The eggs produced both males and females, all of the form *lycia*, which emerged on the following dates :—

Dates of Emergence. 1911.	<i>lycia</i> .	
	Male.	Female.
Jan. 21	2	
„ 22	3	
„ 23	17	2
„ 24	1	
„ 25	18	8
„ 26	5	18
„ 28		3
„ 29		1
Totals	46	32

The individuals of this company are unusually dark, and in many specimens, principally males, the basal half of the fore wing is suffused with a faint fulvous tint varying in depth of shade. In the most extreme of these the fore wing may be called intermediate between *infuscata* and *lycia*. The two varieties in which the suffusion is most pronounced are males, emerging respectively on Jan. 23 and 25. In both of these the subapical bar of the fore wing is of a deeper shade than usual, so that these specimens approach the form *commixta*.

Company 2.

Eggs were found Dec. 24, and hatched Dec. 27.

The eggs produced 47 females, made up of nearly equal numbers of *infuscata* and *lycia*, which emerged on the following dates:—

Dates of Emergence. 1911.	Female <i>infuscata</i> .	Female <i>lycia</i> .
Jan. 30	4	4
„ 31	2	1
Feb. 1	2	3
„ 2	10	12
„ 3	2	2
„ 4	4	1
Totals	24	23

Company 3.

Eggs were found Jan. 1, and hatched Jan 3.

The eggs produced 35 females of the form *infuscata*, which emerged on the following dates:—

Dates of Emergence. 1911.	Female <i>infuscata</i> .
Feb. 1	2
„ 2	11
„ 3	9
„ 4	4
„ 5	3
„ 6	6
Total	35

Company 4.

Eggs were found Jan. 1, and hatched Jan. 3.

The eggs produced males and females of both *infuscata* and *lycia* :—

Dates of Emergence. 1911.	<i>infuscata.</i>		<i>lycia.</i>	
	Male.	Female.	Male.	Female.
Feb. 14	4		2	
„ 15	1		0	
„ 17		1	1 ¹	1 ²
„ 18	1			
„ 19		1	1	
Totals	6	2	4	1

¹ Parent C, of Family 2 (p. 407).

² Parent D, of Family 2 (p. 407).

The individuals of this company were typical and uniform, with the single exception of the male parent, *lycia*, of Family 2, in which the basal half of the fore wing was slightly tinged with fulvous, a variation which appeared in many of its offspring.

Company 5.

The dates of capture and hatching were not kept.

The eggs produced 22 female offspring, of which 6 were *infuscata* and 16 *lycia* :—

Dates of Emergence. 1911.	Female <i>infuscata.</i>	Female <i>lycia.</i>
Feb. 21	1	
„ 22		1
„ 23		4
„ 24	5	11
Totals	6	16

Company 6.

The eggs hatched Jan. 28, 1911.

The eggs produced 3 males of the form *lycia*, which emerged on March 2 and 3 female *lycia* which emerged on March 2, 3, and 4, respectively.

Company 7.

The eggs hatched Feb. 1, 1911.

The eggs produced males and females both of *infuscata* and *lycia*:—

Dates of Emergence. 1911.	<i>infuscata.</i>		<i>lycia.</i>	
	Male.	Female.	Male.	Female.
March 11			4	
„ 13	1		3	
„ 16				1
„ 18				5
„ 19	1	1		
Totals	2	1	7	6

FAMILIES.—We now come to the series of 21 Families, in 19 of which either the female parent or both parents are known.

Family 1.

Parents A and B, both of the form *lycia*, were captured *in cop.* by the river at Idakun, 4 miles north-west of Oni, Dec. 1, 1910. The male A died Dec. 4. Eggs were laid on the back of a leaf, Dec. 2, and the female parent B was killed Dec. 4. The eggs had all hatched by Dec. 9.

The eggs produced 48 female offspring, all of the form *lycia*, which emerged at the dates shown in the following table. The dates of pupation are also included :—

Dates of Pupation. 1911.	Dates of Emergence. 1911.	Female <i>lycia.</i>
Jan. 1.	Jan. 7.	25
„ 2.	„ 8.	12
„ 3.	„ 9.	8
„ 4.	„ 10.	3
	Total	48

Family 2.

Parents C and D both of the form *lycia* (but it has already been pointed out on p. 406 that the male was slightly suffused with fulvous). Both parents belonged to Company 4, and both emerged and paired on Feb. 17. Eggs were laid Feb. 18.

The eggs produced both males and females of the form *lycia* :—

Dates of Emergence. 1911.	<i>lycia</i> .	
	Male.	Female.
March 27	5	1
„ 28	12	11
„ 29	2	1
Totals	19	13

The effect of the male parent was obvious in many specimens, especially in a male emerging March 27, which exhibits the same tendency in higher degree, and approaches *commixta*, like the 2 males of Company 1 (see p. 404). It must be remembered, however, that these two latter differ in other respects, belonging, as they do, to an exceptionally dark series.

Family 3.

Parent E. The female parent, of the form *infuscata*, was captured on the river-bank at Idakun. Eggs were laid Feb. 9–10 and hatched Feb. 13–14. The female parent died Feb. 10.

The eggs produced males and females both of *infuscata* and *lycia*, which emerged on the following dates :—

Dates of Emergence. 1911.	<i>infuscata</i> .		<i>lycia</i> .	
	Male.	Female.	Male.	Female.
March 18	1			
„ 20		2	1	
„ 21	1	3	1	1
„ 22	1	1	2	
„ 23	1	3	2	1
„ 24				4
„ 25				4
„ 26		1		
„ 27		1		2
„ 29	1			1
Totals	5	11	6	13

Family 4.

Parent F. The female parent, of the form *lycia*, was captured in Oni clearing near the lagoon. Two batches of eggs were laid with a day's interval. The first batch began to hatch on Sept. 6, and pupation commenced on Oct. 5.

The eggs of the first batch produced 51 all-female offspring, of which 29 were *infuscata* and 22 *lycia*. One *infuscata* emerged Oct. 12 and the remaining butterflies from this day onwards, but precise dates were not recorded.

The eggs of the second batch hatched Sept. 7-8, and pupation took place from Oct. 5. Of the 18 resulting females, 4 were *infuscata* and 14 *lycia*. These emerged on the following dates :—

Dates of Emergence. 1911.	Female <i>infuscata</i> .	Female <i>lycia</i> .
Oct. 11.	2	2
„ 12.	1	4
„ 13.		1
From „ 11.	1	7
Totals	4	14

Family 5.

Parents G and H, both of the form *infuscata*, were captured *in cop.* in Oni Clearing by the lagoon, Sept. 15, 1911. The male G is a typical West African *infuscata*, although the subapical fore-wing bar is paler than usual, perhaps as a result of wear. In the female, however, the same marking is of a fulvous tint, as in *commixta* and *daira*. Eggs were laid Sept. 18 and hatched Sept. 26. The female parent died Sept. 20. No dates of emergence were kept, but the whole cycle fell well within the wet season, which lasted from about mid-March to Dec. 8, 1911.

The eggs produced 28 female offspring, all of the form *infuscata*—15 with the white subapical bar of the ordinary female *encedon*, 13 with the fulvous bar of the female parent. In two of this latter set, the hind wings are partially white, so that the specimens closely approach the form *commixta*.

It should furthermore be noted that some of the 13 specimens were much worn, but the scales still remaining left no doubt that the bar had been fulvous and not white.

Family 6.

Parent I. The female parent, of the *infuscata* form, was captured in Oni Clearing, April 27, 1912. Eggs were laid between April 30 and May 1, and the butterfly died May 2.

The eggs produced 42 female offspring, which emerged on the following dates. A single male *lycia* may have been accidentally introduced :—

Dates of Emergence. 1912.	Female <i>infuscata</i> .	Female <i>lycia</i> .
May 29	1	2
„ 30	1	1
„ 31	2	5
Unnoted.....	17	13 ¹
Totals	21	21

¹ In addition to the above, a single ♂ *lycia* was found in this category. It is excluded from the table because it seems probable that its appearance was due to accident.

Family 7.

Parent J. The female parent was captured in Oni Clearing, May 5, 1912. This female is much worn, but there is no doubt that it is of the form *commixta*. The pale fulvous fore-wing bar is evident in the specimen. Eggs were laid May 6, and the butterfly died May 8.

The eggs produced 12 female offspring, of which 3 were *commixta* and 9 *lycia*. The date of emergence, June 6, was only noted for a single *lycia*.

Family 8.

Parent K. The female parent, of the form *lycia*, was captured in Oni Clearing, May 7, 1912. Eggs were laid May 7, and the butterfly died May 8.

The eggs produced 28 female offspring, of which 7 were *infuscata* and 21 *lycia*. The dates of emergence were not noted.

Family 9.

Parent L. The female parent, of the form *lycia*, was captured in Oni Clearing on May 8, 1912. Eggs were laid May 9, and the butterfly died May 11.

The eggs produced on June 13, 2 female offspring, of which 1 was *infuscata* and 1 *lycia*. The latter is noticeably darker than its parent.

Family 10.

Parent M. The female parent, a rather dark *lycia*, was captured in Oni Clearing on June 1, 1912. Eggs were laid June 2, and the butterfly died June 4.

The eggs produced 12 female offspring of the form *lycia*, of which 5 emerged July 14 and 7 July 15.

The offspring are uniformly dark like the female parent.

Family 11.

Parent N. The female parent, of the form *infuscata*, was captured in Oni Clearing, June 1, 1912. Eggs were laid June 2, and the butterfly died June 5.

The eggs produced 26 female offspring, of which 12 were *infuscata* and 14 *lycia*. Emergence took place on the following dates:—July 12, *infuscata* 11, *lycia* 12; July 17, *infuscata* 1, *lycia* 1; July 18, *lycia* 1.

Family 12.

Parent O. The female parent, of the form *lycia*, was captured in Oni Clearing on June 8, 1912. Eggs were laid on June 8–9, and the butterfly died June 10.

The eggs produced 41 female offspring, all of the form *lycia*, which emerged as follows:—July 13, eighteen; July 17, six; July 18, fourteen; July 19, three.

Family 13.

Parent P. The female parent, of the form *lycia*, was captured at the edge of the lagoon near Oni Clearing on April 19, 1912. The larvæ produced by the first batch of ova, laid April 21, were reared separately from those of the second batch, laid April 22. The parent died April 24.

The ova of the first batch hatched April 27, and produced 61 female offspring of both forms which emerged on the following dates :—

Dates of Emergence. 1912.	Female <i>infuscata</i> .	Female <i>lycia</i> .
May 24	2	2
„ 25	15	7
„ 26	3	9
„ 28	12	2
„ 29	2	7
Totals	34	27

The ova of the second batch hatched April 28, and produced 26 female offspring of both forms which emerged on the following dates :—

Dates of Emergence. 1912.	Female <i>infuscata</i> .	Female <i>lycia</i> .
May 22	0	2 ¹
„ 25	1	3
„ 26	4	9
„ 27	2	0
„ 28	4	1
Totals	11	15

¹ These 2 *lycia* females became respectively the female parents S and Q, see p. 413.

Both *infuscata* and *lycia* were typical, but the latter varied in the extent of the black pigmentation of the fore wing.

Family 14.

Parents R, Q. The male parent R, of the form *lycia*, captured in Oni Clearing, May 24, 1912, paired May 24 with the female parent Q, of the

form *lycia*, one of the offspring emerging May 22 of the all-female family of parent P. (The male parent R subsequently paired with S.) Eggs were laid May 25 and 26 and the female parent died May 27.

The eggs produced 19 female offspring, all of the form *lycia*, which emerged on the following dates :—June 29, one ; June 30, sixteen ; July 1, two.

Two of the females which emerged on June 30 became respectively the female parents W and Y (see p. 414).

Family 15.

Parents R, S. The male parent R, of the form *lycia*, captured in Oni Clearing, May 24, 1912, paired May 26 with the female parent S, of the form *lycia*, one of the offspring emerging May 22 of the all-female family of parent P. (The male parent R had previously paired with Q.) Eggs were laid May 27–29, and the female parent died June 1.

The eggs produced 19 female offspring, all of the form *lycia*, which emerged on the following dates :—

Dates of Emergence 1912.	Female <i>lycia</i> .
July 1	3
„ 2	4
„ 4	6
„ 7	2
„ 9	4
Total	19

Family 16.

Parents T, U, both of the form *lycia*, were captured *in cop.* in Oni Clearing, May 24. Eggs were laid in 3 batches May 25–27, and the female parent U died May 29.

The eggs produced both males and females, all of the form *lycia*, which emerged on the following dates :—

Dates of Emergence 1912.	<i>lycia.</i>	
	Male.	Female.
June 28	1 ¹	0
„ 29	4 ²	3 ³
„ 30	4	1
July 1	2	1
„ 2	0	1
„ 3	0	1
„ 8	1	1
Totals	12	8

¹ This male became parent V, see below.

² Two of these males became respectively parents X and Z, see pp. 414, 415.

³ One of these females became parent Z', see p. 415.

The series exhibited much variation in the extent of the black pigmentation of the fore-wing and the hind-wing border.

Family 17.

Parents V, W. The male parent V, of the form *lycia*, was one of the offspring, emerging June 28, of the mixed family of parents T, U. The female parent W, of the form *lycia*, was one of the offspring, emerging June 30, of the all-female family of parents R, Q. Pairing took place on June 30. Eggs were laid June 30 and July 1, and the female parent died July 4.

The eggs produced 34 female offspring, all of the form *lycia*. The dates of emergence were not noted.

The family exhibits variation in pigmentation, but to a less extent than that of Family 16.

Family 18.

Parents X, Y. The male parent X, of the form *lycia*, was one of the offspring, emerging June 29, of the mixed family of parents T, U. The female parent Y, of the form *lycia*, was one of the offspring, emerging June 30, of the all-female family of parents R, Q. Pairing took place on

June 30. Eggs were laid in 4 small batches July 2-4, and the female parent died July 6.

The eggs produced 11 female offspring, all of the form *lycia*. The dates of emergence were not noted.

The variation in pigmentation is about the same as that of Family 17.

Family 19.

Parents Z, Z'. The male parent Z, of the form *lycia*, was one of the offspring, emerging June 29, of the mixed family of parents T, U. The female parent Z', of the form *lycia*, was also one of the offspring, emerging June 29, of the same parents T, U. Pairing took place on June 30. Eggs were laid July 1-2, and the female parent died July 5.

The eggs produced both males and females, all of the form *lycia*, which emerged on the following dates :—

Dates of Emergence. 1912.	<i>lycia</i> .	
	Male.	Female.
Aug. 9	10	2
„ 10	2	2
„ 12	4	1
„ 13	4	7
„ 14	4	4
Totals	24	16

The variation in pigmentation is rather greater than in Families 17 and 18.

Family 20.

The parents of this and the next family were not found in Mr. Lamborn's material, and there is no note as to whether they were *infuscata* or *lycia*. A box of specimens appears to have gone astray, and it is probable that these two parents were included in it.

The family, all of which bore the same number ("834"), consists of females of *infuscata* and *lycia* in approximately equal numbers, which emerged on the following dates :—

Dates of Emergence. 1912.	Female <i>infuscata</i> .	Female <i>lycia</i> .
July 4	2	7
„ 5	5	11
„ 6	7	10
„ 8	4	0
„ 11	0	2
„ 12	17	6
Totals	35	36

Family 21.

Parent unknown. The family, all of which bore the same number ("846"), consists of males and females of *infuscata*, which emerged on the following dates :—

Dates of Emergence. 1912.	<i>infuscata</i> .	
	Male.	Female.
July 17	5	3
„ 18	9	0
„ 19	0	1
„ 20	2	1
Totals.....	16	5



Poulton, Edward Bagnall. 1914. "W. A. Lamborn's Breeding Experiments upon *Acraea encedon* (Linn.), in the Lagos District of West Africa, 1910-1912." *The Journal of the Linnean Society of London. Zoology* 32(218), 391-416.

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