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The genetics of the butterfly *Hypolimnas misippus* (L.): The classification of phenotypes and the inheritance of forms *misippus* and *inaria*

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***Hypolimnas misippus* is a polymorphic and mimetic butterfly with a pantropical distribution. The polymorphism is autosomal and female-limited, the several female forms being generally regarded as Batesian mimics of the distasteful, toxic and polymorphic danaine butterfly *Danaus chrysippus*. The female phenotypes of *H. misippus* are described and classified. New data, from the rearing of 140 broods of *H. misippus* in Ghana and Sierra Leone, are analysed together with older material (21 broods) from other parts of Africa. Form *misippus* (genotype *M-*) is found to be genetically dominant to form *inaria* (genotype *mm*). However, a large proportion of *mm* butterflies has an intermediate phenotype, especially in association with white on the hindwing. Evidence is adduced to show that the genes giving hindwing white are variably epistatic over the 'inaria' pattern in the *mm* genotype, producing a phenotype transitional to or even identical to *misippus*. The various intermediate phenotypes are poor mimics of *D. chrysippus*: their abundance, geographical range and, hence, significance have been much underestimated.**

INTRODUCTION

Investigations of the genetics of mimetic polymorphisms in *Papilio dardanus* Brown (Clarke and Sheppard, 1959, 1960*a*, 1960*b*, 1963), *Papilio glaucus* (L.) (Clarke and Sheppard, 1962), *Papilio memnon* L. (Clarke, Sheppard and Thornton, 1968) and *Papilio polytes* (L.) (Clarke and Sheppard, 1972) have shown that the major forms are controlled by various combinations of alleles within a supergene. In contrast, the various forms of the polymorphic nymphalid butterfly *Hypolimnas bolina* (L.) (Clarke and Sheppard, 1975) are controlled at 2 or 3 loci which mainly segregate independently: although linkage between two of the loci is possible, Clarke and Sheppard did not prove it and judged it unlikely. *H. bolina* resembles the Papilios in having polymorphism restricted to the female but differs in that only one of the female forms is mimetic. Clarke and Sheppard (*op. cit.*) suggested that, for their generalisations to be put to a wider test, it would be necessary to investigate a genus other than *Papilio*, in which polymorphism for several mimetic forms occurs. We believe that *Hypolimnas misippus* (L.) (the diadem or danaid eggfly) is eminently suited to this purpose. It resembles *H. bolina* in its female-limited polymorphism but differs in that four, perhaps all, of its many phenotypes are credible mimics of distasteful models belonging to the *Danaus chrysippus-Acraea encedon-Acraea encedana* mimicry ring over much of its very extensive geographical range (Pierre, 1976, 1980).

Our principal aim in this and subsequent papers on the formal and ecological genetics of *H. misippus* is to answer the following questions:

(a) Is the detailed resemblance between mimic and model enhanced by selection for modifiers?
(b) Is the switch control for genotypes located within a supergene?
(c) Is there evidence of selection for linkage?
(d) To what extent has complete dominance evolved between sympatric forms?
(e) Is there evidence for the evolution of epistasis?
(f) How do we explain the widespread occurrence and seasonal abundance of poor mimics?
(g) Why do the mimetic forms fail to match the *Danaus chrysippus* (L.) model in terms both of frequency rankings and biogeography?

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H. misippus has a vast tropical and sub-tropical distribution encompassing Africa south of the Sahara, Asia, Australia, Oceania and the New World. Throughout most of its Old World range the female is generally considered to be a polymorphic Batesian mimic of the danaine butterfly *D. chrysippus*. In the New World, however, it is probably non-mimetic for it bears no more than a superficial resemblance to the American queen (*Danaus gilippus* Cramer) or any other neotropical danaine. The male is monomorphic, non-mimetic and quite unlike all the female forms. It closely resembles several other species of *Hypolimnas*, especially the male of its sister species *H. bolina*. In the Ethiopian and Oriental Regions, the female forms of *H. misippus* and their putative *D. chrysippus* models are often poorly matched with regard to sympatry, frequency rankings or phenology (Edmunds, 1969; Pierre, 1973; Smith, 1976; Gordon, 1982), anomalies which have prompted speculation that the mimetic association may be closer to Müllerian than Batesian (Poulton, 1908; Unamba, 1968; Marsh *et al.*, 1977).

Genetical evidence has accumulated slowly and at irregular intervals over a period of 80 years (1904–83) in widely scattered parts of Africa. Due to the admirable foresight of the late Professor E. B. Poulton, the older material (1904–22) is preserved intact in the Hope Department of Entomology in Oxford. Our perusal of the Oxford collection provided the initial stimulus for further extensive breeding work which will be described here and in subsequent papers.

The new data in this paper come from two breeding programmes. The first was carried out at Freetown, Sierra Leone in 1966–68 by J. A. Unamba under the supervision of Professor D. F. Owen. Unamba died before his work could be published and Professor Owen has kindly made his results available to us. The second programme was undertaken by one of us (I.J.G.) at Cape Coast, Ghana during 1976–81. Our analysis is based on all the material available to us, 121 broods from Ghana, 19 from Sierra Leone, 4 from Kenya, 5 from Tanzania (Tanganyika), 10 from Nigeria, one from Malawi (Nyasaland) and one from Natal, Republic of South Africa, a total of 161 broods.

METHODS

Butterflies reared in Freetown (J.A.U.), Cape Coast (I.J.G.) and Dar es Salaam (Smith, 1976) were obtained by confining mated females on the foodplant, either *Portulaca quadrifida* L. (Portulaceae), *Blepharis maderaspatensis* L., *Ruellia prostrata* Jacq. or *R. cordata* Thunb. (all Acanthaceae), in a muslin sleeve or small cage. Most females laid over 100 eggs in 2–3 days and the maximum exceeded 550. Mean brood size (females only) was 52·7 ($n = 161$), but highly skewed with a median value of 39 and a modal value of 30.

The life cycle in the hot season at Dar es Salaam (mean ambient temperature 30°C) is 2–3 days to hatching, followed by 11 days to pupation, then 6–7 days to eclosion. The total egg to egg development time, recorded in detail for only 4 broods, averages 22·5 days for males and 23·5 days for females but the difference is not significant for this small sample. Generation times at Dar es Salaam, Freetown and Cape Coast were similar and always under one month even in the cooler seasons.

All broods were reared separately in well-ventilated cages. Some broods were ravaged or lost, mainly as a result of virus disease (Dar es Salaam) or the refusal of the larvae to eat in the dry season (Freetown). Broods with less than 8 surviving female offspring are omitted from our analysis as they yield no useful information.

It must be remembered that the male genotype cannot be inferred by inspection. As most male parents were wild, nothing is known of their genetics; a limited amount of information is available in respect of male parents from laboratory reared broods (61 cases) and where the same male sired more than one brood (8 cases). However, with simultaneous segregations occurring at several loci, and the additional complication of epistasis, the use of laboratory-bred males contributed little conclusive information. Consequently, the segregations obtained are largely deduced from the phenotypes of the female parent and her female offspring. Where two or more segregation ratios are statistically valid, the one giving the smallest value of χ^2 is accepted: while it is clear that the method will lead to some misclassification and to an underestimate of heterogeneity, we believe that problems arising from these sources are effectively countered by the quantity and quality of the data.

Twenty-three per cent of wild females ($n = 397$) in Sierra Leone (Smith, 1984) and 5 percent in Ghana ($n = 149$) (Gordon, 1982) were found to carry two or more spermatophores so that mixed paternity may occur. However, segregations from wild mated females ($n = 68$) do not differ from those from single-mated, reared females ($n = 93$) and we suspect that sperm precedence occurs, the eggs being fertilised by the last male to copulate, as in *D. chrysippus* (Smith, 1984) and many other insects.

FEMALE PHENOTYPES

Male *H. misippus* are monomorphic, black with three pairs of white patches, the two larger, one on each wing, ringed with irridescent purple. The female is normally, though probably not universally, polymorphic. The most widespread and generally frequent female form *misippus* (fig. 2) is brownish-orange except for the apical half of the forewing which is black with two white areas, the latter probably homologous with those similarly placed in the male. For analytical purposes the "misippus" forewing is divided into five areas (fig. 1): area 1 is orange, areas 2 and 4 black and areas 3 and 5 white. In conventional form *inaria* all the areas 1–5 are orange except for a black wing margin. Many African populations show continuous variation between the two forms, all of which is ascribable to the variable replacement of orange scales by black or white in areas 2–5. The most "misippus"-like intermediate (table 1) has black scales in area 4 mixed with orange, giving brown (*br*). Orange scales may invade area 3, giving a pale orange (*p*) colour. Areas 3 and/or 4 may be completely orange (*o*), but not necessarily both in the same individual. When areas 3 and 4 are both orange (*oo*), the butterfly is classified as *inaria* without hesitation. However, areas 2 and 5 may remain black and white respectively. In the fullest expression of the "inaria" pattern, first area 5, then area 2, but occasionally in reverse order, are also orange.

The hindwing is also variable. Forms *misippus* and *inaria* have an entirely orange hindwing but *f. alcippoides* has a white patch, which varies in size from a small central spot, or even a few white scales, to near total displacement of orange. An additional source of hindwing variation, which is rare and occurred only in Ghanaian broods, involves a variable suffusion of the orange area by black scales: melanism occurs only in the presence of a large white patch. In heavily melanised females, the resemblance of the hindwing to that in the male is most striking.

The forewing phenotypes are described by combining the symbols *bl*, *br* and *o* for area 4 with *w*, *p* and *o* for area 3 (Edmunds, 1969). There are seven phenotypes—*blw*, *brw*, *ow*, *brp*, *op*, *bro* and *oo*. When combined with a score 0–10 for hindwing white, 77 phenotypes are thus specified. Adding the suffix *M* for melanism increases the theoretical maximum to 154 but by no means all the combinations are recorded: the number of phenotypes seen by us is probably around 100, some 60 of which occur regularly in the four African populations which have been investigated in depth.

The forewing and hindwing phenotypes frequently interact (Edmunds, 1969; Smith, 1976; Gordon, 1982). The *blw* ("misippus") forewing may be associated with all types of hindwing but the *oo* ("inaria") forewing is rarely combined with a hindwing carrying extensive white. On the other hand, there is a strong correlation between white on the hindwing and the intermediate forewing classes (see table 4). Moreover, the orange areas on the forewing of the intermediate forewing classes are often somewhat paler in association with a hindwing carrying extensive white. We hope to show in a later paper that at least some of the genes conferring hindwing white modify the

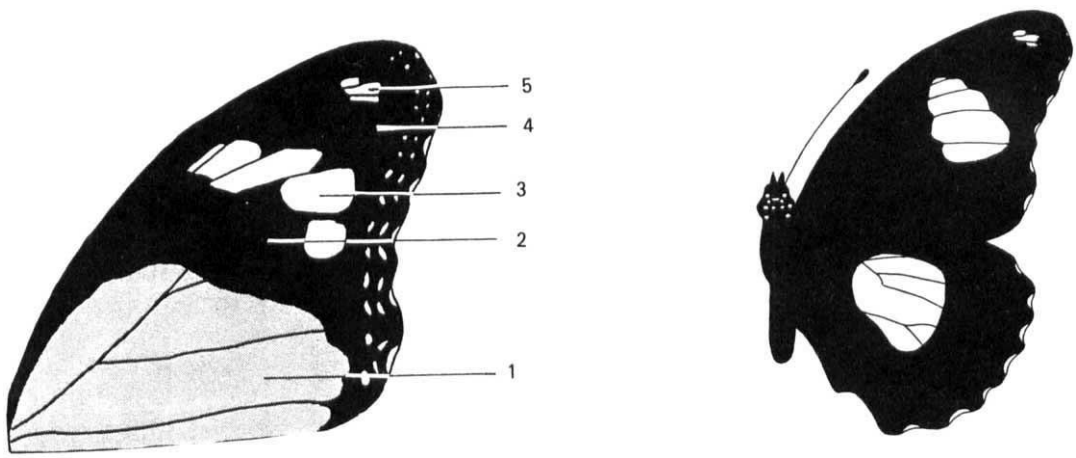

Figure 1 (Left) The five areas of the *Hypolimnas misippus* female forewing described in the text. The example illustrated is form *misippus*. The stippled area (1) is orange. Areas 2 and 4 are black, areas 3 and 5 white as shown. (Right) The monomorphic male is black and white except that the white area on the hindwing is ringed with irridescent purple.

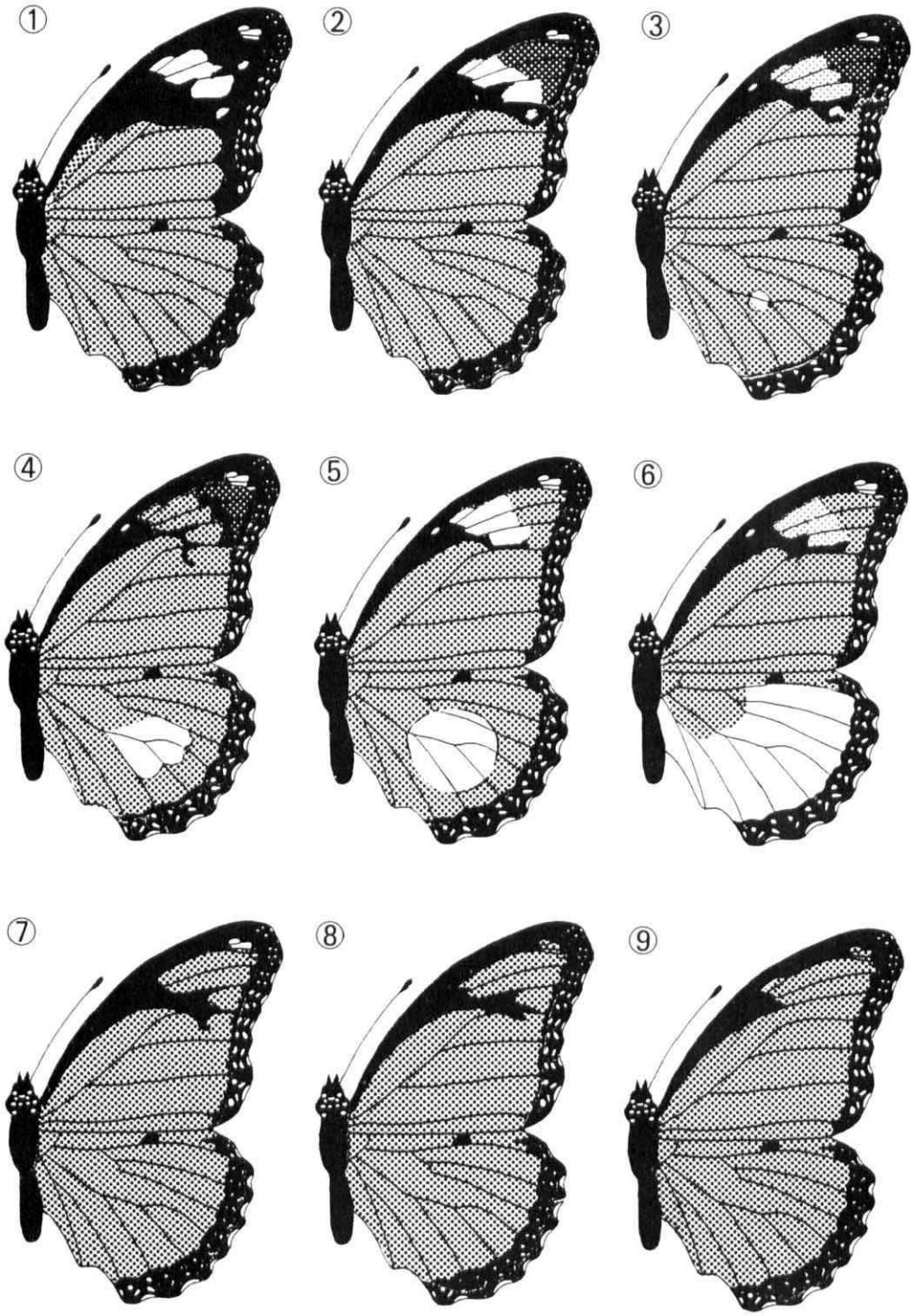

Figure 2 The forewing phenotypes of *Hypolimnas misippus*. The black (*bl*) and white (*w*) areas are as shown. Dark stipple indicates brown (*br*), medium stipple, orange (*c*) and pale stipple, pale orange (*p*). The phenotypes are: 1. *blw* (form *misippus*); 2. *brw*; 3. *brp*; 4. *bro*; 5. *ow*; 6. *op*; 7. *oo* with aree 2 black and area 5 white; 8. *oo* with area 2 black; 9. *oo*. Forms 7-9 are of *inaria* phenotype whereas all the forms 2-9 are of *inaria* (*mm*) genotype. Variation in the extent of hindwing white is shown in 3-6: Number 3 is scored as *brp*2, number 4 as *bro*3 and numbers 5-6 as *ow*5 and *op*8 respectively (see text).

Table 1 Classification of the female phenotypes of *Hypolimnas misippus*

Aree of forewing (fig. 2)					Phenotypic categories		
1	2	3	4	5	Edmunds (1969)	Pierre (1973)	This paper
o	*bl*	*w*	*bl*	*w*	*blw*	*misippus*	*misippus*
o	*bl*	*w*	*br*	*w*	*brw*		
o	*bl*	*w*	*o*	*w*	*ow*		intermediate
o	*bl*	*p*	*br*	*w*	*brp*	*immima*	
o	*bl*	*p*	*o*	*w*	*op*		*inaria*
o	*bl*	*o*	*br*	*w*	*bro*		
o	*bl*	*o*	*o*	*w*	*oo*		
o	*bl*	*o*	*o*	*o*	*oo*	*inaria*	*inaria*
o	*o*	*o*	*o*	*o*	*oo*		

o = orange, *bl* = black, *br* = brown, *p* = pale (orange), *w* = white.

expression of the"inaria" forewing gene to produce the various intermediate phenotypes. The gene giving hindwing melanism also produces a "misippus" (*blw*) or near-"misippus" (*brw*) forewing and is almost completely epistatic to the "inaria" gene (Smith and Gordon, in prep.).

RESULTS

One hundred and sixty-one broods were analysed, of which 23 gave no segregation, 13 segregated for forewing colour only, 57 hindwing colour only and 68 for both fore and hindwing. The breakdown takes account of a few broods where contamination is clear. Occasional contamination resulted from the presence of eggs or small larvae on foodplant gathered from the field. In this paper we are concerned only with the inheritance of forewing colour. All broods in which either the female parent or a proportion of the female offspring displayed hindwing melanism are excluded as this character also affects the forewing.

Sixty non-melanic broods gave no segregation for forewing colour. In 28 broods, where the female parent was *misippus*, all the progenies were *blw* (*misippus*) ($n = 1493$). A further 16 broods from non-"misippus" or *inarie* females also produced entirely *misippus* offspring ($n = 881$). Intermediate phenotypes were absent from all these broods indicating that the "misippus" character behaves as a complete dominant to "inaria". The results also suggest that the intermediate phenotypes are unlikely to be heterozygotes. Sixteen broods from non-"misippus" parents produced entirely non-"misippus" progeny ($n = 509$). We conclude from these results that there is a dominant allele *M*, giving the "misippus" forewing, and a recessive allele *m* which gives non-"misippus" or "inaria" forewings in the homozygous state.

Of the segregating broods, the 19 F2 broods (table 2) give an excellent fit to 3:1 and can be accepted as homogeneous. As all were obtained from *misippus* parents, they confirm the dominance of this character over *inaria*. Eleven broods of the 59 (backcross + F2) segregating for forewing fit both 3:1 and 1:1 hypotheses. Statistically, this is not surprising and their inclusion, according to best fit, in either the F2 (6) or backcross (5) series, produces no significant heterogeneity.

The 40 backcross broods (table 3) are homogeneous ($0{\cdot}7 > P > 0{\cdot}5$) and $\sum \chi^2_{(40)}$ is not significant ($0{\cdot}5 > P > 0{\cdot}3$). However $\chi^2_{(1)}$ for the total progeny test is highly significant ($0{\cdot}01 > P > 0{\cdot}001$) and indicates an overall bias to *misippus* which is small and goes mainly undetected in individual broods. Twenty-six broods are biased in the "misippus" direction compared with only 10 to *inaria* and this imbalance is itself significant ($\chi^2_{(1)} = 7{\cdot}111$; $0{\cdot}01 > P > 0{\cdot}001$). Three individual broods show a significant departure from 1:1, this being no surprise in such a long series. Two of these broods (S136, N151) in fact fit 3:1 but they must be backcross results as the female parents were *inaria*. All three broods segregated either 1:0 (2) or 1:1 (1) for white hindwing and 20 of the remaining 23 broods showing bias to *misippus* also had various proportions of whites among the progeny. We believe the bias is due to variable epistasis, over the "inaria" forewing genotype (*mm*), exercised by the genes controlling hindwing white. These genes tend to convert the forewing pattern into the *misippus* phenotype. The bias thus results from misclassification rather than differential viability.

Table 2 Broods of *H. misippus* segregating 3:1 for forewing colour

Brood number	Maternal phenotype	Female progeny: Hindwing colour	*misippus*	*inaria*	*N*	χ^2
G4	*blw*5	*w*	7	4	11	0·758
G6	*blw*0	*o*	25	5	30	1·111
G23	*blw*0	*o* & *w*	15	3	18	0·667
G27	*blw*1	*o* & *w*	82	27	109	0·009
G41	*blw*3	*o* & *w*	50	26	76	3·439
G53	*blw*3	*w*	45	16	61	0·049
G58	*blw*1	*o* & *w*	85	22	107	1·125
G63	*blw*2	*w*	70	25	95	0·088
G65	*blw*0	*o* & *w*	46	17	63	0·132
G83	*blw*2	*o* & *w*	55	19	74	0·018
G102	*blw*0	*o* & *w*	26	11	37	0·441
G105	*blw*4	*w*	64	20	84	0·063
S124	*blw*2	*o*	13	6	19	0·439
S131	*blw*2	*o* & *w*	17	7	24	0·222
S138	*blw*5	*o* & *w*	19	4	23	0·710
S140	*blw*2	*o* & *w*	51	20	71	0·380
K143	*blw*0	*o* & *w*	37	17	54	1·210
N149	*blw*0	*o* & *w*	13	6	19	0·439
N155	*blw*4	*o* & *w*	14	8	22	1·515
$\sum \chi^2_{(19)}$						12·815
Total progeny			734	263	997	1·011
Heterogeneity $\chi^2_{(18)}$						11·804

Notes: (1) Brood prefixes are: G = Ghana, N = Nigeria, M = Malawi (Nyasaland), S = Sierra Leone, T = Tanzania (Tanganyika), SA = South Africa, K = Kenya in this and the following table. (2) Under 'hindwing colour', *o* = orange and *w* = white.

The epistasis will be examined in more detail in subsequent papers. At this point we are concerned only to substantiate our assertion that it is responsible for misclassification for forewing phenotypes. The data in table 4 show that the presence of hindwing white is accompanied by a significant shift of forewing colour pattern away from *oo* to *brw*. Of the *mm* butterflies with white hindwings, 74·5 per cent had intermediate forewings and 22.5 per cent were *brw*, compared with 48·0 per cent and 3·3 per cent respectively for those with orange hindwings ($\chi^2_{(2)} = 205{\cdot}7$; $P < 0{\cdot}001$).

DISCUSSION

The results leave no doubt that the M locus is autosomal. In butterflies, the female is the heterogametic sex. Therefore, Y-linkage is easily ruled out as all female progeny would necessarily resemble their mothers, from whom they receive their Y chromosome. Segregation would occur only if the locus involved was located on a homologous segment present on both X and Y chromosomes but no case of this type has been recorded for Lepidoptera. On the other hand, as the X chromosome of the female must come from her father, 1:1 segregations in female progenies are expected to occur for X-linked loci but 3:1 ratios, common in our broods, are not possible. It is clear, therefore, that the *M* locus is autosomal but sex-controlled to the female as in the female-limited polymorphism in *H. bolina* (Clarke and Sheppard, 1975).

The results also establish that the "misippus" pattern (*blw*) is fully dominant to "inaria" (*oo*). All the intermediate phenotypes (*brw*, *brp*, *bro*, *ow*, *op*) are genetically "inaria". These latter forms, which comprise the variety *immima* of Bernardi (1959) and Pierre (1973, 1980), have no genetic status. Some broods (*e.g.*, K141) contained entirely *oo* progeny although the female parent was *brw* and close to *misippus* in appearance. In contrast, *blw* mothers never produced all *inaria* progeny. On the other hand, broods T160 and T161, both from *op* parents, consisted almost entirely of intermediates. There is a positive correlation between white on the hindwing and intermediate forewing in field collected specimens (Edmunds, 1969; Smith, 1976; Gordon, 1982) and the same effect is clear in our broods (table 4). This suggests that the expression of the "inaria" pattern in *mm* butterflies is affected by other genes, the primary effect of which is on the hindwing but which also interact

Table 3 Broods of *H. misippus* segregating 1:1 for forewing colour

Brood number	Maternal phenotype	Female progeny				
		Hindwing colour	*misippus*	*inaria*	*N*	χ^2
G1	*op*0	*o* & *w*	10	11	21	0·048
G3	*blw*5	*w*	16	20	36	0·444
G14	*oo*0	*o* & *w*	21	12	33	2·455
G15	*ow*4	*o* & *w*	16	14	30	0·133
G17	*op*1	*o* & *w*	67	63	130	0·123
G18	*op*0	*o* & *w*	60	63	123	0·073
G22	*op*5	*o* & *w*	17	16	33	0·030
G25	*oo*0	*o* & *w*	33	31	64	0·063
G26	*oo*0	*o* & *w*	140	130	270	0·370
G29	*brw*2	*o* & *w*	19	17	36	0·111
G32	*brw*3	*o*	33	21	54	2·667
G35	*brp*0	*o*	16	12	28	0·571
G37	*brp*0	*o*	21	26	47	0·532
G51	*op*4	*o* & *w*	96	71	167	3·743
G54	*op*4	*o* & *w*	41	42	83	0·012
G59	*blw*0	*o* & *w*	31	39	70	0·914
G60	*op*4	*o* & *w*	35	45	80	1·250
G76	*brp*1	*o* & *w*	25	19	44	0·818
G79	*oo*0	*w*	14	15	29	0·034
G81	*blw*0	*o* & *w*	29	30	59	0·017
G84	*brw*1	*o* & *w*	13	7	20	1·800
G85	*bro*0	*o*	6	6	12	0·000
G88	*blw*0	*o* & *w*	8	6	14	0·286
G98	*blw*1	*o* & *w*	58	46	104	1·385
G103	*blw*6	*o* & *w*	10	9	19	0·053
G115	*brp*3	*o* & *w*	30	17	47	3·596
S127	*oo*0	*o* & *w*	21	26	47	0·532
S128	*oo*0	*o* & *w*	4	4	8	0·000
S136	*oo*4	*w*	20	7	27	6·259*
S137	*blw*0	*o* & *w*	56	35	91	4·846*
S139	*oo*3	*o* & *w*	11	9	20	0·200
N144	*blw*0	*o* & *w*	22	19	41	0·220
N146	*oo*0	*o* & *w*	4	7	11	0·818
N147	*blw*3	*o* & *w*	16	11	27	0·926
N150	*oo*0	*o* & *w*	16	14	30	0·133
N151	*ow*10	*w*	21	9	30	4·800*
M152	*blw*0	*o*	55	42	97	1·742
SA153	*bro*2	*o* & *w*	4	4	8	0·000
N154	*blw*0	*o* & *w*	17	16	33	0·030
T159	*blw*3	*o* & *w*	15	9	24	1·500
$\sum \chi^2_{(40)}$						43·535
Total progeny			1147	1000	2147	10·065*
Heterogeneity $\chi^2_{(39)}$						33·470

* Indicates that segregation rejects H_o by $P<0·05$.

epistatically with the M locus. Indeed, the forewing segregations in broods S136 and N151, from *oo*4 and *ow*10 parents respectively, all the progeny of which had substantial amounts of hindwing white, suggest that many of the offspring were phenotypically "misippus" despite being of "inaria" genotype. These two broods, segregating 20:7 and 21:9, fit 3:1 satisfactorily but reject 1:1. However, they must be backcrosses as they came from *inaria* parents. This phenomenon occurred on a smaller scale in many other broods and no doubt explains the excess of "misippus" offspring found in the progeny test on backcross broods. The F2 broods are less prone to this source of bias as only $\frac{1}{4}$ of the progeny is genetically "inaria" and they show no deviation from expectation in the progeny test.

Our data do not support Ford's (1953) general conclusion that F2 segregations for *misippus*: *inaria* approach 2:1. The four broods he analysed segregated 99 *misippus* to 47 *inaria*, an excellent

Table 4 The effect of hindwing white on the forewing phenotype of *mm* (*inaria*) butterflies in the broods detailed in tables 2 and 3

Hindwing phenotype	Forewing phenotype *brw*	Other intermediate	*oo*	Total
white	194	448	220	862
orange	28	384	446	858
Total	222	832	666	1720

$\chi^2_{(2)} = 205{\cdot}7$; $P < 0{\cdot}001$.

fit to 2:1 without significant heterogeneity, and he believed this result indicated selection against the homozygous dominant genotype. By comparison with our broods, 11 of which formally fit 2:1, but introduce no heterogeneity when incorporated into the F2 and backcross series, the correct interpretation for Ford's results is possibly that they were backcrosses showing a deviation towards the "misippus" phenotype due to epistasis exercised by genes at other loci. In particular, two of our 2:1 broods (S136, N151) must be backcrosses as they had *inaria* mothers, both carrying extensive hindwing white, a character which also appeared in all the progeny. Two further clear 1:1 broods (G3, G79) in which the progeny had a high mean score for white segregated normally, a fact which emphasises the variability of the epistasis.

Interactions between fore and hindwing phenotypes may be further investigated in individual broods which segregated for one character only. Two broods (S124, M152) segregated at the M locus but all had orange hindwings: segregation for forewing was absolutely discrete as all progeny were either *blw* or *oo*. On the other hand, two broods (S136, N151) in which all offspring had white hindwings but segregated at the M locus, contained the full range of intermediate forewings in the *inaria-alcippoides* (*mm*) fraction. The difference between the two pairs of broods supports the hypothesis that genes giving white on the hindwing exercise variable epistasis over the M locus in the *mm* genotype.

Many broods (not detailed here) segregated for orange:white hindwing but were all *M*- ("misippus" forewing): the full range of hindwing classes was represented but not a single intermediate forewing (except for a few obvious contaminants). Finally, several broods (not detailed here) had entirely *mm* forewings but segregated for hindwing. The white progeny in most of these broods contained many intermediate forewing phenotypes although in two cases intermediates were few (S126) or absent (K141). The two exceptional broods show that hindwing white is not invariably epistatic over the "inaria" forewing.

To summarise, the *M* allele gives orange over the fore and hindwings except for the black apical half of the forewing and the three white areas. The *m* allele, which is fully recessive, extends the orange pigment over the entire forewing excepting only the black margins. Some, but not all, the genes giving hindwing white are epistatic to the M locus in the *mm* genotype, tending to prevent total displacement of black and/or white on the forewing and sometimes producing a general dilution of orange (broods T160, T161).

It would be premature at this point to embark on a discussion of the *misippus-inaria* polymorphism in relation to mimicry and sexual selection. Suffice it to say that the widespread occurrence of variable intermediates in the broods described here, reared in many different parts of Africa, suggests that factors other than close resemblance to forms *aegyptius* and *dorippus* of *D. chrysippus* may have selective value (Smith, 1976; Gordon, 1982). It is clear that earlier investigators (*e.g.* Pierre, 1973, 1980; Ford, 1953, 1975), with the notable exception of Edmunds (1969), have seriously underestimated the frequency, geographical range and, hence probably, the importance of these forms. The intermediate phenotypes are often abundant and may even be the most ubiquitous forms (Smith, 1976). Their high frequency and diversity, especially at times of peak density, suggests that apostatic selection may be operating.

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