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exist of which four third-order moments have been used in practice (White *et al.*, 1988).

Central moments vary as the orientation of the object changes. However, they can be converted to functions which do *not* vary with rotation of the object under study, and which are therefore known as moment invariants. Moment invariants have so far been formulated only for the first seven central moments. M1 measures size, M2 gives a measure of elongation, while M3 gives a measure of curvature; the parameters of shape measured by M4 to M7 have not yet been adequately understood in qualitative terms (R.J. White, pers. comm.). M2 to M7 can be made size invariant (Hu, 1962, cited by Dudani *et al.*, 1977), and were subject to a modified scaling as given in White *et al.* (1988, below).

Moment invariants have already been shown to be able to distinguish between the leaf shapes of two species of Betula trees and among three branch levels within each species (White *et al.*, 1988). Other shape descriptors have also been used, and although a number of these more clearly recovered within-tree differences, moment invariants do have the advantage that they are applicable to outlines of any object without alteration, and that they can be adjusted to reflect or ignore object size. Moreover, they can describe holes or

FIGURE 10.1 (opposite). The description of shape by moment invariants. In the computation of moment invariants (a) the study object is described in terms of cartesian (x and y) coordinates that coincide with its outline (as shown) or silhouette. Statistical parameters of these coordinates generate central momemnts. For instance, the variance of y gives the second central moment. Here, the variance of the y values of the coordinates 1,1; 3,1; 3,2; and 4,1 *ie.* the variance of 1, 1, 2 and 1 is 0.188. Each central moment is then transformed into a moment invariant that is independent of orientation. The parameters of shape (b) recovered by the first three moment invariants (M1 to M3) are size, elongation, and the degree of concavity or convexity respectively. The parameters of shape recovered by M4 to M7 have not yet been adequately understood in qualitative terms. For further explanation see text.

detached portions of objects, and can also be generalised to describe surface brightness patterns (*ibid.*). These features suggest that moment invariants would be especially suited to the analysis of Lepidopteran wing shape and pattern.

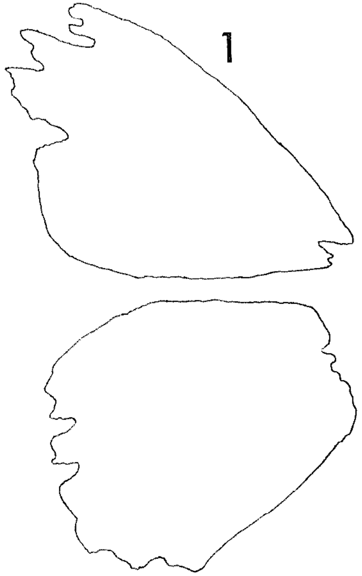
The present investigation set out to assess the extent to which moment invariant analysis could resolve differences between left and right, dorsal and ventral, and forewing and hindwing surfaces. Since a number of specimens had become damaged through natural wear during the course of the breeding programme, the extent to which damage might influence the measurement of the moment invariants was also assessed.

(ii) *Materials and methods*

Monochrome photographs of all the specimens were perused for wing damage or rubbing, and the damages were traced on to paper and the respective specimen recorded. The damages included tears and deletions near the wing margin (edge of wing), and holes within the wing margin (centre of wing). They also included areas from which scales had been lost through rubbing and which appeared as missing wing areas. The recorded damages were perused and classified into representative types. A number of specimens had suffered minor, but overall, rubbing or slight fading.

The preliminary investigation used series of identical monochrome photographs. Each photograph included untreated males no. 003 and no. 004 of STOCK 01 family no. 002, as these specimens were undamaged, and were reproduced from the same set of photographs perused in section 10.1. One photograph depicted their dorsal surfaces, the other their ventral surfaces. Thus eight wing surfaces were recorded for each specimen.

Thirty copies of each photograph were made. Ten of these were under-printed to varying degrees to simulate overall rubbing and fading ('rub' photographs). The remaining 20 were printed with equal exposure; of these, 10 were left unmodified ('control' photographs), the other ten being doctored to simulate the various kinds of damage ('damage' photographs). The 'rub' photographs were numbered on a scale from 1 (printed normally) to 10 (most under-printed). The 'damage' photographs were compiled as follows. The various kinds of damage were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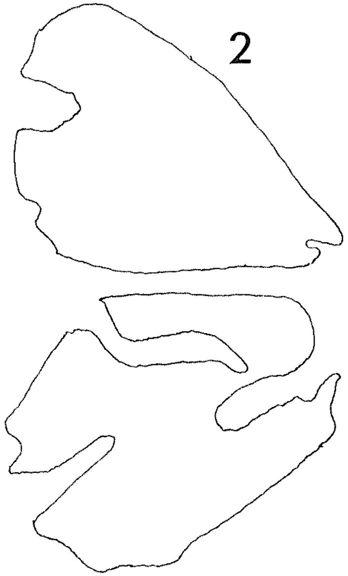
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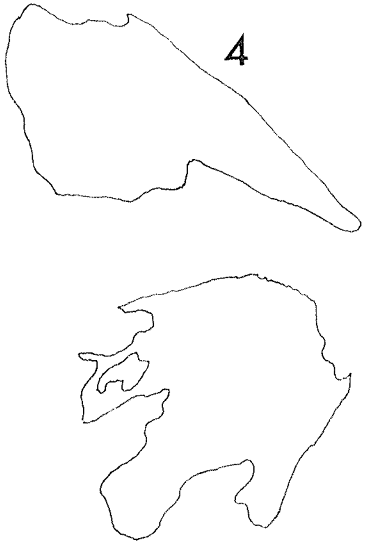
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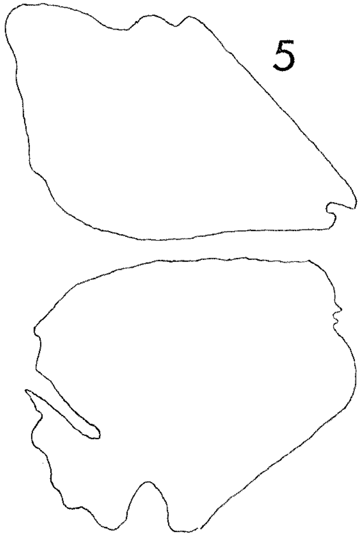
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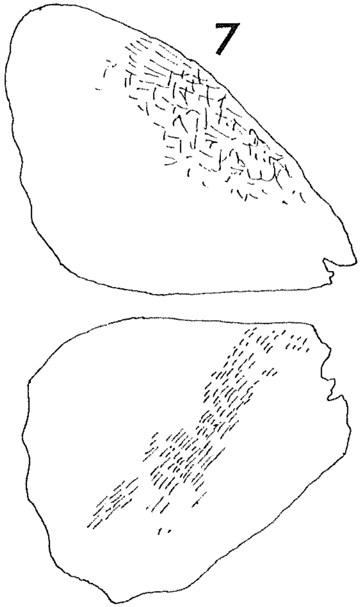
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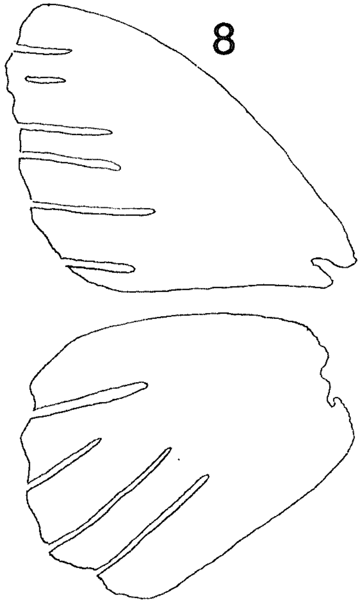
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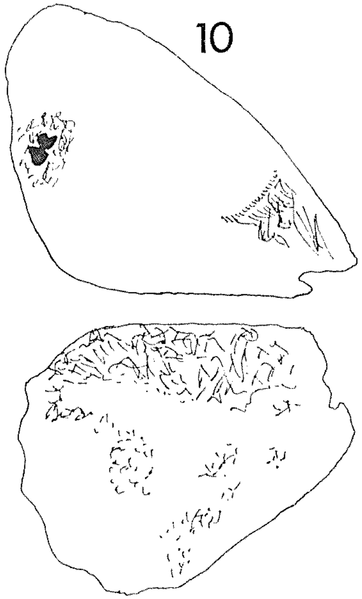
10

traced from monochrome photographs of specimens typifying each damage, and these then traced on to the photographic prints of specimens no. 01002003 and no. 01002004 described above. Ball-point pen was used which leaves the damage visible as an indented outline on the plate. The area corresponding to the damage was then whitened out with 'Tippex' correction fluid. Each damage was superimposed on both the ventral and dorsal surfaces and reversed between left and right. Damages specific to the fore- or hind-wing were retained as such, although as far as possible wings showing similar kinds of damage were reproduced together. The photographs of specimens no. 01002003 and no. 01002004 were given identical series of damages. Thus ten kinds of damage were applied to each specimen, and each kind was given a reference number (Figure 10.2).

The photographs were positioned beneath a Link Electronics type 109A video camera, fitted with a "studio quality" low distortion Vidicon tube and a Fujinon 17.5mm to 105mm zoom lens. A purpose-built interface (Chris Hawkins, after Howard, 1982) served as a digital converter which transformed the analogue television image into digital format.

The moment invariant analysis comprised two stages. The first involved the recording and storage on disc of the digitised image. This stage was run using 'Arbo, version 1.2' software (R.J. White) on a Research Machines 380Z computer with CP/M operating system. The study photographs were illuminated from above by a white fluorescent tube and four tungsten bulbs. 'Arbo, version 1.2 has threshold parameters that can be adjusted to select four cutoff levels of

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FIGURE 10.2 (opposite). A survey of the wing damages over the protocol. The figures are traced, actual size, from photographs of the left dorsal surface of specimen no. 01002003. The damages are numbered as coded for assessing the influence of damage on the measurement of moment invariants. The original specimens from which the damages are derived are listed in Appendix XVI. Damages 7-9 represent localised rubbing; damage 8 depicts rubbing along the wing venation. The dark background (unrubbed) in damage 10 is shaded to emphasise the shape of the marginal forewing rub. For further explanation see text.

greyness; in the present study the thresholds were equally spaced between -10 and 125. During display, the image is scanned vertically from left to right within horizontal sectors of the field, from the topmost sector to the bottom (Figure 10.3e).

The second stage computes the moment invariants. This stage was run using 'Arbo, version 1.6' software (R.J. White) on an IBM PC-compatible using the MS-DOS operating system. 'Cross-wires' are superimposed manually on the digitised image to segregate the four wing surfaces for analysis (Fig. 10.3f). The seven moment invariants are then computed for the images within each sector. M2 to M7 were scaled to render them size invariant as follows (after White *et al.*, 1988):

$$\begin{aligned} M2^{\sim} &= M2^{1/4}/r \\ M3^{\sim} &= M3^{1/6}/r \\ M4^{\sim} &= M4^{1/6}/r \\ M5^{\sim} &= M5^{1/12}/r \\ M6^{\sim} &= M6^{1/8}/r \\ M7^{\sim} &= M7^{1/12}/r \end{aligned}$$

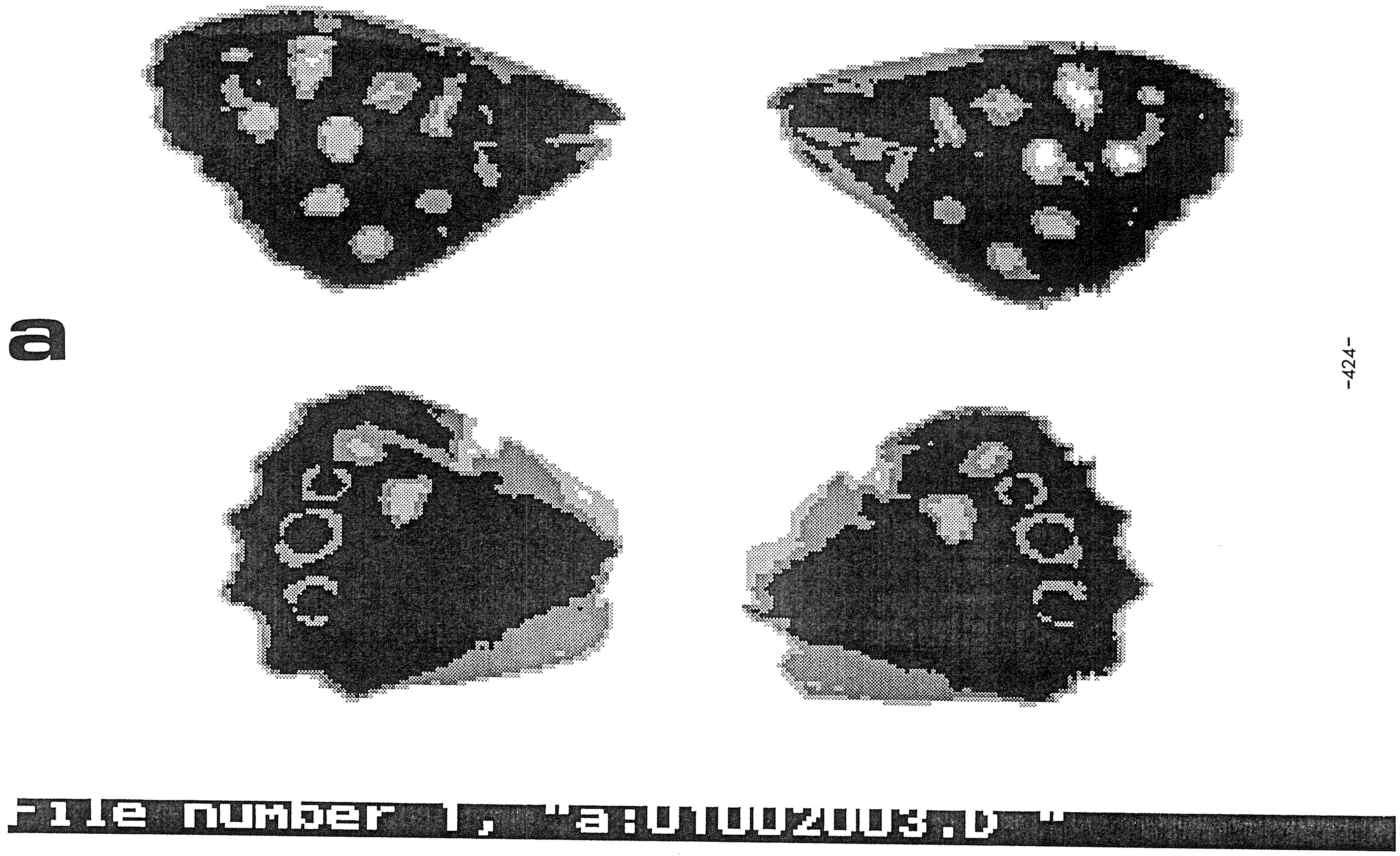
where $r = M1^{1/2}$

The moment invariant data were then transferred to an active file on the University's IBM 3090/150 mainframe computer. The computations were carried out using the SPSS^{x} statistical package.

FIGURE 10.3 (overleaf). Digitised images of the wing pattern.

(a) untreated F_1 male 01 002 003, dorsal surface;
(b) untreated F_1 male 01 002 003, ventral surface;
(c) untreated F_1 male 01 002 004, dorsal surface;
(d) untreated F_1 male 01 002 004, ventral surface;
(e) As for (d), with the image depicted during display;
(f) As for (d), with the cross-wires superimposed;
(g) cold shocked F_1 male 01 004 021, dorsal surface;
(h) cold shocked F_1 male 01 004 021, ventral surface;
(i) assimilated F_2 male 01 012 018, dorsal surface;
(j) assimilated F_2 male 01 012 018, ventral surface.

For further explanation see text


a
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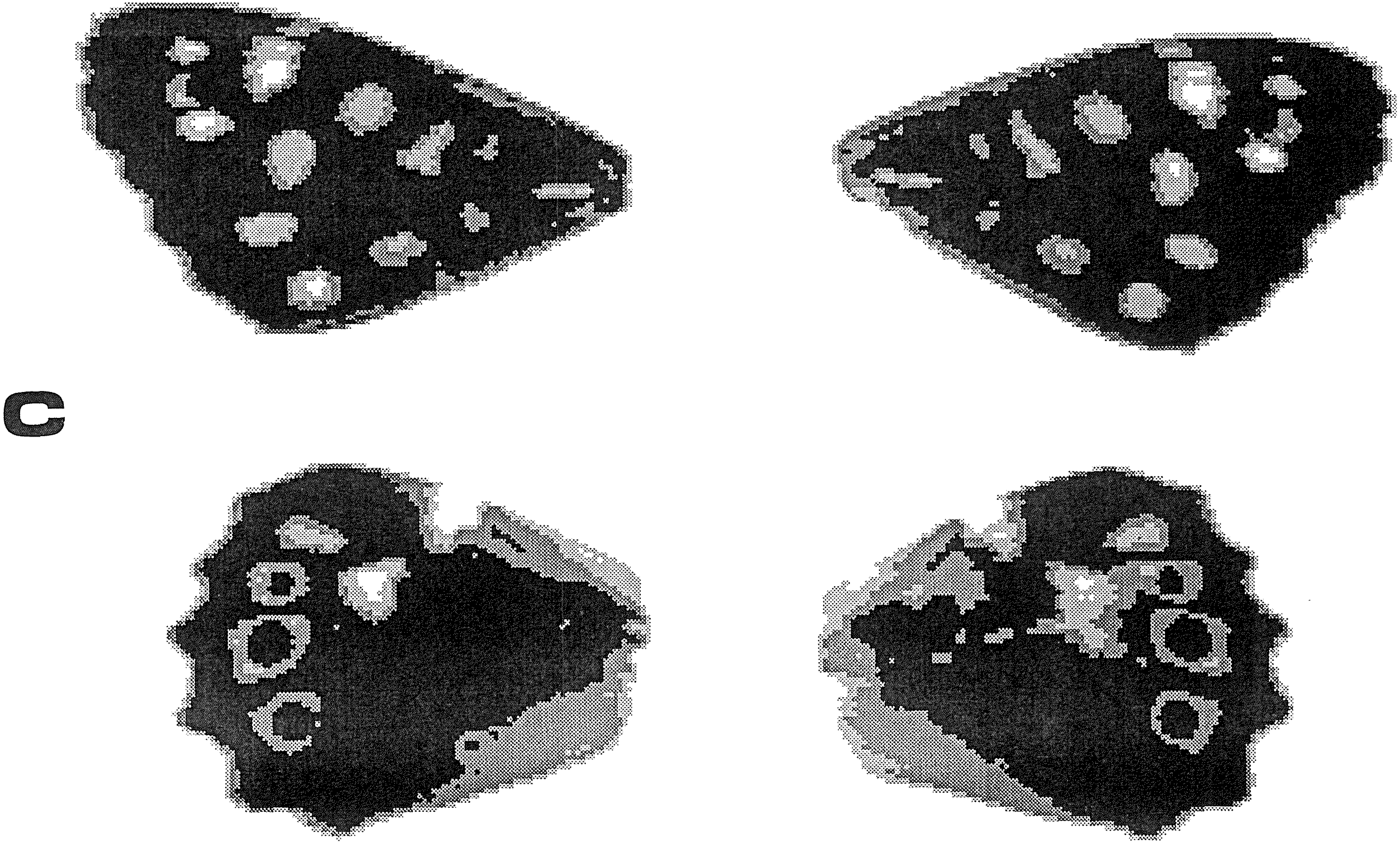
b



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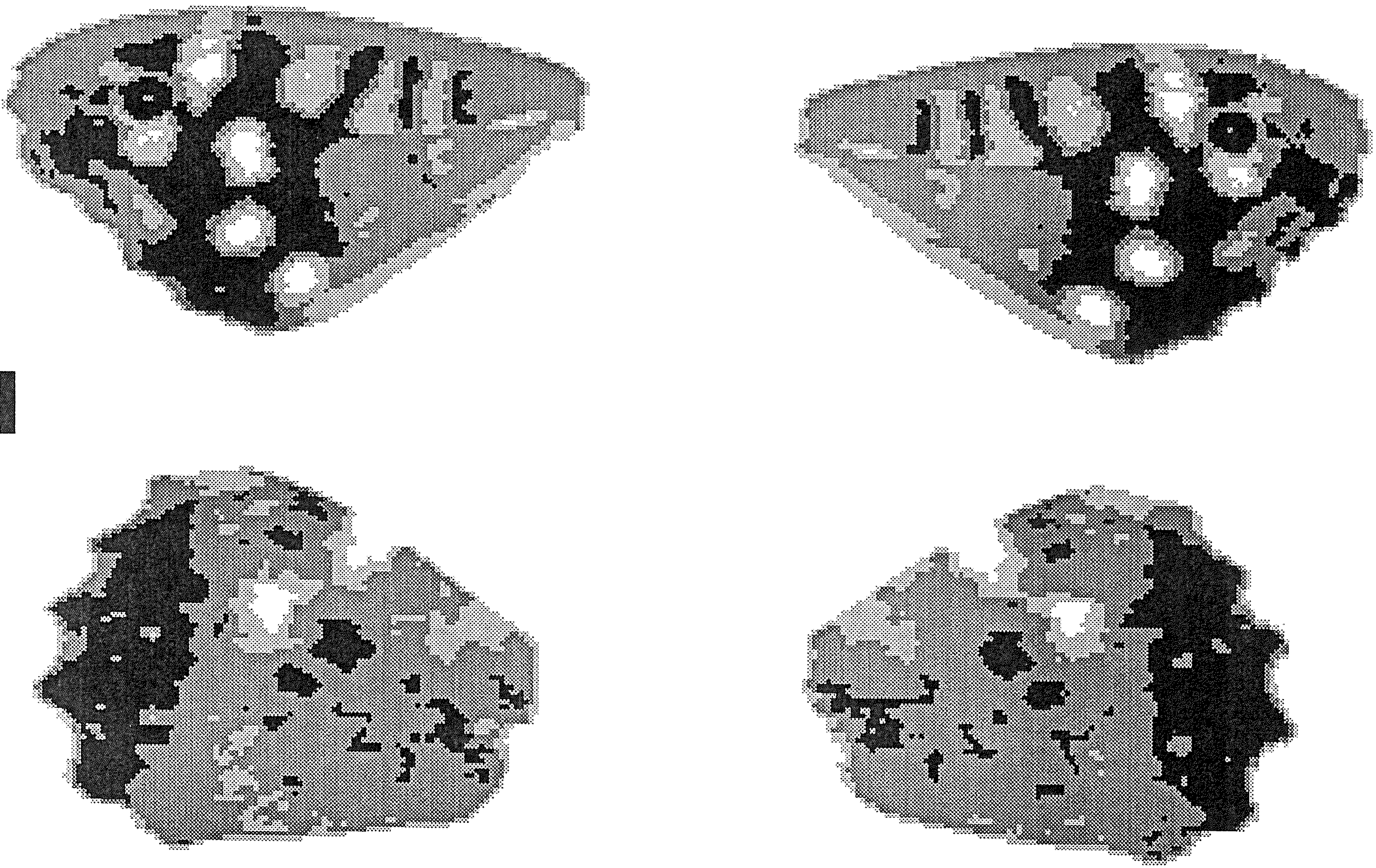

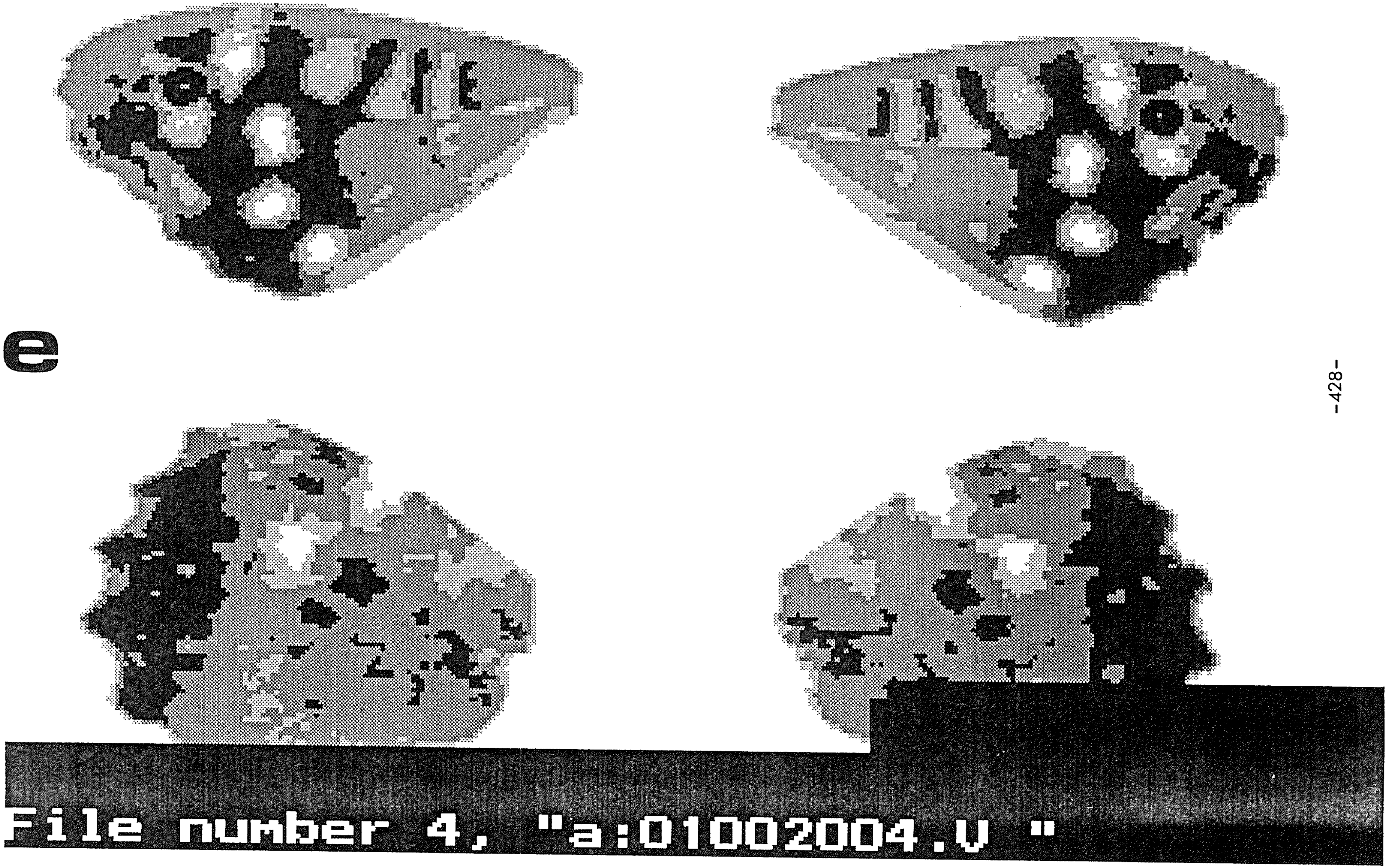
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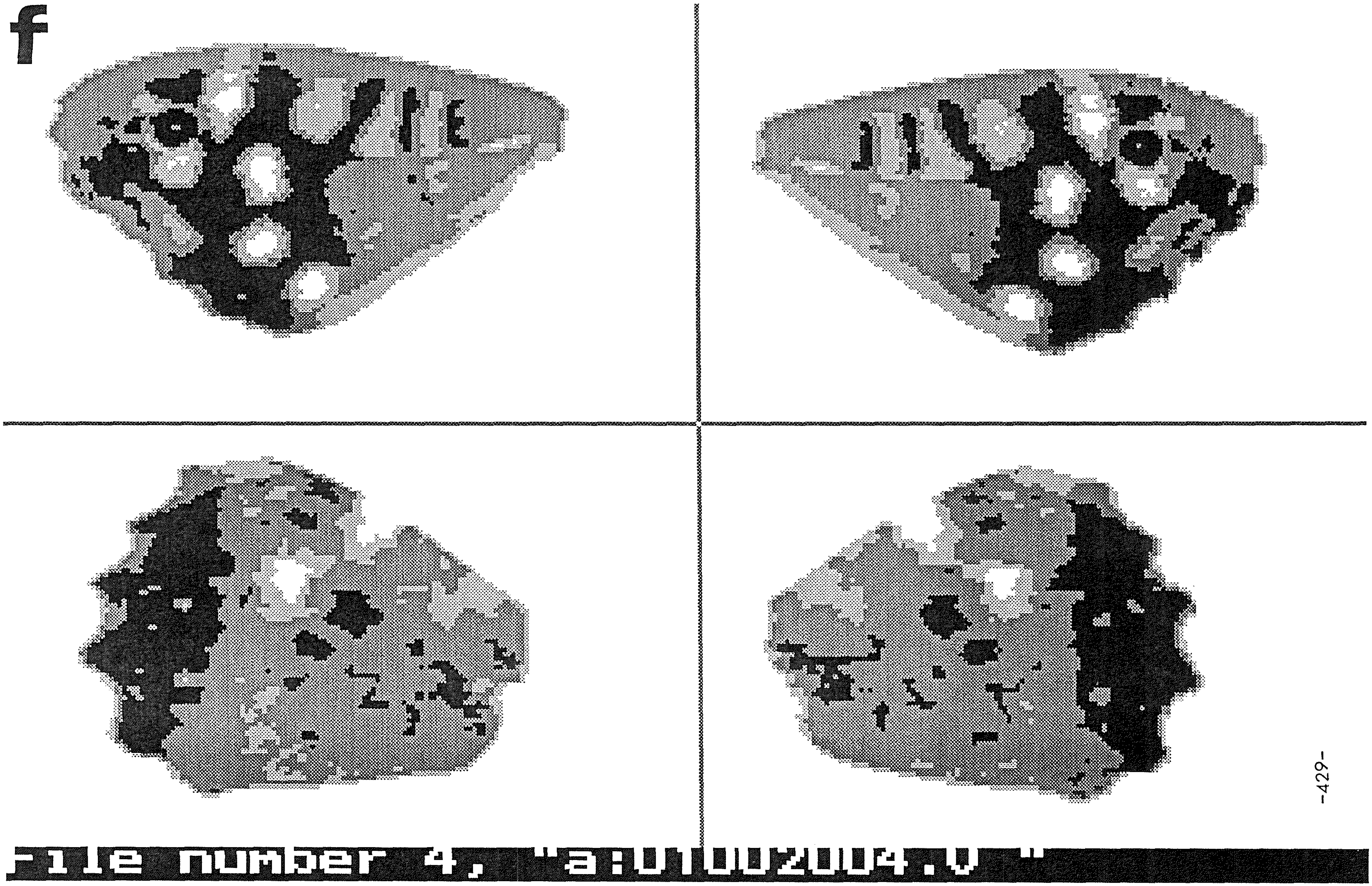

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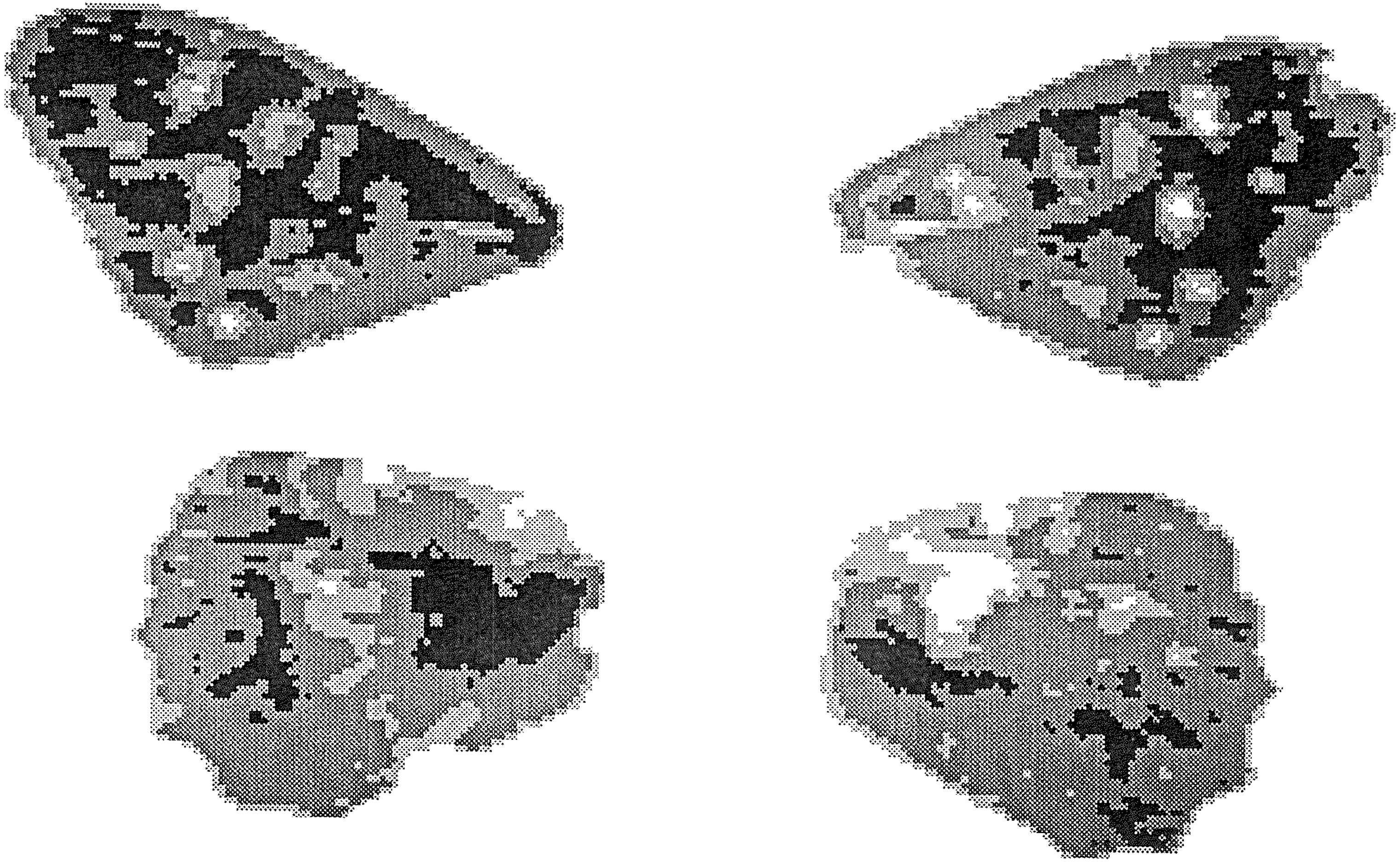
g



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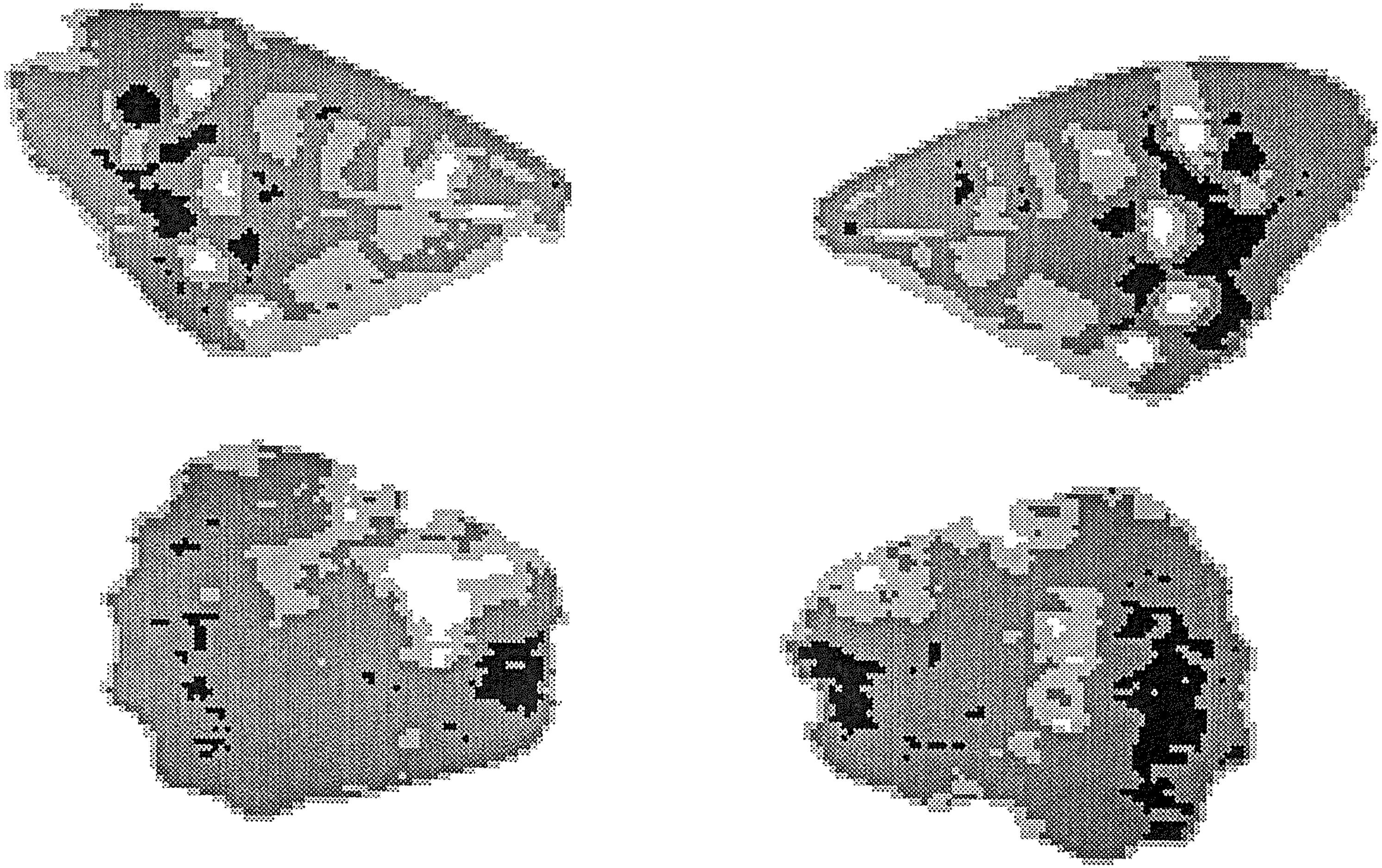
h



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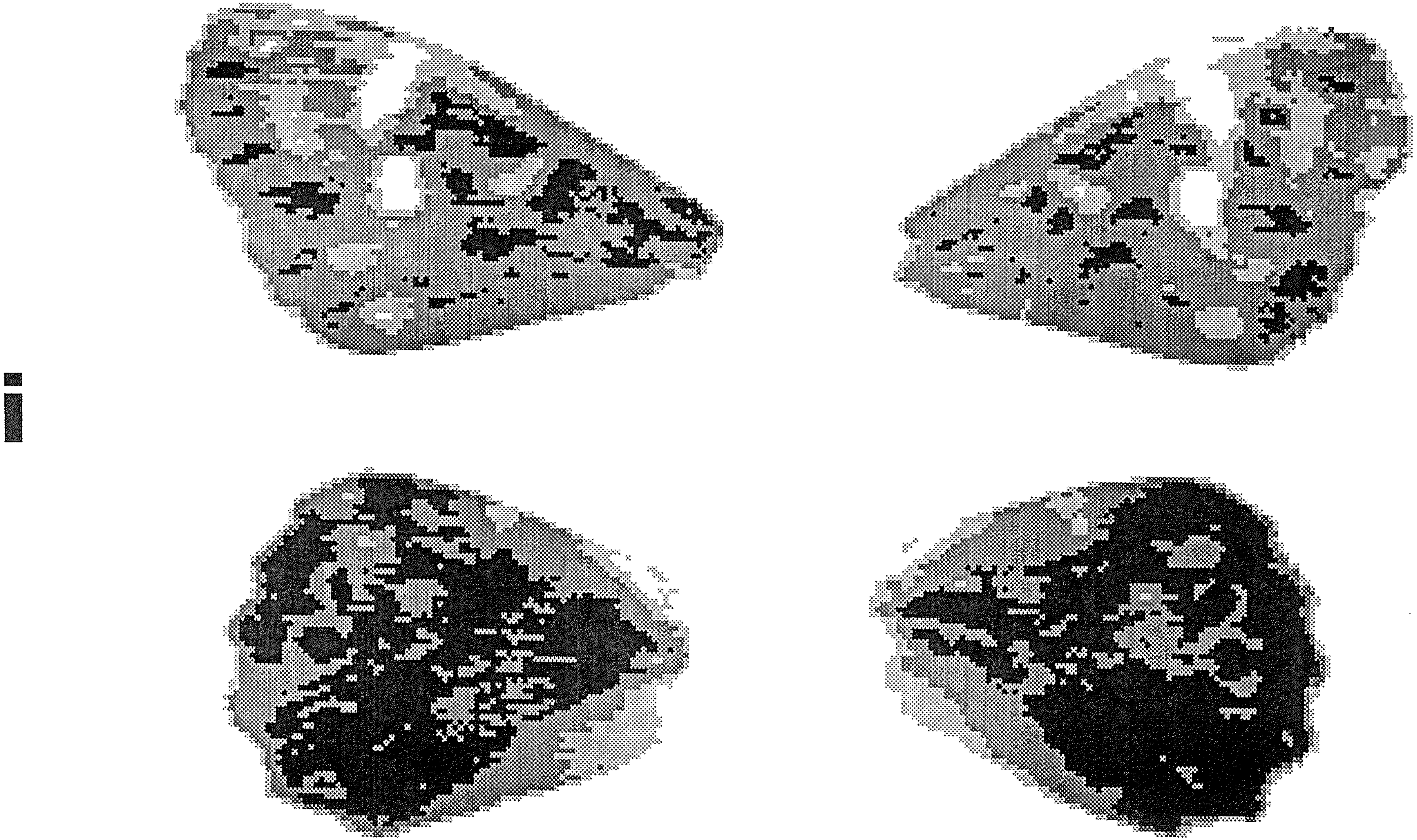

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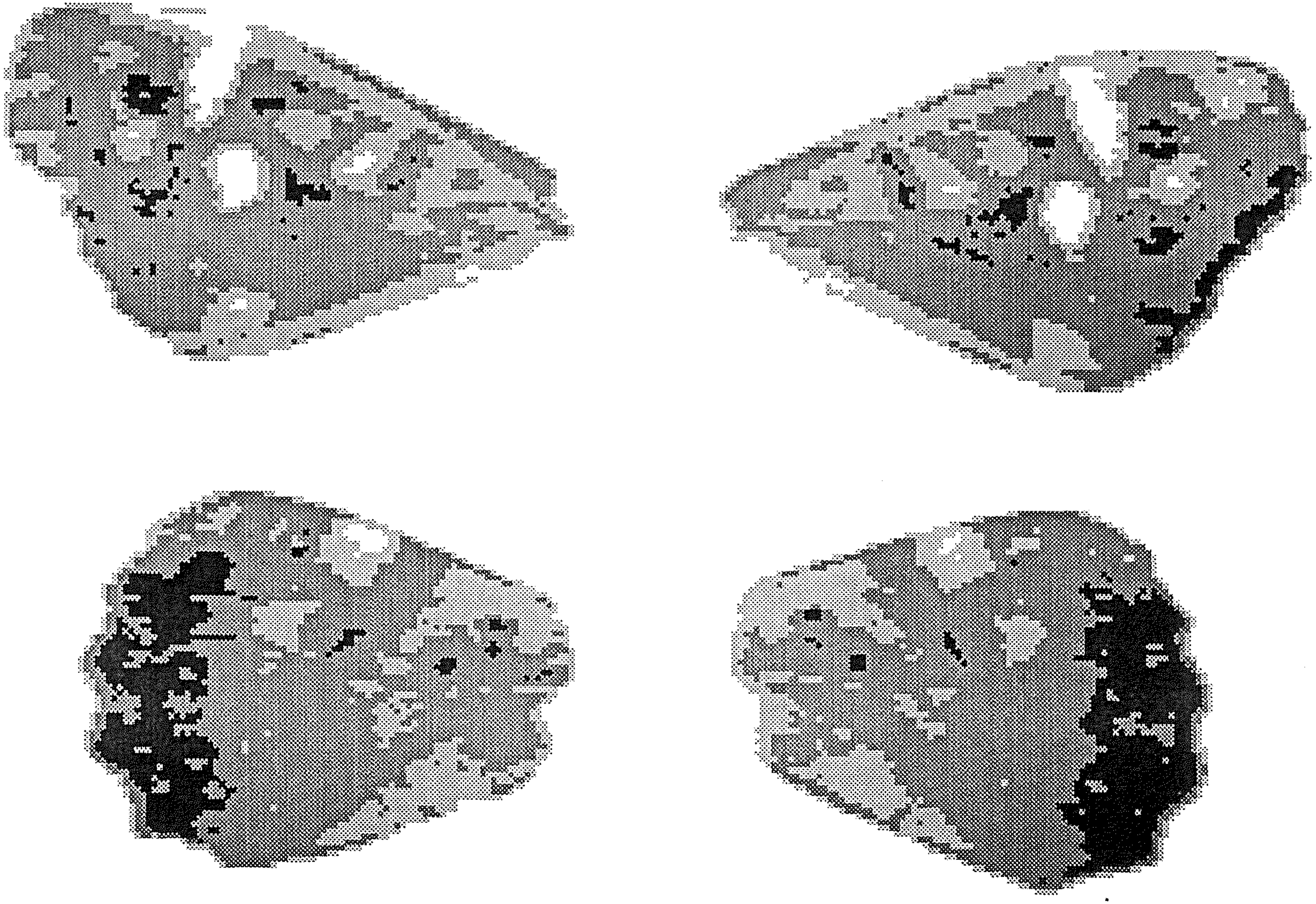


File number 8, "a:01012018.0 "

Results

The seven moment invariants were first compared between the forewing and hindwing (F/H, both surfaces grouped), between the dorsal and ventral surfaces (D/V, both wings and both sides grouped), and between the left and right sides (L/R, both wings and both surfaces grouped). These differences were examined for the individual moments by one-way analysis of variance (one-way ANOVA), and for the moments as a group by multivariate analysis of variance (MANOVA). The results, for the control images only, are shown in Table 10.I.

	M1	M2	M3	M4	M5	M6	M7	Multivariate
forewing/hindwing	***	***	***	***			***	***
dorsal/ventral	***	***	***	***	***	***	***	***
left/right	***	**	**	**				***

TABLE 10.I. Comparison of moment invariants between wing surfaces. M1 to M7 refer to the individual moment invariants, 'Multivariate' to the moment invariants as a group. The significance levels of the differences as estimated by one-way ANOVA and MANOVA respectively are reported: * 0.01<P≤0.05; ** 0.001<P≤0.01; *** P≤0.001. Non-significant differences are indicated by empty cells. For further explanation see text.

It is clear from Table 10.I that the moment invariants can recover differences between the fore- and hindwings, between the dorsal and ventral surfaces, and between the left and right sides.

M1 recovered a difference between the sides. This is unexpected given that M1 provides a measure of size, which would not be expected to differ between left and right. M5 and M6 did not recover any difference between the fore- and hindwings. Since the parameters of pattern resolved by these moments cannot adequately be described in qualitative terms, it is not possible to elaborate on this result in terms of familiar parameters of pattern. However, it is suggested that M5 and M6 as individual moment invariants should be excluded from investigations of forewing/hindwing differences.

The results of the MANOVA show that, *en masse*, the moment invariants are good at recovering axial (F/H, D/V and L/R) differences in wing morphology. This suggests that there are differences between the surfaces in their overall shape and pattern.

Interaction between wing (F/H) and surface (D/V), between wing (F/H) and side (L/R), between surface (D/V) and side (L/R), and between wing (F/H), surface (D/V) and side (L/R) were then examined using multi-way analysis of variance (multi-way ANOVA). The results are shown in Table 10.II.

	M1	M2	M3	M4	M5	M6	M7	Multivariate
side x wing		***	***			**	***	***
side x surface		***	**	**	***	***	*	***
wing x surface	***	***	***	***	***	***		***
wing x surface x side	***	***		***	***	*		***

TABLE 10.II. Interaction among the wing surfaces. M1 to M7 refer to the individual moment invariants, 'Multivariate' to the moment invariants as a group. The significance levels of the interactions as estimated by multi-way ANOVA and MANOVA respectively are reported: * 0.01<P≤0.05; ** 0.001<P≤0.01; *** P≤0.001. Non-significant differences are indicated by empty cells. For further explanation see text.

The results in Table 10.II reveal signifcant interactions among the surfaces. Interaction between wing (F/H) and surface (D/V) could be expected given that *Pararge aegeria* exhibits Oudemans' phenomenon: the fore- and hindwing are visibly more similar to each other on the dorsal surface than they are on the ventral surface (*cf.* Plates 1,2 and 10).

Interaction between wing (F/H) and side (L/R) suggests that the fore- and hindwing differ in their degree of asymmetry. This might be expected given that the levels of fluctuating asymmetry in the wingspan and in the size of pattern elements and interspaces were greater in the hindwing than in the forewing, especially in males (*cf.* section 9.21.iii). That the above interaction was recovered by M2 and M3 but not M1, suggests that the difference between the wings in their level of asymmetry, at least in specimen no. 01002003, is concerned more with curvature and elongation than with size.

Interaction between surface (D/V) and side (L/R) was recovered by all moments except M1. Since dorsal/ventral distinctions appear to be established very early in wing development (Sibatani, 1980; *cf.* section 9.36), such interaction most likely reflects differences between the dorsal and ventral surfaces in their levels of fluctuating asymmetry.

Three-way interaction (wing x surface x side) was recovered by all individual moments *except* M3 and M7. That M1 showed significant two-way interactions and significant three-way interaction suggests that the two-way interactions may coincide so as to render one or more of the eight (F/H x L/R x D/V) surfaces biased towards higher or lower values than the others. ~~That M7 showed showed a significant three-way interaction suggests that its apparent failure to recover any two-way interactions resulted from the latter falling just short of significance. Given a larger sample size, M7 might recover one or more two-way interactions, and this will require further investigation before a firm conclusion can be drawn.~~

The results of the MANOVA show that, *en masse*, the moment invariants are good at recovering two-way and three-way interactions among the wing surfaces.

Pairwise comparisons between the wing surfaces (F/H, D/V, L/R) were therefore repeated except that the surfaces under comparison were now *not* grouped with respect to the excluded variable. For example, comparisons between the left and right sides were conducted separately for each of the dorsal and ventral surfaces rather than for the dorsal and ventral surfaces together. The results are shown in Table 10.III.

The most striking difference between these comparisons and those in which the surfaces were grouped with respect to the excluded variable (*cf.* Table 10.I) is that the individual moments on the whole did *not* differ between the left and right sides on either the dorsal or ventral surface alone. This suggests that the original left-right difference recovered when the dorsal and ventral surfaces were grouped, may have resulted from a random asymmetry (in the specimen or in the photographic plates) coincident in direction on both surfaces, or from uneven illumination at either the photographic or image capture surfaces.

This result also indicates that for the purposes of digital image analysis, the left and right sides can be grouped during forewing/hindwing comparisons on each surface. That M5 differed significantly between the sides on each surface, would suggest that M5 not be used in such comparisons, although it might be particularly useful for recovering asymmetry *within* each of the dorsal and ventral surfaces.

The just significant ($0.01<P\leq0.05$) left/right difference recovered by M3 (dorsal surface only) and M4 (ventral surface only) may have arisen by chance, although analysis of a larger sample will be required before firm conclusions can be drawn.

		M1	M2	M3	M4	M5	M6	M7	Multivariate
Dorsal	L/R			*		**			***
Ventral	L/R				*	***			***
Dorsal	F/H	***	***	***	***		***	***	***
Ventral	F/H	***	***	***	***	***	***	***	***
Forewing	D/V	***		***	***	***		***	***
Hindwing	D/V	***	***	***	***	***	***	***	***

TABLE 10.III. Comparison between individual wing surfaces. M1 to M7 refer to the individual moment invariants, 'Multivariate' to the moment invariants as a group. The significance levels of the differences as estimated by one-way ANOVA and MANOVA respectively are reported: * $0.01<P\leq0.05$; ** $0.001<P\leq0.01$; *** $P\leq0.001$. Non-significant differences are indicated by empty cells. For further explanation see text.

That all the multivariate comparisons were significant at the $P\leq0.001$ level indicates that the moment invariants *en masse* are good at recovering F/H, D/V and L/R differences in overall wing morphology, although the sensitivity of multivariate analyses to surface interactions would call for individual analysis of each of the eight wing surfaces.

The ability of the individual moment invariants to recover artificial damage and simulated fading and rubbing was then examined with one-way ANOVA. The results are shown in Table 10.IV.

	CON v DAM	CON v RUB	CON v RUB v DAM
M1	ns	***	***
M2	ns	ns	ns
M3	ns	***	***
M4	ns	***	***
M5	ns	***	***
M6	ns	***	***
M7	ns	***	***

samples:

CON = control
DAM = damage
RUB = rub

TABLE 10.IV. The detection of damage and rubbing by moment invariant analysis. M1 to M7 refer to the individual moment invariants. The significance levels of the differences as estimated by one-way ANOVA are reported: *** $P \leq 0.001$; ns = not significant. The third column compares all three samples. For further explanation see text.

The most surprising result is that none of the moment invariants recovered any difference between the 'control' and 'damage' samples. Since the applied damages (Figure 10.2) are essentially pattern modifications, the result suggests that moment invariants might be rather refractory to *pattern* differences. However, that they *did* recover forewing/hindwing and left/right differences (within the control sample, Table 10.III), indicates that they are sensitive to *other* parameters of wing morphology, namely size and shape. Here, their apparent inability to recover *pattern* differences might be an *advantage* in that the latter would be less likely to incur bias in analyses of wing size and shape.

In contrast to damage, rubbing was recovered well ($P \leq 0.001$) by all the individual moment invariants except M2. Since the 'rub' sample was under-printed overall, the recovery of rubbing may reflect the relatively larger area of wing image affected. Moreover, moment invariants may be especially sensitive to differences in contrast and overall albedo (*cf.* Rohlf & Ferson, 1985). Indeed, the threshold settings used in the present analysis were such that the wing images of 'rub' samples nos. 9 and 10 were not resolved as differing in greyness from their backgrounds.

M2 measures the degree of elongation, which, since rubbing affected the overall image, would not be expected to differ with the degree of under-printing. M1, which measures size, however, *did* differ between 'rub' and 'control' images (Table 10.IV). It is possible, therefore, that the contours described by wing areas of similar albedo, and so of similar albedo within each 'rub' image, are concentric with the wing border.

Since cold shock can influence wing size and shape (sections 9.28 and 9.30), and since the expressivity and penetrance of such effects would appear to increase with the level of assimilation (section 10.1), it is concluded that moment invariants are a suitable parameter for investigating the occurrence and genetic assimilation of the effects of cold shock on wing size and shape. Yet a number of specimens did exhibit a lightening or darkening of large areas within particular wing surfaces (*cf.* section 9.28.ii), while the interspace colour among STOCK 01 specimens became more orange with inbreeding (section 10.1), when the apparent sensitivity of moment invariants to contrast and albedo could prove suitable for quantifying such effects. In the latter case, however, it would be essential to exclude obviously faded or rubbed non-experimental specimens from analysis.

Simple digitisation of the wing images into discrete levels of greyness itself highlighted certain pattern features (Fig. 10.3). Comparison of untreated male no. 01002003 and cold shocked male no. 01004021 (Fig. 10.3a-b and g-h respectively) clearly shows the loss of definition of the dark dorsal pattern and the loss of the ventral forewing eyespot pupil under cold shock treatment. Here, the ventral hindwing also displays a more uniform distribution of light and dark coloration with a notable reduction in the dark (black) pattern elements. In untreated specimen no. 01002004 (Fig. 10.3c-d) the distinct coloration near the costa and dorsum is clearly visible.

Specimen no. 01012018 (Fig. 10.3i-j) shows that rearing of assimilated individuals under cool temperatures, even in the absence of cold shock *per se*, can lead to further diminution of the dark dorsal pattern with a yet more extreme loss of definition. The interspaces on the posterior ventral forewing and the dark (black) patterning have been almost completely lost, while the ventral hindwing ground colour is more uniform than in either specimens nos. 01002003 or 01004021. Note that in specimens nos. 01004021 and 01012018, the diffusion of the markings is parallel to the transverse venation.

(iv) *The further application of digital analysis*

The foregoing investigation has shown that moment invariants can recover differences between the wing surfaces and that they were influenced by simulated fading and large-scale rubbing. That they were apparently uninfluenced by damage suggested that they might not well recover pattern differences, although the different *nature* of each damage (the 'rub' sample differed only in *degree*) might have obscured an ability to recover pattern differences.

Examination of the influence of particular kinds of damage, perhaps also using artificial patterns, might reveal those kinds of wing damage most likely to bias the analysis of defined wing samples. Moment invariant analyses of real wings might provide further insights into the effects of cold shock, the ways in which these effects are mediated, and their genetic assimilation. Here, a more precise understanding of the influence of particular types of damage would enable the study samples to be constructed so as to adequately exclude those specimens most likely to bias the results. Such real-wing analyses of Pararge aegeria are currently in progress, and the outcomes of these investigations are expected in the near future.

10.4. Genetic assimilation and population structure

Several instances of stray individuals have been reported. Gibson (1944) reports a stray in garden at Petersfield, Hamphsire, one mile from the nearest wood it might inhabit, while females were observed straying onto moorland from a nearby oak woodland in east Inverness-shire on 14th August 1956 (Davidson, 1956). Davidson (*loc. cit.*) suggested that these may have been blown from the Great Glen where it was windy on 9th August and had subsequently experienced light south-westerly winds. Refseth (1973a) suggested that single specimens observed at Stadsbygd, Norway may have strayed up to 100km, although he contended (*loc. cit.*) that these originated from much nearer, yet undiscovered, colonies. It is thus conceivable that female strays, if already mated, could found a new population. And although the species is not normally migrant, females regularly cross open fields (Baker, 1984), females which if mated could therefore spread the new population.

Indeed Barbour (1986) suggests that the spread of the species in south-east Scotland originated with a single stray or human introduction: in 1955, one vagrant was seen at Inverness, 60miles from the nearest known west coast localities, and in 1961 saw two near Inverness suggesting that it was now resident there. By the 1970s the species had become established on the Black Isle and inland south-west to Glen Affric, now occupying an area of about 400 square miles. It then expanded its range to the north, south and east, although its further movement westwards was restricted by mountains. Barbour (1986) estimated its rate of spread as three miles per annum. He argues (*loc. cit.*) that the initial population would be atypical of its parent population, and would spread rather slowly on account of its impoverished gene pool. This would reduce its viability for a number of years, although during this time the population could still spread (*ibid.*).

However, as shown in Chapter Eight, inbreeding does not tend to reduce viability except that of 1st instar larvae - and then only in conjunction with drought or disease, and of the pharate pupa *following cold shock.* As Oliver (1981) points out, genetic load concerns more the genic balance the individual rather than population structure as a whole. Yet even under adverse conditions, populations can recover.

P. aegeria was reintroduced to a locality near Doncaster on the limestone belt in Yorkshire, using 20 fertile females from a locality outside the belt to guard against inbreeding, on at least two separate occasions (Rimington, 1986). Although none were sighted in the appalling spring of 1983, by the end of August 1984 the butterfly was very common. Thus even when faced with a new habitat and having then possibly suffered a drastic decline, the species can still revover (*ibid.*). Moreover, it is possible that the potentially lethal effects of cold shock might become segregated from its developmental prolonging effect (below).

Indeed, Barbour (1986) concedes that the initially slow spread of the founding population above is more likely due to the edge of the population moving at a rate proportional to its radius until it reaches some maximum limiting value. These new populations, while bivoltine like the populations from which they originated, have changed their habitat usage from deciduous woodland typical of the west coast, to coniferous pine forest typical of more inland locations, so implicating a minor evolutionary shift in its climatic tolerance (*ibid.*). Coniferous habitats tend to be cooler than deciduous (Geiger, 1950).

It is therefore conceivable that the species could undergo changes in phenotype or voltinism. On the Isle of Canna, Hebrides, U.K., the species produced two broods for the first time there in 1977, after the climate had been warmer since 1975 (Campbell, 1978).

The above expansion of the species range in Scotland appears to have followed a decline in the previous 100 years, the species having previously been widespread there as well as in Northern England. Indeed, with the exception of subspecies oblita in Argyll (Dennis, 1977), the *original* populations in west Scotland are not taxonomically distinct (Downes, 1948), although it is uncertain as to whether the newer ones (established 1870-1948) are oblita or not (Downes, 1948). During this re-expansion, the species increased even in agricultural areas and highland fringes marked by human activity, again highlighting its tolerance. Downes (1948) argues that the earlier decline resulted from delicate alterations in the biological balance or climatic conditions, rather than to an edge of range effect, since the species occurs further North and West on the continent. But the latter populations *are* taxonomically distinct (Higgins, 1975;

Henriksen & Kreutzer, 1982). Thus it is possible that its decline in Scotland was an edge of range effect, and that the species declined because it could not (or simply did not) adjust, whereas the continental subspecies, in particular Northern ssp. pallida, did, conceivably through genetic assimilation.

Phenotype and voltinism changes might even come about through a simple change in behaviour. The nature of males' territorial flights are certainly known to depend on habitat structure (Wickman & Wiklund, 1983: spiral flights in deciduous woodland; patrolling chase in open coniferous forest), and the micro-habitat in which the females choose to lay their eggs could (*cf.* Shreeve, 1986) influence their susceptibility to later frost exposure; the founder populations at Stadsbygd, Norway too occupy a rather open habitat - namely birchwood with juniper (Refseth 1973a). The way in which such cooler habitats may effect the genetic assimilation of developmental (life-cycle duration and voltinism) and phenotype changes forms the subject of the next two sections. Since large increases in range from originally restricted (British) distributions have also occured in Polygonia c-album and Limenitis camilla (Ford, 1957a) and, more recently, in the Lulworth Skipper, Thymelicus lineola (Thomas & Webb, 1984), the findings have implications for other species.

10.5. Evolution of voltinism strategies

In section 8.13.iii it was postulated that a lineage exposed to winter frost shock and then experiencing a cool summer, could give rise to summer diapause larvae or pupae, and that these might give rise to adults similar in phenotype to ab. cockaynei - as were laboratory specimens nos. 01012018 and 01012109. It was also postulated that this could form the basis of a change from bivoltinism to univoltinism in the species, and this possibility will now be considered more fully.

Since cold shock prolongs pupal development (sections 7.7 and 7.8), winter frost might result in a number of generation 1.i. individuals eclosing rather later than usual. Under a following cool summer, larvae derived from these adults would develop slowly (section 8.13.iii).

Such larvae would appear to have three options open to them. The first is that, as with laboratory specimen no. 01012019, the larva develops slowly to pupate in late summer (August). Since daylength is still greater than the critical for pupal winter diapause (*cf.* Lees & Tilley, 1980), the pupae do not initiate winter diapause, and so eclose in September. Under the cool autumn conditions, the resultant larvae would not develop sufficiently fast to yield winter pupae, and so would overwinter as larvae. These would then eclose as adults of generation 1 part ii.

The second is that the larvae form winter diapause pupae if they pupate later than September (Wiklund et al, 1983), September being the early limit for diapause pupae (Shreeve, 1985). These would more likely experience frost, again prolonging pupal development, which together with the generally prolonging effect of the cooler non-frost temperatures would produce a later-than-usual generation 1.i. Their eclosion might even coincide with generation 1.ii.

The third possibility, as with laboratory specimen no. 01012018 (section 8.13.iii), is that the larva pupates in late August/early September to form a summer diapause pupa. That the photoperiod is still greater than the critical for winter diapause, suggests that in assimilated individuals, cool (but non-frost) temperature can override summer photoperiod. The summer photoperiod still, however, prevents *full* (winter) diapause, but the overriding cool temperature also prevents direct development, the result being that the pupae undergo a *partial* (summer) diapause to eclose in November.

The third option, however, unlike the previous two, does not appear to be typical for the species in nature, and it is proposed that the strategy is stable only as a transitory stage in a transition from bi- to univoltinism. Firstly, the adults might develop within the pupae, only to die before eclosion should the November temperatures suddenly fall (*cf.* Goddard, 1962; Shapiro, 1976, 1977b). Secondly, even if the adults did eclose and breed, the resulting ova, being laid so late in the season, might too succumb to a sudden frost or simply perish in the cooling late autumn/winter climate; eggs need a temperature of at least 6.8°C to hatch (Shreeve, 1985), and oval diapause does not appear to be open to the species (Lees & Tilley, 1980). Thirdly, if there was no such frost and the eggs did hatch before the temperature fell below about 7°C, the resulting larvae would develop too slowly for winter pupation since first instar do not feed below 8.0°C (Lees, 1962). And even if the November to December temperatures did enable them to feed, it is likely that the January temperatures (*cf.* Dennis, 1977) would prevent them doing so - and may even kill them as final instar larvae do not tolerate cold well. Thus, the offspring of summer diapause pupae would almost certainly overwinter as larvae, possibly feeding intermittantly up to their third instar, diapausing, then resume their development in early spring. These would then eclose as adults of generation 1.ii.

Thus under cooler winters and summers, there is a tendency for more individuals to overwinter as larvae and eclose as generation 1.ii, while those that overwinter as pupae produce a later-than-usual generation 1.i, especially should they experience frost early in pupation. With assimilation, their prospective generation 1 (both parts i and ii) would eclose increasingly late in spring, while, under cool summer conditions, their resultant generation 2 larvae (of both parts i and ii) would be present increasingly late in summer and autumn and so be more likely to yield diapause (rather than direct-development) pupae. (Those individuals that might complete adult development in would be least likely to continue the next generation). And of course, these diapause pupae might in turn experience frost. Thus, under generally cooler climatic conditions (as with increasing latitudes and altitudes, or the onset of geological periods), and with assimilation, there is a tendency for the first generation to eclose later and for the second not to eclose until the following spring. Such a shift in voltinism strategy might account for the origin of univoltine races and subspecies, such as race drumensis in Snowdonia, U.K. (Dennis, 1977), and the northernmost subspecies, pallida (Henriksen & Kreutzer, 1982). The larger size of race drumensis suggests that it overwinters as a larva (*cf.* Wiklund *et al.*, 1983); and that it has the appearance of generation 1.i yet flies in July, suggests that its annual brood derived from a generation 1.i lineage whose larvae hatched increasingly late in the season until the cool autumn prevented them pupating in time for winter. Indeed, within its range (above the tree line), the race forms an altitudinal cline (Dennis, 1977).

The next question is, how might assimilation come about, assuming that the lineages must remain true to treatment? (*cf.* section 8.5; this assumption is taken up here to assess the validity of the hypothesis in its least likely formulation). Firstly, as discussed in section 10.4, the minimum number of individuals needed to found a population is a single pair, so an assimilated lineage could originate even if only a very few individuals were affected by frost. Secondly, since adults may wait to eclose if their development coincides with adverse conditions - and adverse conditions (insufficient warmth for adult activity) are more likely under climates where frosts are prevalent - the affected individuals might eclose synchronously. But this would not necessarily prevent them from pairing with unaffected individuals, even were the latter to eclose slightly earlier. However, it is conceivable that a spell of cold weather following the eclosion of unaffected individuals, *further* delays eclosion of the affected ones. Thus, the emergences of the affected and unaffected individuals might become increasingly disparate, possibly dividing the population into two breeding groups. Indeed, temporal subspeciation through [albeit genetic] differences in development rate has been implicated in Maniola jurtina (Thomson, 1971). Then, - as with the hypothetical 'four year acceleration' in periodic cicadas where more and more individuals leave the lagging brood as assimilation proceeds (Lloyd & White, 1974; *cf.* section 3.12), the comparable 'deceleration' in Pararge aegeria would involve more and more individuals leaving the unmodified 'brood' (generation 1.i) and entering the assimilated 'brood'. In this way, transition from bivoltinism to univoltism might be completed. The butterfly certainly has genetically determined 'slow' and 'fast' larval development (Robertson, 1980b).

STOCK 01 families 004 and 012 showed that assimilation of cold shock-mediated prolongation of pupal development was evident after the first generation of treatment, and, in the case of family 012 reared at 14.8°C, that cooler control range ('cool summer') temperatures interacted with assimilation to prolong larval and pupal development after only one generation of treatment. As in Papilio zelicaon (Shapiro, 1976; *cf.* section 2.3), the genetic assimilation of voltinism changes *in nature* can be *completed* in as few as 200 generations.

As explained in section 10.4, even with initially high levels of inbreeding and under adverse conditions, populations can recover. Moreover, inbreeding might facilitate the assimilation of adaptive changes (section 8.10) (prolonged larval and pupal development would be adaptive in preventing the adults eclosing too late in autumn or too early in spring - only to succumb to an imminent frost). Furthermore, canalisation of such responses can result as a very corollary of assimilation, and this is now illustrated using pupal duration as the exemplar.

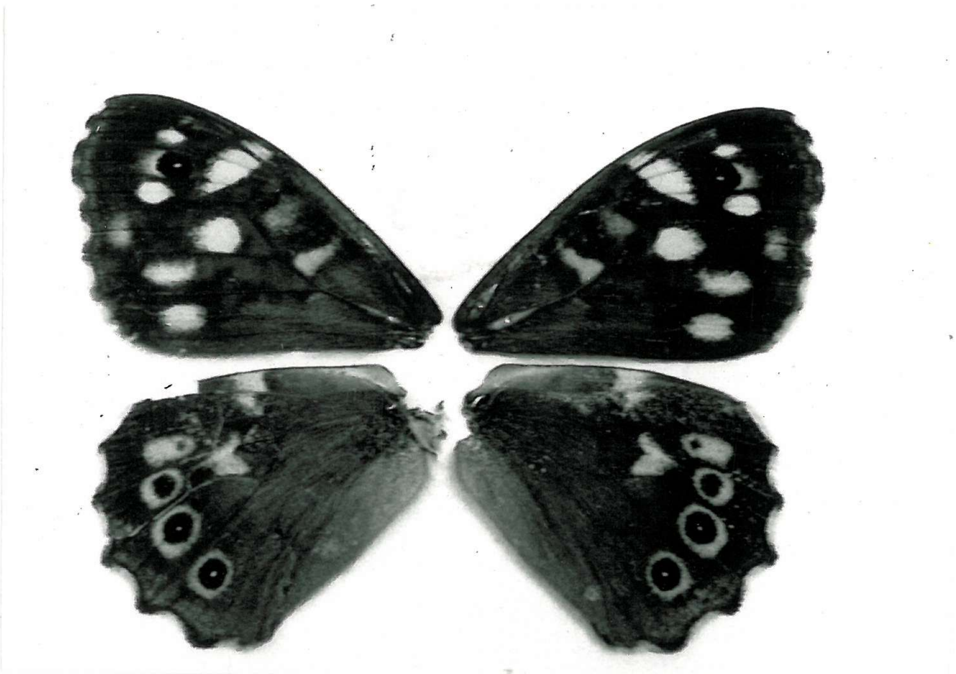
It is suggested that there is a spectrum of susceptibility to cold shock comprising three main classes:

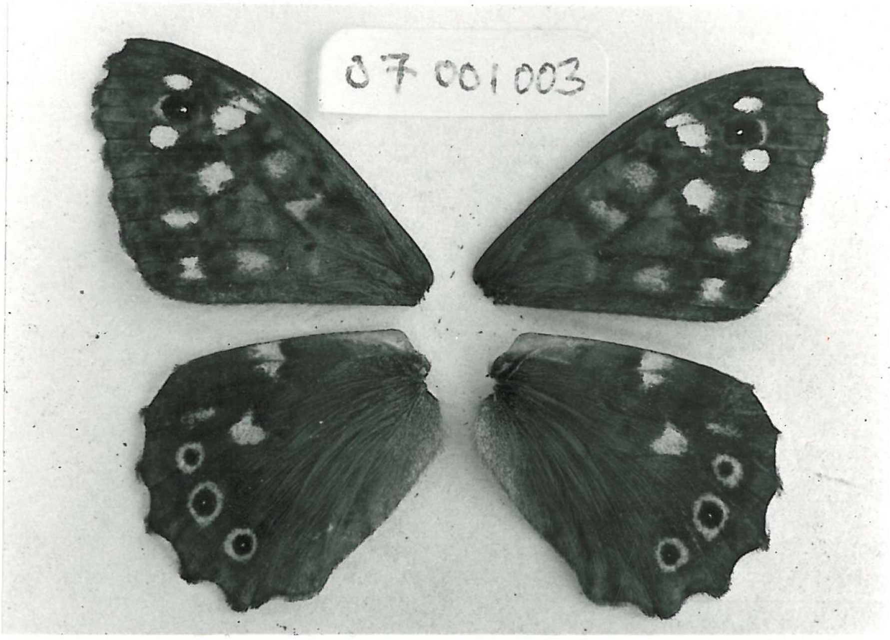
(1) Unreactive
(2) Viably reactive
(3) Inviably reactive

Unreactive individuals are completely canalised against the effects of cold shock; they are unaffected by it. Viably reactive individuals vary in their degree of canalisation against cold shock; their development time is increased to varying extents by cold and they survive the shock. Inviably reactive pupae are killed by treatment; they are effectively uncanalised and their development is so disrupted by cold that it cannot be restabilised.

The model proposes that assimilation shifts some of the otherwise unreactive range towards the viably reactive range so that proportion of unreactive pupae decreases at each generation. At the same time, some of the otherwise viably reactive range are shifted into the inviably reactive range which thus imposes a limit to the degree of reactivity still compatible with life. The result is an increase in the average magnitude of the response which also becomes less variable as the unreactive range gets truncated, as with pharate pupal duration.

The incidence of phenocopies (individuals manifesting the trait with respect to which assimilation is being considered) will remain low if the eliciting stimulus is but occasional, maladaptive, or occurrent only subsequent to reproduction, when there will be no opportunity to segregate the lethal response, so preventing assimilation from progressing beyond the limit of viable expression.

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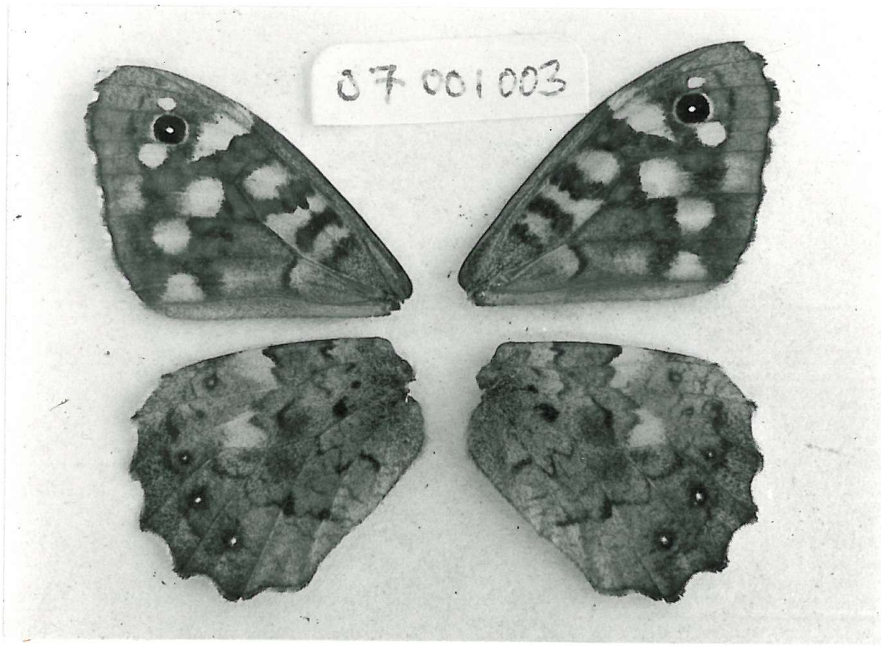
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Hence the potentially lethal effect of cold inherently prevents the assimilation of phenocopies under inappropriate conditions. But when the incidence of phenocopies is high, the lethal effect might be eliminated completely thus enabling their full assimilation. This is more likely to happen when the eliciting stimulus is repetitious or encountered by large numbers of individuals; the phenocopies must necessarily be adaptive lest selection should keep them at low frequency. Yet even were the response maladaptive for the conditions under which the stimulus was initially encountered, it could become further assimilated were the phenocopy animals to choose or encounter a new niche in which the response was acceptable. And to understand this, we must now consider phenotype.

10.6. Evolution of subspecies phenotypes

On account of the similar appearances of a wild-caught ab. cockaynei (*cf.* Russwurm, 1978) to assimilated cool-reared specimen 01012018 (Plate 9), it was suggested that the former might represent a natural case of assimilation - an individual that derived from cold shocked parents and experienced a cool summer as a larva. A similar phenotype was present in the first generation of cold shock treatment in male 01004021 (Plate 9). Of course, it is possible that the wild caught aberrant resulted from a genetic mutation, although its laboratory phenocopy still shows that such phenotypes *can* result from cold shock, and appear through assimilation in the offspring of cold shocked parents.

PLATE 10 (opposite). A wild-caught aberrant and a cold shock phenocopy. (Top) Cold shocked female specimen no. 01004016 showing marbling of the dark dorsal forewing ground colour. (Centre and bottom) Dorsal and ventral surface respectively of a wild-caught second generation male from West Wood, Hursley, Hampshire, with a similar marbling and ripple pattern on both surfaces. For further explanation see text.

The phenotype of cold shocked male 01004021 was very similar to that of subspecies pallida, which typically has a greyer dorsal surface and less distinct ventral markings, while the ventral hindwing is paler with poorly defined markings (Henriksen & Kreutzer, 1982). Since it represents the northernmost limit of the species' range (central-north Norway), where the winter *and* summer climate is cooler, it is possible that this subspecies arose through cold-shock phenocopying and genetic assimilation.

Since cold shock phenotypes may represent *ancestral* facies (Shapiro, 1973b), it is possible that pallida typifies the original condition of Pararge aegeria. P. aegeria thermoregulates by dorsal basking (Shreeve, 1984), and although the pigmentation of pallida is greyer, and hence lighter in overall appearance, the timing of its univoltine eclosion may have enabled it to spread to and colonise cooler climes.

The orange pigmentation of the interspace markings in subspecies aegeria might reduce water loss and radiation damage in warmer climates. In the Satyrid Melanargia galathea, French populations inhabiting warm, dry areas are more heavily pigmented with black, the intensity of this pigmentation correlating more with dryness than temperature (Turner, 1977). Indeed, P. aegeria favours damp localities (Asselbergs, 1978: subspecies aegeria; Wiklund & Persson, 1983: ssp. tircis), and since it thermoregulates by basking its more orange coloration may protect it from *excessive* heat or radiation damage. Since the interspace colour in Southampton STOCK 01 became more orange with inbreeding and typifies other species of the genus (section 10.1), the increasingly pale coloration of subspecies tircis and pallida might represent the derivative forms.

Yet this apparently contradicts the assertion (*cf.* Shapiro, 1973) that cold shock phenocopies represent the ancestral condition. Since orange involves further sequences to white or yellow in the pigment pathway (Ford, 1957a; note that typically red Arctiid and Noctuid 'underwing' moths occasionally sport yellow forms whereas the converse does not apply, *cf.* Skinner, 1984), the complexity principle (Saunders & Ho, 1976, 1981) would suggest that the pale forms are indeed ancestral. But it must be remembered that the species can undergo drastic changes in distribution over periods of the order of centuries, even decades (Downes, 1948; Barbour, 1986), and that

Papilio zelicaon has undergone a voltinism change over two centuries. It is therefore postulated that the pale facies *does* represent the ancestral condition with respect to the species' *phylogeny*, this and its derivative forms then undergoing changes in distribution and, hence, in the potential environmental influences they encounter and so the particular developmental pathways the expression and canalisation of which are built up or broken down.

The orange colour of aegeria may have originated through the dispersal and canalisation of orange-coloured phenocopy, the orange becoming increasingly likely to be expressed under the shorter daylength of southern regions (*cf.* Geiger, 1950; section 9.25), and enabling the species to colonise hotter climes where it would be maintained by its adaptiveness.

Alternatively, the archetypal facies was originally present throughout the species range, the species becoming increasingly orange as the climate became warmer in the more southerly, but not northerly, areas of its (then) distribution.

Indeed, the species does exhibit a phenotypic cline in interspace size and colour, these becoming smaller, less orange, and less distinct through the progression aegeria - tircis - pallida, the width and colour of the elements (dark bands) becoming relatively broader and blacker (versus dark brown) through the cline. In southern Britain, notably Hampshire, orange-tinted specimens (f. intermediana Lempke are found regularly in certain colonies (Russwurm, 1978), that they occur in the generation 1.i (the specimen illustrated in Russwurm, 1978 taken on 17th April, 1967) strongly supporting the influence of the short winter daylength. Moreover, orange tinted interspaces are *typical* of subspecies insula on the Isles of Scilly (Howarth, 1971; Beavis, 1975). On the Isle of Samos, Greece, specimens intermediate in appearance between aegeria and tircis always occur as small series among May and September broods (Asselbergs, 1978), while the indistinct boundary between the two subspecies in central France further implicates an overall intra-species cline. It is conceivable that the differences in chromosome number between the two (Federley, 1938; Bigger, 1960; *cf.* section 5.6) might simply be the result of an environmentally-induced 'genome shock' (*cf.* McClintock, 1984; section 3.12), although such genetic differences need not *per se* result in any alteration of phenotype (*cf.* Oliver, 1971, *re* Lasiommatta [=Pararge] megera).

10.7. Summary and conclusions

The foregoing investigations have demonstrated that early pupal cold shock in Pararge aegeria prolongs early (and so also entire) pupal duration and can result in changes to the adult wing morphology. A model of metamorphosis was proposed that accounted for early-pupal susceptibility to cold shock (and perturbation in general) in terms of metabolic stress during the larval/pupal transition. Cold shock is understood to provide its perturbatory effect through a post-shock surge in ecdysone (EC) turnover following the accumulation of EC during cold treatment. A consideration of the species' ecology suggested that wild pupae might experience natural cold shocks as frost exposure.

The prolonging effect of cold shock on early pupal development was found to increase with genetic assimilation. The timing of several other life cycle stages *not* directly influenced by cold shock, however, also changed progressively with assimilation. It was proposed that cold shock to the [female] parent affected the production and maturation its developing ova. The directions of the assimilated changes undergone by the various life cycle stages suggested that the entire life cycle is adjusted to accommodate the initial changes to oval development. It was found that the influence of rearing (control-range) temperature and its interaction with assimilation could also be accounted for by the above two models.

Normal wing development was then examined and understood in terms of the progressive subdivision of domains within which the determination of pattern and pigmentation describes a reaction-diffusion process. It was proposed that such reaction-diffusion originates at the termen and progresses in an epimorphic fashion, perhaps concurrently with the establishment of the transverse venation. It was suggested that the process describing the reaction-diffusion need not involve a diffusing substance *per se*, but might involve aspects of cellular behaviour such as metabolic activity or mitotic division.

The wing-morphological effects of cold shock were then examined in P. aegeria and a number of other species. It was found to result in developmental failure and shape abnormalities, which were asserted to reflect incompleted stages of cell growth and division. Pattern abnormalities were understood to result from changes in the effective size of the reaction-diffusion domains. Indeed, the natures of the changes so induced were commensurate with a morphocline of pattern changes predicted by progressive increases in the dimensions of reaction-diffusion domains. It was proposed that since the acquisition of pigment depends on scale-cell maturity, thc pattern of cold-mediated changes to cell division and growth is also reflected by changes in coloration.

The relationships between the various pattern elements in normal development, and the changes induced by cold shock, implicated an early dorso-ventral compartmentalisation of the wing as well as rather well-defined anterior and posterior compartments within each surface of each wing.

The frequency and severity of cold-induced changes to the wing, especially changes involving size and shape, showed a general increase with the level of assimilation. The frequency of pattern phenocopies remained more or less constant throughout, the expressivity of the most-affected individuals appeared to increase. This increase was understood to arise through a progressive slowing of wing-cell development in concert with the assimilated decrease in pupal development rate. Individual variation in the manifestation of cold shock effect was understood to reflect individual variation in development rate and hence in the particular stage ongoing at the time of application (and during) treatment. The latter too would change under assimilation.

A number of cold shock and assimilated phenocopies resembled known wild-caught aberrants, suggesting that the species is amenable to genetic assimilation in nature; the ecology of the species was considered and would confirm this contention. The possible role of genetic assimilation in the evolution of known subspecies voltinism strategies and phenotypes was modelled.

In conclusion, it is clear that an understanding of the dynamics of metamorphosis and of wing development in the species help understand and evaluate the kinds of changes it is believed to have undergone during the course of its evolution; such an understanding also allows for predictions as to the kinds of changes it might undergo in the future. For such changes to modelled realisatically however, it is necessary to consider not only the species' development and heredity - the latter possibly involving modes additional to just nuclear DNA, but also its behaviour, ecology and population biology. Describing its evolution in terms of genetic variation and selection alone on the one hand, or totally excluding these on the other, both run the risk of leaving the picture incomplete. Only through a consideration of all facets of the species biology, can its history and evolution be fully understood. More generally, an understanding of the kinds of changes that developmental processes *can* undergo, can help evaluate the evolutionary changes understood to have been undergone by taxa in the past. For example, that cold shock resulted in total hindwing developmental failure, demonstrates that the derivation of the Dipteran haltere from Mecoptera-type wings (and conversely, through an increase in cell division and growth, of the Lepidopteran wing from haltere-type structures) is a realistic possibility.

Future investigations might examine the possibility of genetic assimilation in other Lepidoptera - several species have already been shown to respond to immediate cold shocks in rather similar ways. The development of alternative techniques for analysing wing pattern and shape could facilitate such studies, and indeed is currently in progress.

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Further Readings

Those wishing for a more detailed account of the new biology are recommended Beyond neo-Darwinism: An Introduction to the New Evolutionary Paradigm by Mae-Wan Ho and Peter Saunders, whilst detailed and rather technical accounts of biological structuralism can be found in Biology and Knowledge by Jean Piaget.

A general overview of the neo-Darwinian paradigm is provided in The Theory of Evolution by John Maynard Smith. A more detailed study of its account of molecular evolution is available in Jacques Monod's Chance and Necessity, whilst The Selfish Gene and The Blind Watchmaker, both by Richard Dawkins, present modern interpretations of largely genetically-based evolution.

Darwin's ideas are presented in his own text on The Origin of Species, whilst those of Lamarck are presented in Jordanova's paperback, Lamarck. Those wishing to examine Weismann's tenets for themselves should refer to his The Germ Plasm - A Theory of Heredity. Seasonal polyphenism and genetic assimilation are reviewed in the articles of Waddington (1961) and Shapiro (1984) respectively; the general biology of the Lepidoptera is condensed in the works of Ford (1957a,b), Dennis (1977), and in the collated articles in Vane-Wright and Ackery (1984) all listed under the main references.

What is this thing called Science? by A.F. Chalmers is a very comprehensive yet readable introduction to the nature of Scientific progress whilst a detailed history of evolutionary theory, albeit somewhat scanty on more recent advances, is given in Bowler's Evolution - the history of an idea. This gap is filled in Richard Davenport's An outline of Animal Development which reviews the epistemological problems forcing the current changes, as well as providing clear accounts of morphogenetic fields and epigenesis, whilst Mark Earthey's A Khunian Crisis in neo-Darwinism examines these problems in relation to the nature of scientific progress.

There is no single recommended text that gives an all round critique of the relationship between scientific, sociological and theological epistemologies of biological process. The relevance of physical epistemology to biology is examined in Erwin Schroedinger's What is Life?, whilst The Mind's Eye by Douglas R. Hofstadter and

Daniel C. Dennett gives entertaining yet lucid emphasis to the problems of mechanism and reduction. A critical comparison of political, theological and intellectual progress can be gleaned from Winwood Reade's The Martyrdom of Man - unfortunately now out of print, but a unifying thread between the latter two frameworks is drawn in Davies' God and the New Physics.

APPENDIX I

Life cycle parameters recorded for _Pararge aegeria_

Duration (days) of the egg
Duration (days) of the first larval instar
Larval length (mm) at the first ecdysis
Duration (days) of the second larval instar
Larval length (mm) at the second ecdysis
Duration (days) of the third larval instar
Larval length (mm) at the third ecdysis
Duration (days) of the fourth larval instar
Larval length (mm) at the fourth ecdysis
Duration (days) of the fifth larval instar
The proportion of larvae undergoing five instars
Duration (days) of the entire larval stage
Length (mm) of the pupa
Duration (days) of the prepupa stage
Duration (days) of the prepharate pupal stage
Duration (days) of the pharate pupal stage
Duration (days) of the entire pupal stage
The duration (days) of the life cycle to eclosion
The interval (days) between eclosion and copulation
The interval (days) between copulation and oviposition
The period (days) over which oviposition ensued
The number of eggs laid
Adult longevity (days)
The initial number of eggs in each family
The proportion of eggs hatching in each batch
The relative survival (%) of first instar larvae
The relative survival (%) of second instar larvae
The relative survival (%) of third instar larvae
The relative survival (%) of fourth instar larvae
The relative survival (%) of fifth instar larvae
Relative survival (%) over the entire larval stage
The relative survival (%) of prepupae
The relative survival (%) of prepharate pupae

The relative survival (%) of pharate pupae
Relative survival (%) over the entire pupal stage
Relative survival (%) over the entire life cycle to eclosion
The proportion of pupae displaying dark blotches
The number of males in each family
The number of females in each family
The number of males in each sample
The number of females in each sample
The number of mating pairs in each sample
The number of egg-laying pairs in each sample
The proportion of pairs in each sample yielding ova
The mean number of eggs laid per pair in each sample
The number of egg batches hatching per sample
The proportion of egg batches hatching
The mean proportion of eggs hatching per batch in each sample, infertile batches excluded
The mean proportion of eggs hatching per batch in each sample, infertile batches included

APPENDIX II

Product moment correlation coefficients
of the correlated life cycle characters in Table 6.II.

Characters		R-value	df	Character		R-value	df
OVDUR	I1DUR	-0.11438	53	I2DUR	E3LEN	-0.13581	54
OVDUR	I2DUR	0.10844	53	I2DUR	E4LEN	-0.24855	2
OVDUR	I3DUR	0.21497	54	I2DUR	PLEN	-0.02548	55
OVDUR	I4DUR	0.04496	53	I3DUR	I4DUR	0.29641	54
OVDUR	I5DUR	0.94491	2	I3DUR	I5DUR	0.86603	2
OVDUR	TLDUR	0.05037	51	I3DUR	TLDUR	0.54716	52
OVDUR	PPDUR	-0.01213	50	I3DUR	PPDUR	0,24377	51
OVDUR	PPHDUR	-0.11899	52	I3DUR	E1LEN	0.27471	48
OVDUR	PHDUR	-0.08973	44	I3DUR	E2LEN	-0.29819	52
OVDUR	PDUR	-0.18958	44	I3DUR	E3LEN	0.18127	55
OVDUR	ILONG	-0.19850	8	I3DUR	E4LEN	-0.99662	2
OVDUR	PLEN	-0.08457	55	I3DUR	PLEN	-0.11770	56
I1DUR	I2DUR	0.00300	54	I4DUR	I5DUR	-0.83224	2
I1DUR	I3DUR	0.16595	54	I4DUR	TLDUR	0.53130	53
I1DUR	I4DUR	-0.15943	54	I4DUR	PPDUR	0.14754	52
I1DUR	I5DUR	0.99124	2	I4DUR	E1LEN	0.23088	47
I1DUR	TLDUR	0.59704	53	I4DUR	E2LEN	0.28160	50
I1DUR	PPDUR	0.19572	51	I4DUR	E3LEN	0.04548	54
I1DUR	E1LEN	0.40148	47	I4DUR	E4LEN	0.36836	2
I1DUR	E2LEN	-0.23028	50	I4DUR	PLEN	-0.50716	55
I1DUR	E3LEN	-0.25000	54	I5DUR	TLDUR	0.99485	2
I1DUR	E4LEN	-0.89001	2	I5DUR	PPDUR	1.00000	2
I1DUR	PLEN	-0.00148	55	I5DUR	E1LEN	1.00000	1
I2DUR	I3DUR	0.05891	55	I5DUR	E2LEN	-1.00000	1
I2DUR	I4DUR	-0.06438	53	I5DUR	E3LEN	-1.00000	1
I2DUR	I5DUR	0.75593	2	I5DUR	E4LEN	-0.82199	2
I2DUR	TLDUR	0.23470	52	TLDUR	PPDUR	0.38928	50
I2DUR	PPDUR	0.12452	50	TLDUR	PPHDUR	-0.40438	50
I2DUR	E1LEN	-0.33331	48	TLDUR	PDUR	-0.30466	43
I2DUR	E2LEN	0.00916	51	TLDUR	ILONG	0.51284	8

APPENDIX II (continued)

Characters		R-value	df	Characters		R-value	df
TLDUR	I1DUR	0.59704	50	IN+EX	OVDUR	0.12058	53
TLDUR	E1LEN	0.40167	47	IN+EX	I1DUR	0.97239	53
TLDUR	E2LEN	-0.09940	48	IN+EX	TLDUR	0.60212	50
TLDUR	E3LEN	-0.14463	52	IN+EX	PROV	0.61530	12
TLDUR	E4LEN	-0.87549	2	IN+EX	DOVIP	-0.35780	12
TLDUR	PLEN	-0.44887	53	IN+EX	NOV	-0.52166	12
PPDUR	E1LEN	0.19770	44	IN+EX	ILONG	0.45711	8
PPDUR	E2LEN	-0.17187	47	IN+EX	E1LEN	0.42685	45
PPDUR	E3LEN	-0.13914	51	IN+EX	E2LEN	-0.27270	48
PPDUR	E4LEN	-0.82199	2	IN+EX	E3LEN	-0.23112	52
PPDUR	PLEN	-0.22234	52				
PPHDUR	PHDUR	-0.29137	46				
PPHDUR	PDUR	-0.88347	46				
PPHDUR	E4LEN	0.96862	2				
PHDUR	ILONG	0.72934	8				
DOVIP	NOV	0.89558	12				
E1LEN	E2LEN	0.21746	46				
E1LEN	E3LEN	-0.03442	47				
E1LEN	E4LEN	-1.00000	48				
E1LEN	PLEN	-0.01925	48				
E2LEN	E3LEN	0.09189	51				
E2LEN	E4LEN	1.00000	1				
E2LEN	PLEN	0.13736	56				
E3LEN	E4LEN	1.00000	1				
E3LEN	PLEN	0.28908	56				
E4LEN	PLEN	-0.56949	2				

The character IN+EX refers to the total duration of the oval stage plus the first larval instar. For further explanation see text.

APPENDIX III.i

Constitutive properties of the families and their respective rearing environments and temperatures

FAMILY	GEN	STATUS	Fi	Ai	BATCH	RO	TO	RL	TL	RP	TP	TPPH	RA	TA
01 001	P	Wild	0.000	0.000	N.A.	W	U	W	U	W	U	U	R	A
01 002	F1	Pure	0.000	0.000	0.890	R	A	R	A	R	A	AS	R	A
01 003	F1	Pure	0.000	0.000	0.000	*	*	*	*	*	*	*	*	*
01 004	F1	Pure	0.000	0.000	0.825	R	A	R	A	R	A	AS	R	A
01 005	F2	Pure	0.250	0.000	0.000	I	B	*	*	*	*	*	*	*
01 006	F2	Pure	0.250	1.000	0.000	I	B	*	*	*	*	*	*	*
01 007	F2	Pure	0.250	1.000	0.726	I	B/C	I	B/C	I	B/C	BT/C	G	E
01 008	F2	Pure	0.250	1.000	N.A.	*	*	*	*	*	*	*	*	*
01 009	F2	Pure	0.250	1.000	0.000	I	B	*	*	*	*	*	*	*
01 010	F2	Pure	0.250	0.000	1.000	I	B	I	B	I	B	B	G	E
01 011	F2	Pure	0.250	0.000	0.848	I	B/C	I	B/C	I	B/C	BT/C	G	E
01 012	F2	Pure	0.250	1.000	0.755	I	B/C	I	B/C	I	B/C	BT/C	G	E
01 013	F3	Pure	0.375	0.500	N.A.	G	E	*	*	*	*	*	*	*
01 014	F3	Pure	0.375	0.500	N.A.	G	E	G	E	I	D	D	R	F
01 015	F3	Pure	0.375	2.000	0.000	G	E	*	*	*	*	*	*	*
01 016	F3	Pure	0.375	2.000	0.000	G	E	*	*	*	*	*	*	*
01 017	F3	Pure	0.250	0.250	N.A.	G	E	G	E	G	E	E	*	*
01 018	F3	Pure	0.375	0.000	N.A.	G	E	G	E	I	D	DV	I	D
01 019	F3	Pure	0.000	0.500	N.A.	G	E	G	E	I	D	D	*	*
01 020	F3	Pure	0.375	0.000	0.000	G	E	*	*	*	*	*	*	*
01 021	F4	Pure	0.500	0.000	0.000	G	H	*	*	*	*	*	*	*
01 221	F1	Wild1	0.000	0.000	N.A.	W	I	W	I	W	W	I	G	E
02 001	P	Pure2	0.000	0.000	N.A.	G	*	G	E	G/I	D	DV	I	D
02 002	F1	Pure	0.000	1.000	0.000	I	J	*	*	*	*	*	*	*
02 003	F1	Pure	0.000	1.000	0.000	I	J	*	*	*	*	*	*	*
03 001	P3	Hybrid	0.000	1.000	N.A.	I/G	C/*	I/G	C/E	I	C/D	CV/D	G	H
03 002	F1	Hybrid	0.000	0.750	0.857	I	J	I	J	I	J	JW	I	J
03 003	F2	Hybrid	0.250	0.375	0.821	I	K/L	I	K/L	I	K/L	KX/LX	I	K/L
03 004	F2	Hybrid	0.250	1.750	0.867	I	K/L	I	K/L	I	K/L	KX/LX	I	K/L

APPENDIX III.i (continued)

FAMILY	GEN	STATUS	Fi	Ai	HATCH	RO	TO	RL	TL	RP	TP	TPPH	RA	TA
03 005	F2	Hybrid	0.250	0.375	0.000	I	K	*	*	*	*	*	*	*
03 006	F2	Hybrid	0.250	0.375	0.000	I	K	*	*	*	*	*	*	*
03 007	F2	Hybrid	0.250	1.750	0.453	I	K	I	K	I	K	KX	*	*
03 008	F2	Hybrid	0.250	1.750	0.000	I	K	*	*	*	*	*	*	*
04 001	P	Wild	0.000	0.000	N.A.	W	Z	W	Z	W	Z	Z	G	Z/H
04 002	F1	Pure	0.000	0.000	0.900	I	M	I	M	I	M	M	I	M
05 001	P4	Hybrid	0.000	0.438	N.A.	I	M/K	I	M/K	I	M/K	M/K	I	M/K
05 002	F1	Hybrid	0.000	0.219	0.000	I	K	*	*	*	*	*	*	*
06 001	P	Pure	0.000	0.000	N.A.	G	I	I	N	I	N	NY	I	N
06 002	F1	Pure	0.000	0.000	0.391	I	R	I	R	*	*	*	*	*
06 003	F1	Pure	0.000	1.000	0.952	I	P	I	P	I	P	PY	*	*
07 001	P	Pure	0.000	0.000	N.A.	G	I	G	I	I	P	P	I	P
07 002	F1	Pure	0.000	0.000	0.000	G	I	I	P	*	*	*	*	*
07 003	F1	Pure	0.000	0.000	0.000	I	P	*	*	*	*	*	*	*
01 441	F4	Wild1	0.000	0.000	N.A.	W	U	W	U	W	U	U	P	P
01 442	F4	Wild	0.000	0.000	N.A.	I	P	*	*	*	*	*	*	*
01 443	F1	Reared	0.000	0.000	0.250	I	P	*	*	*	*	*	*	*

The first two digits under family listings denote the relevant stock. RO = oval environment; TO = oval temperature; RL = larval environment; TL = larval temperature; RP = pupal environment; TP = pharate pupal temperature; TPPH = prepharate pupal temperature; RA = adult environment; TA = adult temperature. Rearing environments: G = greenhouse; I = incubator; R = indoor room; W = wild. Temperature codes are listed in APPENDIX III.ii. Where two alternative temperatures (or environments) were used these are separated by a slash; associated cold shock temperatures follow the respective temperature listing. Asterisks denote empty cells. N.A. = not available or not applicable. [1]generation relative to stock 01 parentals; [2]treated as pure as derived from a single captive stock; [3]comprises female 02 001 012 and male 01 012 018; [4]comprises female 03 004 007 and male 04 001 001

APPENDIX 3.ii

Temperature states associated with the respective rearing environments

Indoor Room

A = 18.9 ± 2.08°C
F = 17.4 ± 3.86°C

Greenhouse

E = 16.8 ± 2.08°C
H = 20.3 ± 2.08°C

Incubator

B = 19.3 ± 2.26°C
C = 14.8 ± 6.72°C
D = 20.8 ± 4.24°C
G = 20.8 ± 1.03°C
J = 16.7 ± 9.86°C
K = 17.6 ± 1.26°C
L = 13.9 ± 2.87°C
M = 17.9 ± 1.19°C
N = 19.1 ± 2.99°C
P = 18.0 ± 8.81°C
R = 18.1 ± 2.28°C

Cold Shock

S = -1.2 ± 0.84°C
T = -1.1 ± 1.10°C
V = -1.7 ± 2.09°C
W = -3.0 ± 1.25°C
X = -3.6 ± 1.13°C
K = -2.0 ± 0.00°C

Wild

I = 12°C : British aestival[1]
U = 2°C : British vernal[1]
Z = -13°C : Continental vernal[1]

Mean temperatures (±SD) are shown. For further explanation see text and Appendix 3.i.

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[1] based on data from Dennis (1977)

APPENDIX IV.i

Levels of classification of relevant life cycle characters on the bases of family, sex, rearing temperature and pupal treatment

Character	Classifier				Character	Classifier			
OVDUR	1		3		I2RS	1		3	
I1DUR	1		3		I3RS	1		3	
I2DUR	1		3		I4RS	1		3	
I3DUR	1		3		I5RS	1		3	
I4DUR	1		3		TLRS	1		3	
I5DUR	1		3		PPRS	1		3	
I4I5	1		3		PPHRS	1		3	4
TLDUR	1		3		PHRS	1		3	4
PPDUR	1		3		PRS	1		3	4
E1LEN	1		3		LFCRS	1		3	
E2LEN	1		3		NM	1		3	
E3LEN	1		3		NF	1		3	
E4LEN	1		3		NMS	1		3	4
PLEN	1	2	3		NFS	1		3	4
PPHDUR	1	2	3	4	PECOP	1	2	3	4
PHDUR	1	2	3	4	PAIRS	1		3	4
PDUR	1	2	3	4	OVPR	1		3	4
PNBT	1	2		4	PROV	1	2^F	3	4
LFCY	1	2	3		DOVIP	1	2^F	3	4
ILONG	1	2	3	4	MOV	1	2^F	3	4
NOVA	1		3		NOHTC	1		3	4
HTCH	1		3		MHTCH	1		3	4
I1RS	1		3		MHTCA	1		3	4

Classifiers are the groups for which the character was scored separately: 1 = family; 2 = sex; 3 = rearing temperature; 4 = pupal treatment. F = females only. For example HTCH was recorded for each rearing temperature within each family but entered similarly for both sexes and all treatments.

APPENDIX IV.ii

Case selection codes for life cycle parameters examined for genetic assimilation

(i)

Classifier				Selector
1	2	3	4	NONE
1	2^{F}	3	4	GNDR = 2
1	2		4	STK = 6
1	2	3		CHSE1 = 1
1				CHSE2 = 3
1		3		CHSE2 = 2 or 3
1		3	4	CHSE2 = 1 or 2 or 3

(ii)

Selector	Parameters
NONE	PPHDUR PHDUR PDUR PECOP ILONG
GNDR = 2	PROV DOVIP MOV
STK = 6	PNBT
CHSE1 = 1	PLEN LFCY
CHSE2 = 3	NOVA ASV FIN GEN
CHSE2 = 1/2	ASVP
CHSE2 = 2/3	HTCH I1RS I2RS I3RS I4RS I5RS TLRS PPRS LFCRS FNE PF OVDUR I1DUR I2DUR I3DUR I4DUR I5DUR TLDUR PPDUR E1LEN E2LEN E3LEN E4LEN I4I5
CHSE2 = 1/2/3	MHTCA MHTCH PPHRS PHRS PRS PFS FNS OVPR PAIRS FECUND FERT NOHTC

(iii)

Selection criteria	Selector codes
FAM REAR SEX PLTT	None
PLTT	CHSE2 = 1
FAM	CHSE2 = 3
FAM REAR	CHSE2 = 2/3
FAM SEX	CHSE1 = 1, CHSE2 = 3
FAM PLTT	CHSE2 = 1/3
FAM REAR SEX	CHSE1 = 1
FAM REAR PLTT	CHSE2 = 1/2/3
FAM SEX PLTT	CHSE1 = 1, CHSE2 = 1/3
REAR	CHSE2 = 2
REAR SEX	CHSE1 = 1, CHSE2 = 2
REAR PLTT	CHSE2 = 1/2
REAR SEX PLTT	CHSE1 = 1, CHSE2 = 1/2
SEX	GNDR = M/F
SEX PLTT	CHSE1 = 1, CHSE2 = 1

(i) Classifiers are as described in APPENDIX IV.i. The selectors instruct the SPSS^x statistical package to select for analysis only those cases necessary for examination of the variable(s) under comparison without redundancy of information. For example, pupal length was scored separately for each sex under each rearing temperature within each family; its classifiers as defined in APPENDIX IV are thus 1 2 and 3. These classifiers correspond to the selector code CHSE1 = 1. During analyses involving pupal length, therefore, SPSS^x was instructed to select for analysis only those cases for which the variable CHSE1 took the value 1. (ii) Life cycle characters (as defined in TABLE 8.II) and their respective selector codes. (iii) The selector codes corresponding to the constitutive parameters of family (FAM), rearing temperature (REAR), sex (GNDR), and pupal treatment (PLTT) alone and in combination.

APPENDIX V.i

Relationships among constititive parameters, pupal treatment, rearing environments and temperatures

(A)

dependent (1) and discriminant (2) groups

(1)	(2)	n	Wilks-L	Chi-sq[1]	Df	Sig.	P-exact
PDRR	OVRR	52	0.04711	148.18	3	****	0.0000
PDRR	TLRR	32	0.03982	91.866	3	****	0.0000
PLTT	OVRR	50	0.70842	16.030	3	**	0.0011
PLTT	TLRR	50	0.69836	16.695	3	***	0.0008
PLTT	PDRR	50	0.66253	19.144	3	***	0.0003
ILRR	PLTT	39	0.93485	2.4235	2	NS	0.2974

[1] to five *significant* figures

APPENDIX V.i (cont.i)

(B)

Variable (1) and independent (2) groups

(1)	(2)	n	Chi-squared	Df	Sig.	P-exact
GEN	OVRR	50	10.8857	3	*	0.0124
FIN	OVRR	50	8.3218	3	*	0.0398
AI	OVRR	50	8.2302	3	*	0.0415
AIP	OVRR	50	18.6475	3	***	0.0003
OVTT	OVRR	45	17.7298	3	***	0.005
TLTT	OVRR	32	12.3419	3	**	0.0063
PPHTC	OVRR	26	7.9728	2	*	0.0186
PPHTE	OVRR	16	2.2287	2	NS	0.3281
PDTT	OVRR	31	17.5612	3	***	0.0005
AIP	TLRR	50	17.7898	3	***	0.0005
OVTT	TLRR	31	12.2640	3	**	0.0065
TLTT	TLRR	32	13.4187	3	**	0.0038
PPHTC	TLRR	26	7.2636	2	*	0.0265
PPHTE	TLRR	16	2.4441	2	NS	0.2946
PDTT	TLRR	31	17.1393	3	***	0.0007
AIP	PDRR	50	17.2378	3	***	0.0006
OVTT	PDRR	30	11.6187	3	**	0.0088
TLTT	PDRR	32	11.8510	3	**	0.0079
PPHTC	PDRR	26	0.8373	2	NS	0.6579
PPHTE	PDRR	16	1.6879	1	NS	0.1939
PDTT	PDRR	31	10.5824	3	*	0.0142
FIN	PLTT	45	7.2967	2	*	0.0260
AI	PLTT	45	8.3162	2	*	0.0156
PPHT	PLTT	49	31.7421	2	****	0.0000
PPHTC	ILRR	19	1.6345	2	NS	0.4416
PPHTE	ILRR	13	8.6081	2	*	0.0135
ILTT	ILRR	23	9.4131	2	**	0.0090

APPENDIX V.i (cont.ii)

(C)

Nonparametric correlations

(1)		n	Spearman-R	Df	Sig.	P-exact
GEN	FIN	47	0.7172	46	***	0.000
GEN	AI	47	0.3169	46	*	0.015
GEN	AIP	45	0.4522	44	***	0.001
GEN	OVTT	45	0.2865	44	*	0.028
FIN	AI	47	0.3022	46	*	0.019
FIN	AIP	45	0.4256	44	**	0.002
AI	PPHTC	26	-0.3518	25	*	0.039
AI	PPHTE	16	-0.4360	15	*	0.046
OVTT	TLTT	30	0.8964	29	***	0.000
OVTT	PPHTC	24	0.5802	23	***	0.001
OVTT	PPHTE	14	0.7415	13	***	0.001
OVTT	PDTT	29	0.7380	28	***	0.000
TLTT	PPHTC	26	0.6284	25	***	0.000
TLTT	PPHTE	16	0.6931	15	***	0.001
TLTT	PDTT	31	0.7118	30	***	0.000
PPHTC	PDTT	26	0.9058	25	***	0.000
PPHTE	PDTT	16	0.7478	16	***	0.000

(A) Wilk's Lambda values are reported with Chi-square statistics of the separation between groups as defined by the dependent variable; (B) Chi-square statistics of Kruskall-Wallis nonparametric one-way ANOVA after correcting for ties. In both (A) and (B) chi-squared degrees of freedom are shown. (C) Spearman rank correlation coefficients with degrees of freedom. In all cases total sample sizes (n) and exact probabilities are reported and their significance levels summarised: * 0.01<P0.05; ** 0.001<P<0.01; *** 0.0001<P<0.001; **** P<0.0001.

APPENDIX V.ii

Nonparametric correlation between life cycle parameters (column 1) and generation (GEN) or inbreeding coefficient (FIN)

(1)		n	Spearman-R	Df	Sig.	P-exact
NOVA	GEN	39	-0.4219	38	**	0.004
OVDUR	GEN	19	-0.4517	18	*	0.026
OVDUR	FIN	19	-0.6125	18	**	0.003
PLEN	GEN	43	-0.2927	42	*	0.028
PPHDUR	GEN	66	0.0679	65	NS	0.294
PPHDUR	FIN	66	0.1132	65	NS	0.185
PHDUR	GEN	71	0.5822	70	***	0.000
PHDUR	FIN	71	0.5545	70	***	0.000
PDUR	GEN	66	0.1077	65	NS	0.195
PDUR	FIN	66	0.1412	65	NS	0.129
I1RS	GEN	15	-0.4444	14	*	0.048
I1RS	FIN	15	-0.7598	14	***	0.001
I2RS	GEN	15	-0.7598	14	***	0.001
I2RS	FIN	15	0.7244	14	***	0.001
I5RS	FIN	11	0.5539	10	*	0.039
TLRS	FIN	28	0.3571	27	*	0.031
PPHRSC	FIN	26	0.0689	25	NS	0.369
PPHRSE	FIN	16	-0.7150	15	***	0.001
PRSC	FIN	26	0.1573	25	NS	0.221
PRSE	FIN	16	-0.6277	15	**	0.005
PF	GEN	21	-0.5900	20	**	0.002
PFS	GEN	48	-0.3657	47	**	0.005
PFS	FIN	48	-0.3300	47	*	0.011
FNS	GEN	48	-0.2893	47	*	0.023
FNS	FIN	48	-0.2754	47	*	0.029
PAIRS	GEN	39	-0.1929	38	NS	0.120
OVPR	FIN	27	-0.4085	26	*	0.017
NOHTC	GEN	20	-0.1098	19	NS	0.322
NOHTC	FIN	20	-0.0908	19	NS	0.352

APPENDIX V.ii (cont.)

(1)		n	Spearman-R	Df	Sig.	P-exact
MHTCH	GEN	16	-0.4523	15	*	0.039
FERT	FIN	19	0.4921	18	*	0.016

Spearman-R gives Spearman rank correlation coefficients. Sample sizes (n) are shown in addition to degrees of freedom. Exact probabiliteis are reported and their significance levels summarised: * $0.01<P<0.05$; ** $0.001<P<0.01$; *** $P<0.001$. Non-significant correlations are shown only where necessary for comparison.

APPENDIX V.iii

Nonparametric regression of life cycle parameters (column 1) on independent temperature and constitutional parameters (column 2)

(1)	(2)	n	Kendall-W	Chi-square	Df	Sig.	P-exact
OVDUR	AI	19	1.0000	18.9999	1	-****	0.0000
OVDUR	OVTT	18	1.0000	18.0000	1	-****	0.0000
HTCH	OVTT	35	1.0000	35.0000	1	****	0.0000
I1RS	OVTT	14	1.0000	14.0000	1	***	0.0002
I1RS	TLTT	13	1.0000	13.0000	1	***	0.0003
I2RS	OVTT	14	1.0000	14.0000	1	-***	0.0002
I2RS	TLTT	13	1.0000	13.0000	1	-***	0.0003
13RS	OVTT	14	1.0000	14.0000	1	-***	0.0002
13RS	TLTT	13	1.0000	13.0000	1	-***	0.0003
I4RS	OVTT	14	1.0000	14.0000	1	***	0.0002
I4RS	TLTT	13	1.0000	13.0000	1	-***	0.0003
I5RS	OVTT	11	1.0000	11.0000	1	***	0.0009
I5RS	TLTT	11	1.0000	11.0000	1	***	0.0009
TLRS	OVTT	26	1.0000	26.0000	1	****	0.0000
TLRS	TLTT	26	1.0000	26.0000	1	****	0.0000
PPRS	OVTT	25	1.0000	24.9999	1	****	0.0000
PPRS	TLTT	25	1.0000	24.9999	1	****	0.0000
I1DUR	AI	14	1.0000	14.0000	1	***	0.0002
I1DUR	OVTT	13	0.4793	6.2308	1	-*	0.0126
I1DUR	TLTT	12	0.4444	5.3333	1	-*	0.0209
I2DUR	AI	12	1.0000	12.0000	1	***	0.0005
I2DUR	OVTT	12	0.4444	5.3333	1	-*	0.0209
I2DUR	TLTT	11	0.4050	4.4545	1	-*	0.0348
I3DUR	AI	10	1.0000	12.0000	1	-***	0.0005
I3DUR	TLTT	11	0.4050	4.4545	1	-*	0.0348
I4DUR	AI	12	1.0000	12.0000	1	***	0.0005
I5DUR	AI	9	1.0000	9.0000	1	**	0.0027
TLDUR	AI	19	1.0000	18.9999	1	-****	0.0000
TLDUR	OVTT	19	1.0000	18.9999	1	-****	0.0000

APPENDIX V.iii (cont.i)

(1)	(2)	n	Kendall-W	Chi-square	Df	Sig.	P-exact
TLDUR	TLTT	19	1.0000	18.9999	1	-****	0.0000
PPDUR	AI	23	0.6403	14.7272	1	-****	0.0000
PPDUR	OVTT	22	1.0000	21.9999	1	-****	0.0000
PPDUR	TLTT	23	1.0000	22.9999	1	-****	0.0000
E1LEN	AI	11	1.0000	11.0000	1	-***	0.0009
E1LEN	OVTT	11	1.0000	11.0000	1	-***	0.0009
E1LEN	TLTT	11	1.0000	11.0000	1	-***	0.0009
E2LEN	AI	10	1.0000	10.0000	1	-**	0.0016
E2LEN	OVTT	10	1.0000	10.0000	1	-**	0.0016
E2LEN	TLTT	10	1.0000	10.0000	1	-**	0.0016
E3LEN	AI	11	1.0000	11.0000	1	-***	0.0009
E3LEN	OVTT	11	1.0000	11.0000	1	***	0.0009
E3LEN	TLTT	11	1.0000	11.0000	1	***	0.0009
E4LEN	AI	8	1.0000	8.0000	1	-**	0.0047
I4I5	OVTT	13	1.0000	13.0000	1	-***	0.0003
I4I5	TLTT	13	1.0000	13.0000	1	-***	0.0003
NOVA	AI	39	0.9001	35.1025	1	****	0.0000
NOVA	AIP	20	1.0000	19.9999	1	****	0.0000
NOVA	OVTT	32	0.3906	12.5000	1	-***	0.0004
NOVA	TLTT	21	0.6553	13.7619	1	-***	0.0002
NOVA	PDTT	21	0.6553	13.7619	1	-***	0.0002
NOVA	ILTT	16	0.5625	9.0000	1	***	0.0027
NOVA	PPHTC	16	0.5625	9.0000	1	-***	0.0027
PLEN	AI	43	1.0000	43.0000	1	-****	0.0000
PLEN	OVTT	39	0.9001	35.1025	1	-****	0.0000
PLEN	TLTT	43	0.9091	39.0930	1	-****	0.0000
LFCY	AI	28	1.0000	27.9998	1	-****	0.0000
LFCY	AIP	28	1.0000	27.9998	1	-***-	0.0000
LFCY	OVTT	28	1.0000	27.9998	1	-****	0.0000
LFCY	TLTT	28	1.0000	27.9998	1	-****	0.0000
LFCY	PDTT	28	1.0000	27.9998	1	-****	0.0000
LFCY	ILTT	23	1.0000	22.9999	1	-****	0.0000

APPENDIX V.iii (cont.ii)

(1)	(2)	n	Kendall-W	Chi-square	Df	Sig.	P-exact
LFCY	PPHTC	24	1.0000	23.9999	1	-****	0.0000
MOV	AI	21	1.0000	21.0000	1	****	0.0000
MOV	AIP	21	1.0000	21.0000	1	****	0.0000
MOV	OVTT	19	0.3352	6.3683	1	-*	0.0116
MOV	TLTT	21	0.3832	8.0476	1	-**	0.0046
MOV	PDTT	20	0.2500	4.9999	1	-*	0.0253
MOV	ILTT	18	0.3086	5.5555	1	-*	0.0184
MOV	PPHTE	7	1.0000	7.0000	1	-**	0.0082
DOVIP	AI	10	1.0000	10.0000	1	**	0.0016
DOVIP	AIP	10	0.9000	9.0000	1	**	0.0027
DOVIP	OVTT	9	0.5000	4.5000	1	*	0.0339
DOVIP	TLTT	10	0.5444	5.4444	1	-*	0.0196
DOVIP	PDTT	10	0.5444	5.4444	1	*	0.0196
DOVIP	ILTT	9	0.6049	5.4444	1	-*	0.0196
DOVIP	PPHTE	5	1.0000	5.0000	1	*	0.0253
PROV	AI	14	0.8571	12.0000	1	***	0.0005
PROV	OVTT	13	1.0000	13.0000	1	***	0.0003
PROV	TLTT	14	1.0000	14.0000	1	-***	0.0002
PROV	PDTT	14	1.0000	14.0000	1	-***	0.0002
PROV	ILTT	13	1.0000	13.0000	1	-***	0.0003
PROV	PPHTC	6	1.0000	6.0000	1	-*	0.0143
PROV	PPHTE	5	1.0000	5.0000	1	*	0.0253
PPHDUR	AI	66	1.0000	65.9999	1	****	0.0000
PPHDUR	AIP	66	1.0000	65.9999	1	****	0.0000
PPHDUR	OVTT	61	0.1423	8.6721	1	-**	0.0032
PPHDUR	TLTT	66	0.2975	19.6363	1	-****	0.0000
PPHDUR	PDTT	66	0.2975	19.6363	1	-****	0.0000
PPHDUR	PPHTC	38	0.1773	6.7368	1	-**	0.0094
PPHDUR	PPHTE	24	1.0000	23.9999	1	-****	0.0000
PHDUR	AI	71	0.9445	67.0563	1	****	0.0000
PHDUR	AIP	71	0.0378	2.6825	1	NS	0.1015
PHDUR	OVTT	71	0.9394	61.0615	1	-****	0.0000
PHDUR	TLTT	71	0.9445	67.0563	1	-****	0.0000

APPENDIX V.iii (cont.iii)

(1)	(2)	n	Kendall-W	Chi-square	Df	Sig.	P-exact
PHDUR	PDTT	70	0.9437	66.0571	1	-****	0.0000
PHDUR	PPHTC	38	1.0000	38.0000	1	-****	0.0000
PHDUR	PPHTE	26	1.0000	26.0000	1	-****	0.0000
PDUR	AI	66	1.0000	65.9999	1	****	0.0000
PDUR	AIP	66	1.0000	65.9999	1	****	0.0000
PDUR	TLTT	66	0.0918	6.0605	1	-*	0.0138
PDUR	PDTT	66	0.1111	7.3333	1	-**	0.0068
PDUR	PPHTC	38	0.1773	6.7368	1	-**	0.0094
PDUR	PPHTE	24	1.0000	23.9999	1	-****	0.0000
PECOP	AI	31	0.3729	11.5600	1	-***	0.0007
PECOP	AIP	31	0.2688	8.3333	1	-**	0.0039
PECOP	OVTT	28	1.0000	27.9998	1	-****	0.0000
PECOP	TLTT	31	1.0000	31.0000	1	****	0.0000
PECOP	PDTT	31	1.0000	31.0000	1	****	0.0000
PECOP	ILTT	31	1.0000	31.0000	1	****	0.0000
PECOP	PPHTC	14	1.0000	14.0000	1	-***	0.0002
PECOP	PPHTE	13	1.0000	13.0000	1	***	0.0003
ILONG	AI	32	1.0000	32.0000	1	****	0.0000
ILONG	AIP	32	0.8789	28.1250	1	****	0.0000
ILONG	TLTT	32	0.1914	6.1250	1	*	0.0133
ILONG	PDTT	31	0.2341	7.2581	1	-**	0.0071
ILONG	ILTT	29	0.2675	7.7585	1	-**	0.0053
ILONG	PPHTC	14	1.0000	14.0000	1	***	0.0002
ILONG	PPHTE	12	1.0000	13.0000	1	***	0.0003
MHTCA	AIP	23	1.0000	22.9999	1	-****	0.0000
MHTCA	OVTT	21	0.8186	17.1904	1	-****	0.0000
MHTCA	TLTT	23	0.8336	19.1738	1	-****	0.0000
MHTCA	PDTT	22	0.8264	18.1817	1	-****	0.0000
MHTCA	ILTT	21	0.8186	17.1904	1	-****	0.0000
MHTCA	PPHTC	9	1.0000	9.0000	1	-**	0.0027
MHTCA	PPHTE	8	1.0000	8.0000	1	**	0.0047
MHTCH	AI	16	0.1042	1.6667	1	-NS	0.1967
MHTCH	AIP	16	1.0000	66.0000	1	-****	0.0001

APPENDIX V.iii (cont.iv)

(1)	(2)	n	Kendall-W	Chi-square	Df	Sig.	P-exact
MHTCH	OVTT	14	0.7347	10.2857	1	-**	0.0013
MHTCH	TLTT	16	0.7656	12.2500	1	-***	0.0005
MHTCH	PDTT	16	0.7656	12.2500	1	-***	0.0005
MHTCH	ILTT	15	0.7511	11.2667	1	***	0.0008
MHTCH	PPHTC	5	1.0000	5.0000	1	-*	0.0253
MHTCH	PPHTE	7	1.0000	7.0000	1	-**	0.0082
PFS	AIP	48	0.9792	47.0000	1	-****	0.0000
PFS	OVTT	43	0.9091	39.0930	1	****	0.0000
PFS	TLTT	48	0.9184	44.0833	1	****	0.0000
PFS	PDTT	47	0.8370	39.3404	1	-****	0.0000
PFS	PPHTC	26	1.0000	26.0000	1	-****	0.0000
PFS	PPHTE	14	1.0000	14.0000	1	***	0.0002
FNS	AI	48	0.1333	6.4000	1	-*	0.0114
FNS	OVTT	43	0.5890	25.3256	1	-****	0.0000
FNS	TLTT	48	0.6267	30.0833	1	****	0.0000
FNS	PDTT	47	0.5545	26.0638	1	-****	0.0000
FNS	PPHTC	26	0.8521	22.1538	1	****	0.0000
FNS	PPHTE	14	1.0000	14.0000	1	***	0.0002
OVPR	AI	27	0.7101	19.1737	1	****	0.0000
OVPR	AIP	27	0.2424	6.5453	1	*	0.0105
OVPR	OVTT	25	0.8067	20.1666	1	-****	0.0000
OVPR	TLTT	27	0.8205	22.1537	1	****	0.0000
OVPR	PDTT	26	0.6785	17.6400	1	-****	0.0000
OVPR	ILTT	25	1.0000	24.9999	1	****	0.0000
OVPR	PPHTC	12	1.0000	12.0000	1	-***	0.0005
OVPR	PPHTE	9	1.0000	9.0000	1	-**	0.0270
PAIRS	AI	39	0.1313	5.1212	1	-*	0.0236
PAIRS	AIP	39	0.3231	12.6000	1	-***	0.0004
PAIRS	OVTT	34	0.7496	25.4848	1	-****	0.0000
PAIRS	TLTT	39	0.7800	30.4210	1	****	0.0000
PAIRS	PDTT	38	0.6835	25.9729	1	-****	0.0000
PAIRS	ILTT	33	0.8825	29.1212	1	****	0.0000
PAIRS	PPHTC	18	1.0000	18.0000	1	-****	0.0000

APPENDIX V.iii (cont.v)

(1)	(2)	n	Kendall-W	Chi-square	Df	Sig.	P-exact
PAIRS	PPHTE	14	1.0000	19.0000	1	***	0.0002
FECUND	AI	26	0.4476	11.6363	1	***	0.0006
FECUND	AIP	26	0.8077	21.0000	1	-****	0.0000
FECUND	OVTT	24	1.0000	23.9999	1	****	0.0000
FECUND	TLTT	26	1.0000	26.0000	1	-****	0.0000
FECUND	PDTT	26	0.8521	22.1538	1	-****	0.0000
FECUND	ILTT	25	1.0000	24.9999	1	-****	0.0000
FECUND	PPHTC	12	1.0000	12.0000	1	-***	0.0005
FECUND	PPHTE	9	1.0000	9.0000	1	-**	0.027
FERT	AI	19	0.1579	2.9999	1	NS	0.0833
FERT	AIP	19	0.9474	17.9999	1	****	0.0000
FERT	OVTT	17	1.0000	17.0000	1	-****	0.0000
FERT	TLTT	19	1.0000	18.9999	1	****	0.0000
FERT	PDTT	18	1.0000	18.0000	1	****	0.0000
FERT	ILTT	17	1.0000	17.0000	1	-****	0.0000
FERT	PPHTC	8	1.0000	8.0000	1	-**	0.0047
FERT	PPHTE	6	1.0000	6.0000	1	*	0.0143
NOHTC	AI	20	0.4167	8.3332	1	**	0.0039
NOHTC	AIP	20	0.5921	11.8420	1	***	0.0006
NOHTC	OVTT	18	0.9444	17.0000	1	-****	0.0000
NOHTC	TLTT	20	0.9500	18.9999	1	-****	0.0000
NOHTC	PDTT	19	0.9474	17.9999	1	-****	0.0000
NOHTC	ILTT	18	1.0000	18.0000	1	-****	0.0000
NOHTC	PPHTC	9	1.0000	9.0000	1	-**	0.0027
NOHTC	PPHTE	6	1.0000	6.0000	1	-*	0.0143

Kendall-W gives Kendall's coefficient of concordance. Sample sizes (n) are shown in addition to degrees of freedom. Exact probabilities are reported and their significance levels summarised: * $0.01<P<0.05$; ** $0.001<P<0.01$; *** $0.0001<P<0.001$; **** $P<0.0001$; '-' show negative relationships. Non-significant regressions are shown only where necessary for comparison.

APPENDIX V.iv

Life cycle parameters (Column 1)
differing between the stocks, rearing
environments, pupal treatments or sexes (Column 2)

(1)	(2)	n	Chi-squared	Df	Sig.	P-exact
PPRS	STK	27	13.4284	5	*	0.0197
PPHRS	OVRR	47	7.8502	2	*	0.0197
PPHRS	TLRR	45	6.9934	2	*	0.0303
PPHRS	PDRR	45	6.8329	2	*	0.0328
PHRS	OVRR	45	6.1277	2	*	0.0467
PHRS	TLRR	43	7.8184	2	*	0.0201
PHRS	PLTT	43	7.6904	2	*	0.0214
PHRS	PDRR	43	6.6873	2	*	0.0353
LFCRS	OVRR	39	8.9370	3	*	0.0301
LFCRS	TLRR	28	8.9393	3	*	0.0301
LFCRS	PDRR	28	10.6214	3	*	0.0140
FNE	PLTT	25	7.3690	2	*	0.0251
FNE	OVRR	25	6.8006	2	*	0.0334
FNS	TLRR	48	12.1637	3	**	0.0068
FNS	PDRR	48	12.2298	3	**	0.0066
PF	OVRR	45	9.5001	2	**	0.0087
OVPR	ILRR	26	3.1960	2	NS	0.2023
FERT	ILRR	18	6.4927	2	*	0.0389
PLEN	GNDR	43	7.4675	1	**	0.0063
PPHDUR	STK	66	11.2760	4	*	0.0236
PPHDUR	PLTT	66	10.5253	2	**	0.0052
PPHDUR	OVRR	66	12.3958	2	**	0.0020
PPHDUR	TLRR	66	13.8683	2	***	0.0010
PHDUR	STK	71	25.1525	6	***	0.0003
PHDUR	OVRR	71	13.7504	3	**	0.0033
PHDUR	PLTT	71	2.7584	2	NS	0.2518
PDUR	STK	66	8.8533	4	NS	0.0649
PDUR	PLTT	66	12.2959	2	**	0.0021
PDUR	OVRR	66	9.7407	2	**	0.0077

APPENDIX V.iv (continued)

(1)	(2)	n	Chi-squared	Df	Sig.	P-exact
PDUR	TLRR	66	9.7751	2	**	0.0075
PECOP	STK	31	10.9728	4	*	0.0269
ILONG	PLTT	32	12.6888	2	**	0.0018
ILONG	OVRR	32	9.1914	3	*	0.0269
ILONG	TLRR	32	8.9530	3	*	0.0299
ILONG	PDRR	32	8.8395	2	*	0.0120
ILONG	ILRR	30	8.4380	2	*	0.0147
LFCY	PLTT	52	1.1937	2	NS	0.5505
LFCY	OVRR	52	0.0058	1	NS	0.9394
LFCY	TLRR	52	0.0058	1	NS	0.9394
LFCY	PDRR	52	0.0058	1	NS	0.9394
LFCY	ILRR	41	1.1937	2	NS	0.9835

Chi-square statistics refer to Kruskall-Wallis nonparametric one-way ANOVA after correcting for ties. Total sample size (n) and Chi-squared degrees of freedom are shown. Exact probabilites are reported and their significance levels summarised: * 0.01<P<0.05; ** 0.001<P<0.001; *** P<0.001. Non-significant differences are shown only where necessary for comparison.

APPENDIX 6.VI

Life cycle parameters of animals undergoing the various stages and surviving control and experimental treatments respectively.

	originals			control			coldshock				
Sample	$\bar{X}$	SD	n	$\bar{X}$	SD	n	$\bar{X}$	SD	n	Chi^{2}control	Chi^{2}cold
OVDUR											
01002*	10.0	0.46	71	9.4	0.80	5	9.8	0.56	14	0.423	0.076
01004*	10.2	0.73	47	8.2	3.72	5	10.1	0.57	9	0.278	0.012
01007B	8.4	0.87	39	8.7	0.47	3	NA			0.092	NA
01007C	8.3	0.56	22	8.0	0.00	1	NA			0.287	NA
01010B	8.7	0.94	3	8.0	0.00	1	NA			0.555	NA
01011B	8.6	1.13	23	7.8	1.77	6	8.0	0.00	1	0.145	0.282
01011C	8.8	0.43	16	9.0	0.00	3	NA			0.216	NA
01012B	8.7	1.28	45	7.2	1.17	5	9.5	1.50	4	0.748	0.165
01012C	8.7	0.65	29	8.7	0.47	3	NA			0.000	NA
03002	12.8	1.09	48	13.7	0.47	6	13.4	0.49	7	0.575	0.252
06003	9.6	0.73	40	9.0	0.00	3	9.0	0.00	2	0.676	0.676
I1DUR											
01002	9.9	3.07	50	9.6	3.20	5	10.6	3.63	13	0.005	0.022
01004*	7.1	1.31	43	7.2	1.07	6	7.7	1.41	9	0.003	0.097
01007B	8.4	3.50	20	10.7	5.25	3	NA			0.133	NA
01007C	12.5	1.50	2	11.0	0.00	1	NA			1.000	NA
01010B	7.0	0.00	1	7.0	0.00	1	NA			0.000	NA
01011B	6.6	2.34	13	6.5	2.63	6	NA			0.001	NA
01011C	17.3	8.26	3	17.3	8.26	3	NA			0.000	NA
01012B	7.3	2.19	27	6.2	1.60	5	9.2	2.49	4	0.164	0.328
01012C	4.4	0.57	22	NA			NA			0.001	NA
03002	9.1	2.24	17	7.4	1.11	8	9.8	1.33	5	0.462	0.072
06003	7.9	2.49	39	3.7	0.94	3	7.0	0.00	2	2.490	0.131

APPENDIX 6.VI (cont.i)

	originals			control			coldshock				
Sample	$\bar{X}$	SD	n	$\bar{X}$	SD	n	$\bar{X}$	SD	n	Chi^{2}control	Chi^{2}cold
I2DUR											
01002*	6.6	2.33	46	5.6	0.80	5	5.8	1.03	13	0.165	0.099
01004*	7.2	4.09	41	6.5	1.61	6	NA			0.025	NA
01007B	7.1	3.18	18	7.7	3.86	3	NA			0.014	NA
01007C	9.0	0.00	3	18.0	0.00	1	NA			(1)***	NA
01011B	7.1	1.86	13	7.5	1.61	6	NA			0.026	NA
01011C	21.5	8.50	2	13.0	0.00	1	NA			1.000	NA
01012B	10.1	4.20	17	8.3	3.49	4	13.0	0.00	1	0.109	0.447
01012C	14.0	4.24	3	15.5	4.50	2	NA			0.059	NA
03002	9.1	2.24	17	6.8	0.40	5	7.1	1.12	7	0.000	0.023
06003	9.0	6.64	27	3.7	0.94	3	6.5	0.50	2	0.626	0.141
I3DUR											
01002*	9.4	3.38	44	9.3	1.50	4	8.7	2.81	13	0.001	0.025
01004*	7.8	2.86	38	6.7	2.49	6	4.7	1.41	9	0.084	0.945
01007B	7.2	2.12	12	7.5	2.50	2	NA			0.008	NA
01007C	9.0	0.00	3	9.0	0.00	1	NA			0.000	NA
01011B	7.1	1.86	13	7.5	1.61	6	NA			0.007	NA
01011C	23.5	7.50	2	16.0	0.00	1	NA			1.000	NA
01012B	9.6	2.24	13	8.0	2.00	2	8.0	0.00	1	0.284	0.510
01012C	19.3	8.34	3	23.0	8.00	2	NA			0.103	NA
03002	9.1	2.24	17	6.8	0.40	5	7.1	1.12	7	1.022	0.638
06003	17.0	8.96	21	5.0	0.00	3	15.0	4.00	2	2.490	0.131
I4DUR											
01002*	12.6	4.35	32	11.2	3.54	5	13.2	2.72	13	0.062	0.014
01004*	11.7	3.01	31	9.3	4.53	6	8.1	2.60	9	0.195	0.819
01007B	8.8	1.30	4	10.0	0.00	2	NA			0.852	NA
01007C	20.3	3.68	3	16.0	0.00	1	NA			1.365	NA
01011B	9.3	1.25	3	9.5	1.50	2	NA			0.010	NA
01011C	21.5	8.50	2	13.0	0.00	1	NA			0.008	NA
01012B	8.2	0.90	6	9.0	0.00	1	8.0	1.00	2	0.748	0.165
01012C	36.3	16.54	3	36.3	16.54	3	NA			0.000	NA
03002	9.4	1.39	14	9.2	1.21	6	10.0	1.41	6	0.012	0.092
06003	17.0	8.96	21	5.0	0.00	3	15.0	4.00	2	0.626	0.141

APPENDIX 6.VI (cont.ii)

	originals			control			coldshock				
Sample	$\bar{X}$	SD	n	$\bar{X}$	SD	n	$\bar{X}$	SD	n	Chi^{2}control	Chi^{2}cold
I5DUR											
01002*	10.7	1.25	3	11.0	0.00	1	11.5	0.50	2	0.058	0.353
01004*	12.0	0.00	1	NA			NA			NA	NA
01007B	5.0	0.00	2	NA			NA			NA	NA
01007C	9.0	0.00	1	9.0	0.00	1	NA			0.000	NA
01011B	21.0	0.00	1	NA			NA			NA	NA
01011C	18.0	0.00	1	18.0	0.00	1	NA			0.000	NA
01012C	23.0	0.00	1	23.0	0.00	1	NA			0.000	NA
06003	25.5	19.50	2	NA			NA			NA	NA
PPDUR											
01002*	1.5	0.50	5	1.8	0.40	5	1.4	0.49	14	0.220	0.020
01004*	1.1	0.31	18	1.2	0.40	5	1.0	0.00	9	0.039	0.104
01007B	1.3	0.43	4	1.0	0.00	2	NA			0.487	NA
01007C	1.0	0.00	4	NA			1.5	0.50	2	NA	1.000
01011B	1.5	0.50	4	1.7	0.47	3	NA			0.085	NA
01011C	2.0	0.00	4	2.0	0.00	3	NA			0.000	NA
01012B	1.5	0.50	10	2.0	0.00	1	NA			1.000	NA
01012C	2.3	0.47	3	2.3	0.47	3	NA			0.000	NA
03002	1.3	0.45	14	1.3	0.47	6	1.1	0.35	7	0.000	0.123
06003	1.8	0.69	6	1.7	0.47	3	2.0	1.00	2	0.014	0.027
E1LEN											
01002*	5.4	0.84	37	4.4	0.76	3	5.6	0.60	12	0.779	0.038
01004*	4.8	0.78	36	4.7	0.80	6	5.2	0.62	9	0.008	0.161
01007B	4.6	0.65	8	NA			NA			NA	NA
01007C	4.5	0.50	2	4.0	0.00	1	NA			1.000	NA
01011B	5.0	0.75	9	4.9	0.92	5	NA			0.007	NA
01011C	4.8	0.62	2	4.5	0.00	1	NA			0.234	NA
01012B	6.0	0.00	11	4.3	0.43	4	4.0	0.00	2	15.630***	(1)***
01012C	4.4	0.57	22	NA			NA			NA	NA
03002	4.7	0.46	16	4.6	0.46	8	4.7	0.40	5	0.024	0.000
06003	4.5	0.81	31	5.5	1.47	3	4.8	0.75	2	0.356	0.074

APPENDIX 6.VI (cont.iii)

	originals			control			coldshock				
Sample	X	SD	n	X	SD	n	X	SD	n	Chi^{2}control	Chi^{2}cold
E2LEN											
01002*	8.4	1.21	39	7.6	1.16	5	8.7	0.84	17	0.228	0.041
01004*	8.7	0.86	38	9.0	0.65	6	8.7	0.74	12	0.077	0.000
01007B	7.5	0.96	11	7.7	1.32	3	7.5	0.00	1	0.015	0.000
01011B	8.8	2.18	10	10.0	1.90	5	NA			0.172	NA
01011C	9.0	0.00	1	NA			NA			0.000	NA
01012B	8.0	1.46	12	7.2	0.62	5	10.0	2.00	2	0.254	0.652
01012C	2.3	0.47	3	2.3	0.47	3	NA			0.000	NA
03002	8.1	0.60	14	8.6	0.65	4	7.9	0.49	7	0.319	0.067
06003	7.5	1.03	22	8.7	0.24	3	7.0	0.50	2	1.287	0.191
E3LEN											
01002*	13.2	1.92	41	14.4	0.77	5	13.4	2.14	18	0.337	0.005
01004*	14.2	2.10	36	14.5	0.81	6	15.1	1.59	13	0.018	0.117
01007B	11.5	1.44	7	12.0	0.00	1	NA			0.121	NA
01011B	14.2	2.01	3	14.7	2.01	3	NA			0.031	NA
01011C	13.2	0.47	3	NA			NA			NA	NA
01012B	10.9	1.24	4	NA			12.5	0.00	1	NA	NA
01012C	10.9	1.02	4	11.2	1.03	3	NA			0.000	NA
03002	13.0	0.81	15	13.2	0.38	6	13.0	1.04	7	0.050	0.000
06003	10.7	1.42	20	12.0	0.82	3	10.5	1.00	2	0.629	0.013
E4LEN											
01002*	15.2	1.37	6	NA			15.2	1.75	2	NA	0.000
01004*	17.0	0.00	1	NA			NA			NA	NA
01007C	14.5	1.08	3	13.5	0.00	1	NA			0.857	NA
01012C	14.5	0.00	1	NA			NA			NA	NA
06003	14.5	0.96	7	NA			15.5	0.00	1	NA	1.085

APPENDIX 6.VI (cont.iv)

	originals			control			coldshock				
Sample	$\bar{X}$	SD	n	$\bar{X}$	SD	n	$\bar{X}$	SD	n	Chi^{2}control	Chi^{2}cold
PLEN											
01002*	12.0	0.78	21	12.3	0.40	5	12.1	0.68	14	0.117	0.009
01004*	12.1	1.29	21	12.8	0.47	6	12.3	0.97	9	0.260	0.015
01007B	9.4	1.36	5	11.0	0.00	2	NA			1.384	NA
01007C	11.5	0.00	1	11.5	0.00	1	NA			0.000	NA
01011B	11.4	1.03	7	12.0	0.71	4	11.0	0.00	1	0.230	0.151
01011C	10.9	1.19	4	11.3	1.03	3	NA			0.065	NA
01012B	10.8	1.20	13	11.1	1.24	4	11.1	0.89	4	0.030	0.040
01012C	12.0	0.71	3	12.0	0.71	3	NA			0.000	NA
01014	10.8	0.75	2	10.8	0.75	2	NA			0.000	NA
01018	10.6	1.68	15	11.8	0.47	6	12.2	0.25	2	0.473	0.887
02001	11.3	0.87	22	11.5	0.71	8	11.6	0.45	6	0.032	0.094
03002	12.6	0.35	14	12.5	0.41	6	12.7	0.25	7	0.034	0.054
03003K	10.6	1.50	7	11.5	0.00	1	10.3	0.47	3	0.360	0.036
03003L	9.9	2.05	7	12.5	0.00	1	12.0	0.00	2	1.609	1.049
03004K	10.3	1.72	13	11.6	0.65	4	10.0	0.00	1	0.500	0.030
03004L	10.3	1.86	16	10.0	1.00	2	12.1	0.22	4	0.020	0.924
03007K	10.3	1.86	16	10.0	1.00	2	12.1	0.22	4	0.543	NA
06001	11.2	0.68	99	11.3	0.79	25	11.3	0.56	38	0.009	0.013
06003	11.4	0.45	6	11.8	0.24	3	11.0	0.00	1	0.615	0.790

APPENDIX 6.VI (cont. vi)

Sample	originals			survivors			originals			survivors			Chi^{2}control	ChiS2cold
	$\overline{X}$	SD	n	$\overline{X}$	SD	n	$\overline{X}$	SD	n	$\overline{X}$	SD	n		
PPHDUR														
01002*	11.2	1.17	5	11.2	1.17	5	13.9	2.28	15	14.1	2.22	14	0.000	0.004
01004*	12.1	1.81	7	11.8	1.77	6	14.7	0.94	12	14.7	0.94	9	0.014	0.000
01007B	11.0	0.00	2	11.0	0.00	2	NA			NA			0.000	NA
01007C	21.0	0.00	1	21.0	0.00	1	NA			NA			0.000	NA
01011B	10.2	0.83	4	10.2	0.83	4	16.0	0.00	1	16.0	0.00	1	0.000	0.000
01011C	20.3	0.47	3	20.3	0.47	3	NA			NA			0.000	NA
01012B	10.2	1.30	4	10.2	1.30	4	17.5	2.06	4	17.5	2.06	4	0.000	0.000
01012C	29.0	13.44	3	29.0	13.44	3	NA			NA			0.000	NA
01014	11.0	0.00	2	11.0	0.00	2	NA			NA			NA	NA
01018	8.7	0.75	6	8.7	0.75	6	12.0	0.00	2	12.0	0.00	2	0.000	0.000
02001	10.0	0.53	6	10.0	0.58	5	14.6	2.50	8	14.6	2.66	7	0.000	0.000
03002	12.8	2.61	6	12.8	2.61	6	14.9	1.36	7	14.9	1.36	7	0.000	0.000
03003K	13.0	0.00	2	13.0	0.00	1	20.0	1.41	3	20.0	1.41	3	0.000	0.000
03003L	35.0	0.00	1	35.0	0.00	1	43.0	2.00	2	43.0	2.00	2	0.000	0.000
03004K	12.5	1.12	4	12.5	1.12	4	17.5	0.50	2	18.0	0.00	1	0.000	0.000
03004L	29.0	0.00	2	29.0	0.00	2	29.2	1.30	4	29.2	1.30	4	0.000	0.000
03007K	13.0	0.00	1	13.0	0.00	1	NA			NA			0.000	NA
06001	12.7	1.33	26	12.4	0.81	24	16.6	1.82	37	16.4	1.58	34	0.037	0.007
06003	12.0	0.82	3	12.0	0.82	3	17.0	0.00	1	17.0	0.00	1	0.000	0.000

Means ($\overline{X}$), standard deviations (SD) and sample sizes (n) are reported. Significance of Chi$^2_{(1)}$ values are non-significant unless indicated thus: *** = P<0.001. Sample postscripts refer to rearing temperature as coded in Appendix III. For further explanation see text.

*Family 002 and 004 control groups = no foil treatment.

(1)Chi^{2}value not computable as variances = 0.000

APPENDIX VII (overleaf)

Pupal stage durations in each sample of the assimilation protocol

The mean, standard deviation (SD), range of the prepharate, pharate and entire pupal durations are reported together with sample size (n); NA = data not available. The respective pupal treatments are indicated prior to the stock and family listings: N = no foil, C = foil, E = cold shock. Where samples within a family were reared at alternative temperatures the respective temperature code follows the stock and family listing: b = 19.3°C, c = 14.8°C; k = 17.6°C, l = 13.9°C. The rearing temperatures used with each of the remaining families are given in Appendix III.

	PREPHARATE				PHARATE				PUPAL			
	Mean	SD	Range	n	Mean	SD	Range	n	Mean	SD	Range	n
N 01002	11.2	1.17	9-12	5	3.0	1.41	2-5	5	13.7	1.70	11-16	6
C 01002	12.2	1.64	10-14	8	3.3	1.28	2-6	7	15.6	1.40	13-17	7
E 01002	13.9	2.28	10-19	15	2.6	0.90	1-4	14	16.6	2.16	13-22	14
C 01010	NA				NA				12.0	0.00	12	1
E 01007	11.0	0.00	11	2	3.0	1.00	2-4	2	14.0	1.00	13-15	2
N 01004	12.1	1.81	9-14	7	1.8	0.69	1-2	6	13.7	1.70	11-16	6
C 01004	12.8	1.09	10-14	8	2.0	0.58	1-3	6	15.2	0.37	15-16	6
E 01004	14.7	0.94	13-16	12	2.2	0.42	2-3	9	16.9	0.74	16-18	9
C 01011b	10.3	0.69	9-11	4	2.5	0.25	2-3	4	13.5	1.26	12-16	6
E 01011b	16.0	0.00	16	1	2.0	0.00	2	1	18.0	0.00	18	1
C 01012b	10.3	1.30	8-11	4	3.0	0.71	2-4	4	13.4	1.36	11-15	5
E 01012b	17.5	2.06	16-21	4	3.0	0.71	2-4	4	20.5	1.66	19-23	4
C 01018	8.7	0.75	8-10	6	2.5	1.26	1-4	6	11.2	1.07	10.13	6
E 01018	12.0	0.00	12	2	3.5	0.50	3-4	2	15.5	0.50	15-16	2
C 01014	11.0	0.00	11	2	2.0	0.00	2	2	13.0	0.00	13	2
C 01011c	20.3	0.47	20-21	3	4.0	0.82	3-5	3	24.3	0.94	23-25	3
C 01012c	27.0	12.14	19-48	4	3.0	0.82	2-4	3	32.0	14.17	21-52	3
C 02001	10.0	0.53	9-11	7	2.0	0.00	2	6	12.0	0.58	11-13	6
E 02001	15.3	1.91	12-19	7	1.9	0.33	1-2	8	17.2	2.11	14-21	6
C 03002	12.8	2.61	11-16	6	2.0	0.00	2	6	14.8	2.61	13-19	6
E 03002	14.9	1.36	12-16	7	1.9	0.35	1-2	7	16.7	1.67	13-18	7
C 03003k	13.0	0.00	13	2	2.0	0.00	2	1	15.0	0.00	15	1
E 03003k	20.0	1.41	19-22	3	3.0	0.00	3	3	23.0	1.41	22-25	3
C 03003l	5.0	0.00	5	1	4.0	0.00	4	1	9.0	0.00	9	1
E 03003l	13.0	2.00	11-15	2	5.0	1.00	4-6	2	18.0	3.00	15-21	2
C 03004/7k	12.6	1.02	11-14	5	2.2	0.40	2-3	5	14.8	0.83	14-16	4
E 03004/7k	17.5	0.50	17-18	2	4.0	0.00	4	4	22.0	0.00	22	1
C 03004/7l	29.0	0.00	29	2	5.0	1.00	4-6	2	34.1	1.00	33-35	2
E 03004/7l	29.3	1.30	28-31	4	3.5	0.50	3-4	4	32.8	1.79	31-35	4
C 04001	12.0	0.00	12.0	1	1.0	0.00	1	1	13.0	0.00	13	1
C 06001	12.7	1.33	11-18	26	1.7	0.56	1-3	23	14.1	0.78	13-16	23
E 06001	16.6	1.82	15-22	37	1.7	0.54	1-3	30	18.1	1.76	16-24	30
C 06003	12.0	0.82	11-13	3	1.7	0.47	1-2	3	13.7	0.94	13-15	3
E 06003	17.0	0.00	17	1	2.0	0.00	2	1	19.0	0.00	19	1

APPENDIX VIII

t-values and degrees of freedom [ ] of duration differences within samples

(i) between foil and cold shock treatments (table 8.XV)

Sample[1]	PREPHARATE	PHARATE	PUPAL
01002	[21] 1.851	[19] 1.453	[19] 1.101
01004	[18] 4.137	[13] 0.771	[13] 5.119
01011	[3] 4.130	[3] 1.000	[5] 1.458
01012	[6] 5.724	[6] 0.000	[7] 6.896
01018	[6] 5.652	[6] 1.004	[6] 5.053
02001	[12] 7.002	[12] 0.727	[10] 5.739
03002	[11] 1.841	[11] 0.687	[11] 1.570
03003 K	[3] 6.080	[2][2]	[2] 3.276
03003 L	[1] 2.828	[1] 0.707	[1] 2.121
03004/7 K	[5] 5.915	[7] 8.649	[3] 8.916
03004/7 L	[4] 0.289	[4] 2.449	[4] 0.796
06001	[61] 9.305	[51] 0.000	[41] 10.138
06003	[2] 3.520	[2] 0.387	[2] 6.905

(ii) between family 01004 and its F_2 (table 8.XVI)

Sample	PREPHARATE	PHARATE	PUPAL
004 x 011 C	[10] 4.070	[8] 1.569	[10] 3.127
004 x 012 C	[10] 3.473	[8] 2.400	[9] 3.084
011 x 012 C	[6] 0.000	[6] 1.286	[9] 0.124
004 x 011 E	[11] 0.399	[8] 0.159	[8] 0.495
004 x 012 E	[14] 3.790	[11] 2.546	[11] 5.509
011 x 012 E	[3] 0.364	[3] 0.704	[3] 0.753

[1] Rearing temperature K = 17.6°C, L = 13.9°C

[2] both samples of zero variance

APPENDIX VIII (cont.i)

(iii) between STOCK 01 F_3 and F_1 - F_2 (table XVII)

Sample	PREPHARATE	PHARATE	PUPAL
F_3 018 x 004 F_1 C	[12] 7.801	[10] 0.871	[10] 8.533
F_3 018 x 011 F_2 C	[8] 3.333	[8] 0.000	[10] 3.361
F_3 018 x 004 F_1 E	[12] 3.845	[9] 3.762	[9] 2.426
F_3 018 x 011 F_2 E	[1][2]	[3] 1.500	[1] 3.536
F_3 018 x 014 F_2 C	[6] 3.939	[6] 0.510	[6] 2.161
F_3 014 x 004 F_1 C	[8] 2.162	[6] 0.000	[6] 1.000
F_3 014 x 011 F_2 C	[4] 1.265	[4] 0.208	[6] 0.510
F_3 014 x 012 F_2 C	[4] 0.672	[4] 1.757	[5] 0.373
F_3 018 x 012 F_2 C	[8] 2.445	[8] 0.698	[9] 2.958
F_3 018 x 012 F_2 E	[4] 3.330	[4] 0.814	[4] 3.701

(iv) between temperature, treatment and A_i (table 8.XVIII)

Constants	Variable	PREPHARATE	PHARATE	PUPA	LARVA	LIFE CYCLE
A_i=0 C	15°C v 19°C	[5] 17.496	[5] 2.905	[7] 12.286	[8] 20.441	[7] 19.834
A_i=1 C	15°C v 19°C	[5] 2.761	[5] 0.000	[6] 2.974	[11] 9.410	[6] 7.474
19°C A_i=0	Foil v Cold	[6] 5.803	[6] 0.355	[7] 6.896	[14] 3.242	[7] 5.455
19°C A_i=1	Foil v Cold	[3] 3.434	[3] 0.500	[5] 1.413	[6] 1.796	[5] 1.013
15°C C	A_i=0 v Ai=1	[4] 1.059	[4] 1.408	[4] 0.884	[5] 1.300	[4] 1.403
19°C C	A_i=0 v Ai=1	[6] 0.126	[6] 1.115	[9] 0.122	[14] 1.474	[9] 0.540
19°C E	A_i=0 v A_i=1	[3] 0.364	[3] 0.482	[3] 0.753	[6] 2.207	[3] 0.812

[2] both samples zero variance

APPENDIX VIII (cont.ii)

(v) between A_i and temperature (°C) in STOCK 03 F_2 (table 8.XIX)

Constants		Variable	PREPHARATE	PHARATE	PUPAL
18°C	C	x A_i	[5] 0.497	[4] 0.224	[3] 0.120
18°C	E	x A_i	[3] 2.106	[5][2]	[2] 0.409
14°C	C	x A_i	[1][2]	[1] 0.707	[1] 17.678
14°C	E	x A_i	[4] 11.692	[4] 2.449	[4] 7.411
A_i=0.4	C	x °C	[ ][3]	[ ][3]	[ ][3]
A_i=0.4	E	x °C	[3] 4.293	[3] 2.000	[3] 2.404
A_i=1.8	C	x °C	[5] 20.283	[5] 5.544	[4] 23.685
A_i=1.8	E	x °C	[4] 11.052	[6] 1.936	[3] 3.017

(vi) between stocks under corresponding treatments (table 8.XXI)

Samples[4]	PREPHARATE	PHARATE	PUPAL
(002) 01 x 02 C	[13] 3.354	[11] 2.442	[11] 5.783
(004) 01 x 02 C	[13] 6.113	[10] 0.000	[10] 11.234
(002) 01 x 02 E	[20] 1.399	[20] 2.093	[18] 0.570
(004) 01 x 02 E	[17] 0.920	[15] 1.611	[13] 0.394
(002) 01 x 04 C	[7] 0.151	[6] 0.591	[6] 0.756
(004) 01 x 04 C	[7] 0.422	[5] 0.667	[5] 2.648
(002) 01 x 06 C	[32] 0.924	[28] 4.780	[28] 3.655
(004) 01 x 06 C	[32] 0.193	[27] 1.157	[27] 3.312
(002) 01 x 06 E	[50] 4.497	[42] 4.131	[42] 0.197
(004) 01 x 06 E	[47] 3.449	[37] 5.546	[37] 1.975
02 x 04 C	[6] 1.070	[5][2]	[5] 0.563
02 x 06 C	[31] 5.196	[27] 1.290	[27] 6.110
02 x 06 E	[42] 1.717	[36] 0.991	[34] 1.433
04 x 06 C	[25] 0.177	[22] 0.149	[22] 0.348

[1] Rearing temperature K = 17.6°C, L = 13.9°C

[2] both samples zero variance

[3] only one individual only per sample

[4] respective STOCK 01 families: 002 or 004

APPENDIX IX

Wing characters scored for *Pararge aegeria*

Character	Location	Type
MFW	The 1° forewing examined	
FSPAN	Maximum base-termen[1] distance parallel to forewing dorsum at $M^1{:}M^2$	Length
PAT1	FW_D $E^3{:}M^1$ 1a	P/A
PAT2	FW_D F:J 1	P/A
PAT3	FW_D $E^3{:}M^1$ 2	Length
PAT3C	FW_D $E^3{:}M^1$ 2	Colour
PAT4	FW_D $M^1{:}M^2$ 2	Length
PAT4C	FW_D $M^1{:}M^2$ 2	Colour[2]
PAT5	FW_D $E^1{:}E^2$ 2	P/A
PAT6	FW_D $E^2{:}E^3$ 3	Length
PAT6C	FW_D $E^2{:}E^3$ 3	Colour
VEN7	FW v5 from d2/d3 fusion to termen[1] and parallel to v5 at $U{:}U_D$	Length
SPC8	FW_D s5 from v6/d2/d3 fusion to termen[1] and parallel to v5 at U:U	Length
SPC8C	FW_D s5	Colour
PAT9A	FW_D $(U{:}U)_a$ 5	Length
PAT9AC	FW_D $(U{:}U)_a$ 5	Colour
PAT9B	FW_D $(U{:}U)_b$ 5	Length
PAT9BC	FW_D $(U{:}U)_b$ 5	Colour
PAT10	FW_D OC 5	Length
PAT10C	FW_D OC 5	Colour
PAT11	FW_D cOC 5	Length
PAT11C	FW_D cOC 5	Colour
PAT12	FW_D $U{:}M^1$ 5	Length
PAT12C	FW_D $U{:}M^1$ 5	Colour
PAT13	FW_D $(U{:}U)_b + (U{:}M^1)_a$ 5	P/A
PAT14	FW_D $E^1{:}E^2$ 5	P/A
PAT14C	FW_D $E^1{:}E^2$ 5	Colour

APPENDIX IX (cont.i)

Character	Location	Type
PAT15	FW_D I:F 5 midway between v5 and v6 and parallel to v5 at $E^1:E^2$	Length
PAT15C	FW_D I:F 5 midway between v5 and v6	Colour
PAT16	FW_D V:F 5 parallel to v5 at $E^1:E^2$	Length
PAT16C	FW_D V:F 5	Colour
SPC17	FW s0 from $v4_b$ to median $vein_b$ and parallel to v2-v3 sector of median	Length
SPC17C	FW s0	Colour[3]
PAT18	FW_D $D^1:M^2$ 0 parallel to v2-v3 sector of median vein	Length
PAT18C	FW_D $D^1:M^2$ 0	Colour
PAT19	FW_D $M^2:D^2$ 0 parallel to v2-v3 sector of median vein	Length
PAT19C	FW_D $M^2:D^2$ 0	Colour
PAT9AU	FW_V $(U:U)_a$ 5	Length
PAT9AUC	FW_V $(U:U)_a$ 5	Colour
PAT9BU	FW_V $(U:U)_b$ 5	Length
PAT9BUC	FW_V $(U:U)_b$ 5	Colour
PAT10U	FW_V OC 5	Length
PAT10UC	FW_V OC 5	Colour
PAT11U	FW_V cOC 5	Length
PAT11UC	FW_V cOC 5	Colour
PAT12U	FW_V $U:M^1$ 5	Length
PAT12UC	FW_V $U:M^1$ 5	Colour
PAT13U	FW_V $(U:U)_b + (U:M^1)_a$ 5	P/A
FSPANA	as for FSPAN (2° FW)[1]	
PAT9AA	as for PAT9A (2° FW)	
PAT9AAC	as for PAT9AC (2° FW)	
PAT9BA	as for PAT9B (2° FW)	
PAT9BAC	as for PAT9BC (2° FW)	
PAT10A	as for PAT10 (2° FW)	
PAT10AC	as for PAT10C (2° FW)	
PAT11A	as for PAT11 (2° FW)	

APPENDIX IX (cont.ii)

Character	Location	Type
PAT11AC	as for PAT11C (2° FW)	
PAT12A	as for PAT12 (2° FW)	
PAT12AC	as for PAT12A (2° FW)	
PAT13A	as for PAT13 (2° FW)	
HWIN	The 1° hindwing examined	
HSPAN	Maximum base-termen[1] distance parallel to hindwing costa at ($U{:}M^1$)	Length
VEN21	HW v2 from median vein to termen[1] and parallel to v2 at $E^3{:}U_D$	Length
SPC22	HW_D s2 from v2/median vein fusion to termen[1] and parallel to v2 at $E^3{:}U$	Length
SPC22C	HW_D s2	Colour[2]
PAT23	HW_D $E^3{:}U$ 2	Length
PAT23C	HW_D $E^3{:}U$ 2	Colour
PAT24	HW_D OC 2	Length
PAT24C	HW_D OC 2	Colour
PAT25	HW_D cOC 2	Length
PAT25C	HW_D cOC 2	Colour
PAT26	HW_D I:F 2 midway between v2 and v3 and parallel to v2 at $E^3{:}U^2$	Length
PAT26C	HW_D I:F 2	Colour
PAT27	HW_D V:F 2 parallel to v2 at $E^3{:}U^2$	Length
PAT27C	HW_D V:F 2	Colour
PAT28	HW_D $E^3{:}U$ 3	Length
PAT28C	HW_D $E^3{:}U$ 3	Colour
PAT29	HW_D OC 3	Length[4]
PAT29C	HW_D OC 3	Colour
PAT30	HW_D cOC 3	Length[4]
PAT30C	HW_D cOC 3	Colour
PAT31	HW_D $E^3{:}U$ 4	Length
PAT31C	HW_D $E^3{:}U$ 4	Colour
PAT32	HW_D OC 4	Length[4]
PAT32C	HW_D OC 4	Colour

APPENDIX IX (cont.iii)

Character	Location	Type
PAT33	HW_D cOC 4	Length[4]
PAT33C	HW_D cOC 4	Colour
PAT34	HW_D E^3:U 5	Length
PAT34C	HW_D E^3:U 5	Colour
PAT35	HW_D OC 5	Length
PAT35C	HW_D OC 5	Colour
PAT36	HW_D cOC 5	P/A
PAT37	HW_D U:M^1 4-5 parallel to v5	Length
PAT37C	HW_D U:M^1 4-5	Colour
PAT38	HW_D U:M^1 6-7 parallel to v7	Length
PAT38C	HW_D U:M^1 6-7	Colour
PAT39	HW_D OC 1-8	Meristic
PAT39A	HW_D (cOC OC E^3:U [1° or 2°]) 1-8	Meristic
PAT54[5]	HW_V D^2_a 4 present on either or both wings (1) or totally absent (0)	P/A
PAT55	HW_V D^2_p 4 present on either or both wings (1) or totally absent (0)	P/A
PAT56	HW_V D^1 4 present on either or both wings (1) or totally absent (0)	P/A
PAT57	HW_V M^1 4 present on either or both wings (1) or totally absent (0)	P/A
PAT58	HW_V OC 1c present on either or both wings (1) or totally absent (0)	P/A
PAT59	HW_V OC 2 present on either or both wings (1) or totally absent (0)	P/A
PAT60	HW_V OC 3 present on either or both wings (1) or totally absent (0)	P/A
PAT61	HW_V OC 4 present on either or both wings (1) or totally absent (0)	P/A
PAT62	HW_V OC 5 present on either or both wings (1) or totally absent (0)	P/A
PAT63	HW_V OC 5 present on either or both wings (1) or totally absent (0)	P/A

APPENDIX IX (cont.iv)

Character	Location	Type
PAT64	HW$_v$ [1° or 2°] OC 1a-8	Meristic
HSPANA	as for HSPAN (2° HW)	
PAT28A	as for PAT28 (2° HW)	
PAT28AC	as for PAT28C (2° HW)	
PAT29A	as for PAT29 (2° HW)	
PAT29AC	as for PAT29C (2° HW)	
PAT30A	as for PAT30 (2° HW)	
PAT30AC	as for PAT30C (2° HW)	
PAT31A	as for PAT31 (2° HW)	
PAT31AC	as for PAT31C (2° HW)	
PAT32A	as for PAT32 (2° HW)	
PAT32AC	as for PAT32C (2° HW)	
PAT33A	as for PAT33 (2° HW)	
PAT33AC	as for PAT33C (2° HW)	
FWOC	1° FW$_D$ PAT9A + PAT9B + PAT10	Length
FWOCU	as for FWOC (1° FW$_v$)	
FWOCA	as for FWOC (2° FW)	

Scoring is for: linear dimension = Length; colour TYPE-1 and TYPE-2 = Colour; presence (1) or absence (0) = P/A; or count = Meristic. Length (mm) is measured parallel to the sector of vein posteriorly bordering the respective character (with colour features the maximum continuous colour field) unless otherwise indicated. 1° wings are scored for all characters, 0^{ry} wings only for those used to investigate asymmetry, and denoted (dorsal view) as left (L) or right (R). For further explanation see text.

[1] Fringe excluded; [2] PAT4C$_2$, SPC22C$_1$ and SPC22C$_2$ reliability improved by macroscopic scoring; [3] PAT18 and PAT19 excluded; [4] presence/absence also scored; [5] numbers 40-53 omitted for historical reasons.

APPENDIX X

Pigment composition of the map colours

Map colour	Water colour pigment[1]		Ratio
	Name	No.	
WHITE	Chinese White	001	
PALE BLUE-GREY	Chinese White	001	>10
	Ultramarine	123	1
	Ivory Black	034	1
PALE YELLOW-GREY ..	Chinese White	001	5
	Lemon Yellow	651	1
	Ivory Black	034	<1
CREAM	Chinese White	001	>10
	Lemon Yellow	651	1
PALE YELLOW	Chinese White	001	5
	Lemon Yellow	651	1
GOLDEN YELLOW$_1$ .... $_2$	Chinese White	001	2
	Lemon Yellow	651	2
	Vermillion	588	1_1 $>1_2$
PALE ORANGE-YELLOW	Chinese White	001	4
	Yellow Ochre	663	1
ORANGE-YELLOW	Chinese White	001	1
	Lemon Yellow	651	1
	Vermillion	588	1
ORANGE	Chinese White	001	1
	Lemon Yellow	651	1
	Vermillion	588	2
ORANGE-BROWN	Yellow Ochre	663	5
	Burnt Sienna	221	1
OCHRE	Yellow Ochre	663	2
	Viridian	382	<1
RED-BROWN	Burnt Sienna	221	—
LIGHT GREY-BROWN ..	Chinese White	001	5
	Burnt Sienna	221	1
	Ivory Black	034	1
DARK GREY-BROWN	Chinese White	001	<1
	Burnt Sienna	221	2
	Ivory Black	034	2

APPENDIX X (continued)

Map colour	Water colour pigment		Ratio
	Name	No.	
DARK BROWN	Burnt Sienna Ivory Black	221 034	1 2
BLACK	Ivory Black	034	___

[1] Rowney & Company Ltd., London

[2] Black Map Background

APPENDIX XI

Transformations applied to the relevant wing characters examined in _Pararge_ _aegeria_

Character	Transformation	Rationale
PAT9AC	$Y^{-0.4491}$	Interaction
PAT9B	$Y^{-0.1990}$	Interaction
PAT9BC	$Y^{-0.2654}$	Interaction
PAT10C	$Y^{0.8553}$	Interaction
PAT11C	$Y^{-4.1219}$	Interaction
PAT12C	$Y^{-0.4187}$	Interaction
PAT14C	$Y^{-0.2338}$	Interaction
PAT15C	$Y^{-0.3651}$	Interaction
SPC17	$Y^{-1.0138}$	Interaction
PAT18	$Y^{-0.2896}$	Interaction
PAT18C	$Y^{-0.2418}$	Interaction
PAT19C	$Y^{-0.3847}$	Interaction
PAT9BU	$Y^{-0.2110}$	Interaction
PAT9BUC	$Y^{-0.2654}$	Interaction
PAT10UC	$Y^{0.8105}$	Interaction
PAT11UC	$Y^{0.1826}$	Interaction
PAT9AAC	$Y^{-0.4089}$	Interaction
PAT9BA	Ln Y	Interaction
PAT9BAC	$Y^{-0.1902}$	Interaction
PAT10AC	$Y^{0.8989}$	Interaction
PAT11AC	$Y^{-0.5906}$	Interaction
PAT9AAC	$Y^{-0.4089}$	Interaction
SPC22C	$Y^{0.9185}$	Interaction
PAT23C	$Y^{-0.4087}$	Interaction
PAT24	Ln Y	Interaction
PAT24C	$Y^{0.6858}$	Interaction
PAT26	$Y^{-0.4121}$	Interaction
PAT33	$Y^{-2.0000}$	Not normal
PAT34	$Y^{-0.2833}$	Interaction

APPENDIX XI (continued)

Character	Transformation	Rationale
PAT34C	$Y^{-0.4787}$	Interaction
PAT37C	$Y^{0.6556}$	Interaction
PAT38C	$Y^{-0.6790}$	Interaction
PAT39	$Y^{0.7166}$	Interaction
PAT39A	$Y^{0.1105}$	Interaction
PAT64	$Y^{-0.4044}$	Interaction
PAT28AC	$Y^{-2.0000}$	Not normal
PAT29AC	$Y^{1.1302}$	Interaction
PAT33A	$Y^{-0.1597}$	Interaction

Transformations:

Y = variable;
Ln = Natural logarith of Y;
Y^x = Y raised to the power X.

Rationale (reasons for their application):

Interaction = corrected for non-additivity;
Not normal = character not normally distributed.

For further explanation see text.

APPENDIX XII

Directional Asymmetries

	UNTREATED				FOIL				COLD SHOCK			
	Male	Female	002	004	Male	Female	002	004	Male	Female	002	004
FSPAN	-1.383	-0.659	-0.188	-1.697	-2.045*	-2.007	-2.039	-2.018	-0.045	-2.403	-1.648	-1.179
FWOC	7.207	14.270	2.621	15.114*	4.346*	3.124	7.598	0.618	0.431	1.111	-0.793	3.287
PAT9A	15.563**	33.666*	14.650*	28.240*	18.620*	15.122	19.429	15.030	-1.111	-0.032	-6.575	8.703
PAT9B	-11.010	-3.573	-32.660	10.777	-24.785	-39.895	-14.828	-45.674	-6.611	-23.862	-16.202	-17.831
PAT10	6.600*	-1.519	1.107	4.850	0.935	-3.008	2.063	-3.291	1.084	2.589	2.309	1.503
PAT11	3.853	-14.622	-23.274	14.469	3.397	-3.109	-4.102	4.225	10.353*	24.723	26.814	7.479
PAT12	86.625**	82.809	25.134	114.826*	2.258	30.932	20.289	11.127	15.204	29.500	-12.015	77.477
PAT9AC	11.180	12.416	0.000	20.866	4.605	-5.714	0.000	-0.157	-7.009	-3.009	-7.743	0.000
PAT9BC	-4.762	9.524	7.143	-5.714	8.525	-5.000	-5.000	8.525	0.000	2.592	2.592	0.000
PAT10C	0.366	0.000	0.549	0.000	-0.733	-0.449	-1.329	0.000	0.000	0.183	0.183	0.000
PAT11C	36.977	0.000	0.000	44.372	28.205	0.000	0.000	28.205	18.750	0.000	0.000	18.750
PAT12C	-18.506	-18.182	-13.636	-22.207	-16.667	0.000	0.000	-16.667	1.000	31.841	-6.093	57.901
HSPAN	-3.975	1.020	-5.030	-0.135	0.191	0.396	1.853	-1.023	1.429	2.472*	0.971	3.097**
PAT28	7.690	2.032	3.398	7.729	2.188	2.788*	1.978	2.863	2.183	0.272	-0.587	3.020*
PAT29	-2.591	-2.630	-1.981	-3.102	-1.178	-0.755	-0.674	-1.246	2.203	-3.699	-3.987	1.900
PAT30	-0.300	0.962	1.344	-1.314	3.600	2.772	2.939	3.460	35.713	-1.829	18.408	6.808
PAT31	6.349*	-0.330	6.245	2.425	1.730	2.647	2.208	2.096*	5.581	6.485	3.652	9.364
PAT32	1.705	4.172	2.570	2.494	1.984	0.625	2.695	0.259	1.316	0.273	3.106	-2.449
PAT33	33.333	-10.303	2.020	35.556	-133.370	-121.053	-42.792***	-172.500	0.000	55.491*	27.783	38.792
PAT28C	27.778	0.000	20.833	16.667	-6.667	0.000	0.000	-6.667	1.481	2.778	0.168	4.815
PAT29C	-0.366	1.465	-0.549	0.879	0.366	0.440	0.000	0.733	0.281	-0.366	-0.200	0.005
PAT30C	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
PAT31C	27.778	0.000	20.833	16.667	-6.667	0.000	0.000	-6.667	14.486	0.000	5.926	8.148
PAT32C	0.000	0.000	-0.549	0.440	-0.741	0.440	0.000	-0.375	-5.049	0.000	-4.131	0.000
PAT33C	-178.947	0.000	0.000	-89.474	0.000	0.000	0.000	0.000	63.248	-31.667	37.949	-47.500

The magnitude (%) and direction of asymmetries are shown. Negative values indicate a greater value for the left side (dorsal view). Two-tailed significance: * 0.01 < P < 0.05; ** 0.001 < P < 0.001; *** P < 0.001. For further explanation see text.

APPENDIX XIII

Antisymmetries

	UNTREATED				FOIL				COLD SHOCK			
	Male	Female	002	004	Male	Female	002	004	Male	Female	002	004
FSPAN	1.570	1.953	1.383	2.426	2.039	2.018	2.045	2.007	2.604	1.830	0.879	3.238
FWOC	7.207	19.541	6.574	15.114	4.566	10.727	10.779	4.523	6.345	6.464	7.080	5.420
PAT9A	16.697	36.253	17.237	29.374	18.914	24.963	24.234	19.521	15.315	14.414	16.133	12.737
PAT9B	38.642	6.448	33.324	23.580	60.458	66.299	30.247	90.502	61.793	43.927	44.609	60.768
PAT10	6.600	15.373	6.618	12.436	3.360	7.936	2.864	7.587	4.693	4.729	3.995	5.795
PAT11	22.771	30.271	30.347	21.210	15.865	19.371	9.513	24.080	12.819	25.165	28.211	8.632
PAT12	5.050	9.752	4.374	8.523	3.153	2.845	3.476	2.627	1.909	8.923	7.089	6.661
PAT9AC	12.000	38.448	28.704	22.672	0.000	17.701	12.939	5.714	12.938	6.250	15.172	7.176
PAT9BC	7.143	5.714	4.762	9.524	5.000	3.525	8.525	5.000	14.551	0.000	0.000	14.551
PAT10C	1.673	0.000	1.115	0.000	1.329	0.000	0.733	0.449	0.183	0.000	0.000	0.183
PAT11C	0.000	44.372	36.977	0.000	0.000	28.205	28.205	0.000	0.000	18.750	18.750	0.000
PAT12C	13.636	22.207	18.506	18.182	0.000	16.667	16.667	0.000	28.685	57.901	42.056	39.249
HSPAN	4.934	2.577	8.151	0.946	2.491	7.164	2.077	6.730	2.315	3.635	2.629	3.433
PAT28	10.038	3.069	5.000	9.887	3.279	2.788	2.107	3.847	3.461	5.086	5.147	3.567
PAT29	5.571	2.926	5.169	4.305	3.183	0.755	2.492	1.736	6.581	10.087	11.359	5.416
PAT30	3.118	4.038	2.883	3.814	11.822	8.505	10.454	10.199	48.397	13.381	33.253	20.218
PAT31	6.493	1.595	6.462	3.580	2.660	3.917	4.397	2.259	10.377	6.685	6.615	10.934
PAT32	3.130	10.463	4.311	6.586	3.761	2.218	3.258	2.895	6.575	7.851	8.498	5.526
PAT33	166.667	16.364	135.354	97.778	133.370	121.053	42.792	172.500	88.889	64.055	84.926	59.670
PAT28C	20.833	16.667	27.778	0.000	0.000	6.667	6.667	0.000	9.259	13.704	11.481	11.111
PAT29C	0.549	0.879	0.366	0.000	0.000	0.733	0.366	0.440	0.599	0.494	0.281	0.733
PAT30C	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
PAT31C	20.833	16.667	27.778	0.000	0.000	6.667	6.667	0.000	5.926	8.148	14.486	0.000
PAT32C	0.549	0.440	0.000	1.465	0.000	1.107	0.741	0.440	4.131	0.000	5.049	0.000
PAT33C	0.000	89.474	178.947	0.000	0.000	0.000	0.000	0.000	37.949	47.500	63.248	31.667

The magnitudes (%) of the asymmetries are shown. For further explanation see text

APPENDIX XIV.i

Family and sex differences in fluctuating asymmetry

	002	004	t-value	Male	Female	t-value
FSPAN	3.0%	0.7%	1.979[7]ns	0.1%	0.0%	2.707[7]*
FWOC	14.7%	93.6%	0.157[7]ns	25.0%	27.9%	3.322[7]*
PAT9A	2.8%	18.9%	4.275[8]**	1.6%	30.6%	2.752[8]ns
PAT9B	67.8%	16.4%	6.432[7]***	54.0%	0.5%	2.224[7]ns
PAT10	31.3%	15.2%	0.197[8]ns	17.7%	15.5%	1.126[8]ns
PAT11	95.0%	10.8%	0.698[7]ns	45.8%	66.9%	3.811[7]**
PAT12	0.4%	13.1%	1.061[7]ns	12.2%	5.4%	4.360[7]**
PAT13[1]	25.0%	0.0%	12.500[1]***	33.3%	0.0%	16.652[1]***
PAT9AC	0.0%	82.4%	17.704[4]***	44.3%	0.0%	16.114[4]***
PAT11C	0.0%	[A]	[A]	44.4%	0.0%	[B]
HSPAN	20.3%	1.6%	3.211[7]*	85.9%	12.4%	3.238[7]*
PAT28	39.2%	2.2%	1.597[7]ns	5.4%	18.3%	3.804[7]**
PAT29	12.1%	6.1%	1.278[6]ns	16.3%	0.0%	0.784[6]ns
PAT30	0.8%	0.0%	0.000[3]ns	0.4%	0.0%	0.492[3]ns
PAT31	40.1%	41.2%	0.502[7]ns	21.6%	30.7%	0.042[7]ns
PAT32	57.7%	6.1%	4.522[7]**	68.8%	2.7%	3.184[7]*
PAT33	7.6%	0.1%	0.606[4]ns	2.7%	0.0%	2.604[4]ns
PAT28C	[B]	[B]	[B]	[A]	0.0%	[A]
PAT30C	0.0%	0.0%	0.000[6]ns	0.0%	0.0%	0.000[6]ns
PAT31C	[B]	[B]	[B]	[A]	0.0%	[A]
PAT33C	0.0%	[B]	[B]	[B]	0.0%	[B]
PAT39[1]	50.0%	0.0%	25.000[1]***	33.3%	0.0%	16.652[1]***

[1] Frequency of left/right difference; chi-square values are shown

[A] = sample of zero variance

[B] = insufficient sample size

Levels of fluctuating asymmetry (%) are reported. T-values of the differences are given with their degrees of freedom in parentheses. 2-tailed significance levels: * $0.01<P,0.05$; ** $0.001<P<0.01$; *** $P<0.001$. For further explanation see text.

APPENDIX XIV.ii

Differences in fluctuating asymmetry between untreated and foil treated samples in each sex

	MALES			FEMALES		
	None	Foil	t-value	None	Foil	t-value
FSPAN	0.1%	0.0%	0.959[9] ns	0.0%	0.1%	2.611[7]*
FWOC	25.0%	22.8%	0.636[10]ns	27.9%	15.3%	0.726[6]ns
PAT9A	1.6%	3.2%	1.481[10]ns	30.6%	27.9%	0.135[7]ns
PAT9B	54.0%	40.4%	11.141[10]***	0.5%	13.8%	4.414[6]ns
PAT10	17.7%	3.8%	3.449[10]**	15.5%	99.1%	3.647[7]**
PAT11	45.8%	79.1%	1.209[10]ns	66.9%	27.3%	1.320[6]ns
PAT12	12.2%	2.8%	1.573[9] ns	5.4%	4.4%	0.255[7]ns
PAT13[1]	33.3%	0.0%	16.652[1] ***	0.0%	0.0%	0.000[1]ns
PAT9AC	44.3%	0.0%	17.508[4] ***	0.0%	[B]	[B]
PAT10C	0.0%	[B]	[B]	0.0%	[B]	[B]
PAT11C	44.4%	[B]	[B]	0.0%	0.0%	0.000[5]ns
PAT12C	[A]	[B]	[B]	[B]	0.0%	[B]
HSPAN	85.9%	48.1%	1.864[9] ns	12.4%	98.7%	3.439[6]*
PAT28	5.4%	10.1%	1.417[10]ns	18.3%	0.8%	3.484[6]*
PAT29	16.3%	2.6%	4.060[10]**	0.0%	0.0%	0.000[2]ns
PAT30	0.4%	6.8%	3.525[7] **	0.0%	12.6%	0.784[5]ns
PAT31	21.6%	27.3%	0.494[9] ns	30.7%	61.7%	1.007[6]ns
PAT32	68.8%	6.7%	5.927[10]***	2.7%	84.7%	3.575[5]*
PAT33	2.7%	92.0%	4.490[6] **	0.0%	0.0%	0.000[2]ns
PAT28C	[A]	[B]	[B]	0.0%	0.0%	0.000[7]ns
PAT30C	0.0%	0.0%	0.000[10]ns	0.0%	0.0%	0.000[5]ns
PAT31C	[A]	[B]	[B]	0.0%	0.0%	0.000[6]ns
PAT33C	[B]	0.0%	[B]	0.0%	0.0%	0.000[1]ns
PAT39[1]	46.8%	8.6%	26.340[1] ***	0.0%	35.0%	17.500[1]***

[1] Frequency of left/right difference; chi-square values are shown

[A] = sample of zero variance

[B] = insufficient sample size

Legend as for Appendix XIV.i. For further explanation see text.

APPENDIX XIV.iii

Differences in fluctuating asymmetry between foil and cold treated samples in each sex

	MALES			FEMALES		
	Foil	Cold	t-value	Foil	Cold	t-value
FSPAN	0.0%	0.0%	3.566[12]**	0.1%	0.0%	2.716[15]*
FWOC	22.8%	51.6%	2.598[12]*	15.3%	8.6%	1.624[15]ns
PAT9A	3.2%	17.2%	4.524[12]***	27.9%	12.9%	2.263[15]*
PAT9B	40.4%	99.0%	4.734[12]***	13.8%	40.4%	3.302[15]**
PAT10	3.8%	10.1%	2.623[12]*	99.1%	3.3%	12.057[15]***
PAT11	79.1%	19.8%	4.833[12]***	27.3%	14.7%	1.730[14]ns
PAT12	2.8%	5.7%	1.885[12]ns	4.4%	12.1%	2.785[15]*
PAT13[1]	0.0%	44.0%	22.000[1] ***	0.0%	16.7%	8.350[1] **
PAT9AC	0.0%	95.2%	16.764[3] ***	[B]	0.0%	[B]
PAT9BC	[B]	6.4%	[B]	[B]	[B]	[B]
PAT11C	[B]	69.4%	[B]	0.0%	22.0%	[B]
PAT12C	[B]	26.8%	[B]	0.0%	56.1%	[B]
HSPAN	48.1%	3.2%	6.883[12]***	98.7%	24.6%	5.855[13]***
PAT28	10.1%	70.9%	6.189[12]***	0.8%	20.7%	1.684[15]ns
PAT29	2.6%	38.9%	6.925[11]***	0.0%	8.5%	0.838[12]ns
PAT30	6.8%	9.7%	0.932[12]ns	12.6%	4.9%	2.574[15]*
PAT31	27.3%	36.3%	0.797[12]ns	61.1%	47.1%	0.875[12]ns
PAT32	6.7%	91.5%	8.853[12]***	84.7%	11.1%	3.514[12]**
PAT33	92.0%	2.4%	4.530[6] **	0.0%	3.7%	0.942[7]ns
PAT28C	[B]	0.0%	[B]	0.0%	0.0%	0.000[5] ns
PAT30C	0.0%	0.0%	0.000[11]ns	0.0%	0.0%	0.000[15]ns
PAT31C	[B]	0.0%	[B]	0.0%	0.0%	0.000[13]ns
PAT33C	0.0%	[B]	[B]	0.0%	[B]	[B]
PAT39[1]	8.6%	10.0%	0.105[1] ns	35.0%	33.3%	0.042[1] ns

[1] Frequency of left/right difference; chi-square values are shown
[B] = insufficient sample size

Legend as for Appendix XIV.i. For further explanation see text.

APPENDIX XV

Variability of the wing characters

(i) *Family differences*

	002			004			
	V^*	s_{V^*}	n	V^*	s_{V^*}	n	t-value
PAT9BC	0.0	0.00	4	8.3	2.40	6	3.458[8] **
SPC22C	0.0	0.00	4	2.5	0.72	6	3.472[8] **
PAT24C	0.0	0.00	4	1.3	0.38	6	3.421[8] **

(ii) *Untreated and foil treated sample differences*

		UNTREATED			FOIL			
		V^*	s_{V^*}	n	V^*	s_{V^*}	n	t-value
Males	PAT8C	1.9	0.55	6	0.0	0.00	5	3.455[10]**
	PAT26	9.1	2.63	6	0.7	0.20	6	3.185[10]**
Females	SPC22C	2.3	0.33	4	0.0	0.00	5	6.970[7] ***

Coefficients of variation (V^*) are reported with their standard errors (s_{V^*}) and sample sizes (n). T-values of the differences are given with their degrees of freedom in parentheses. 2-tailed significance levels: * $0.01<P<0.05$; ** $0.001<P,0.01$; *** $P<0.001$. For further explanation see text.

over/

APPENDIX XV (continued)

(iii) *Foil and cold treated sample differences*

		FOIL			COLD			
		V^*	s_{V^*}	n	V^*	s_{V^*}	n	t-value
Males	PAT4C	25.2	7.69	6	0.0	0.00	6	3.277[10]**
	PAT10C	1.0	0.30	6	0.0	0.00	8	3.333[12]**
	PAT18C	2.7	0.78	6	15.3	3.90	8	3.168[12]**
	PAT10UC	0.9	0.27	6	0.0	0.00	8	3.333[12]**
	PAT9BAC	0.0	0.00	6	3.9	0.98	8	3.980[12]**
	PAT24	6.2	1.79	6	22.0	4.92	10	3.018[14]**
	PAT25	5.5	1.59	6	39.9	8.92	10	3.797[14]**
	PAT26	0.7	0.20	6	5.1	1.20	9	3.617[13]**
	PAT29	3.3	0.95	6	14.3	3.37	9	3.142[13]**
	PAT32	4.9	1.41	6	34.3	8.08	9	3.584[13]**
	SPC22C	0.9	0.27	6	0.0	0.00	8	3.333[12]**
	PAT27C	0.0	0.00	6	35.1	10.41	7	3.372[11]**
	PAT32C	0.9	0.26	6	18.0	4.38	9	3.897[13]**
	PAT29A	3.3	0.95	6	16.1	3.79	9	3.376[13]**
	PAT32A	8.7	2.51	6	32.7	7.31	10	3.105[14]**
Females	PAT3	4.8	1.52	5	14.2	2.78	13	2.967[16]**
	PAT6	3.7	1.17	5	33.6	6.59	13	4.122[16]***
	PAT8C	0.0	0.00	5	1.5	0.30	13	5.000[16]***
	PAT15C	3.3	1.06	5	23.2	6.09	13	3.219[16]**
	PAT18C	4.6	1.43	5	20.7	4.40	13	3.480[16]**
	FWOCU	6.5	2.06	5	19.7	3.86	13	3.017[16]**
	PAT9AU	13.1	4.14	5	51.0	10.00	13	3.502[16]**
	PAT10U	5.5	1.74	5	20.2	3.96	13	3.399[16]**
	PAT9BUC	5.5	1.92	4	18.0	3.65	13	3.013[15]**
	PAT11A	5.0	1.58	5	35.8	7.63	11	3.952[14]**
	PAT27C	0.0	0.00	5	1.7	0.41	8	4.164[11]**
	PAT36	0.0	0.00	5	346.5	67.95	13	5.099[16]***

Legend as for APPENDIX XV (i).

APPENDIX XVI

Specimens exemplifying the damages used in moment invariant analysis

DAMAGE CODE	SPECIMEN	WING	DAMAGE TYPE
1	03 002 007	R.Hw	
	03 002 011	R.Hw	
2	01 002 018	R.Fw	
	01 002 021	R.Hw	
2	01 004 018	R.Hw	
2	03 002 013	R.Hw	
3	01 001 002	R.Fw	Holes
	01 001 004	R.Fw	Holes
	03 002 001	L.Hw	Hole
	03 004 025	L.Hw	Hole
4	01 001 006	L.Fw	
	01 111 004	L.Hw	
	07 001 001	R.Fw	
5	01 001 001	L.Fw	
	03 002 009	L.Fw	
6	03 004 025	R.Fw	deletion
	07 001 008	L.Fw	
7	01 004 020	L.Fw	
	06 001 035	L.Fw	
8	01 001 006	L.Fw	rubs along veins
	01 001 013	L.Fw	rubs along veins
	02 001 007	L.Fw	rubs along veins
9	01 004 021	R.Fw	rub
	06 001 001	L.Fw	
	06 001 001	L.Fw	
	06 001 002	L.Fw	rub
	06 001 002	L.Fw	
10	01 001 013	R.Fw	rub
	01 001 013	R.Fw	basal rubs
	01 004 012	L.Fw	
	03 003 002	R.Fw	

Only damage types not distinct in Fig. 10.2 are qualified