

## "SEX-RATIO" IN *PIERIS* HYBRIDS

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Those lepidopterists who have worked with interspecific hybrids will be aware that in many instances female hybrids are very difficult to obtain. This is in accordance with the rule of Haldane (1922) that in all such hybrids it is the heterogametic (XY) sex which is the less vigorous, less numerous, and less fertile. In hybrid Pieridae, developmental disturbances which affect only the female range from mere changes in the incidence or length of diapause to its indefinite extension leading to death (Bowden, 1957). In experimental conditions it may easily happen that diapause pupae, which would eventually have produced imagines, are meanwhile adversely affected by those conditions and die before they can do so. A sex-ratio effect which is to some extent spurious can thus be produced.

Therefore, in assessing numerical breeding results, that is, the numbers of the sexes (as of other phenotypes) reaching the imaginal state, it is useful to have some estimate of the losses that have occurred, and particularly to know at what stages of development they took place. Losses in the egg, or of very young larvae, point to lethal combinations, especially if losses are few among more mature larvae. At least in *Drosophila*, some lethal factors do become operative in the last larval instar (Hadorn, 1961), but in *Pieris* losses which increase during the feeding of a brood can often be recognized as due to a bacterial or other disease; blacking-off commonly follows among the pupae. Losses at the time of pupation are by no means always due to infection; particularly when not preceded by larval losses, deaths at this stage also may be attributable to lethals. Of course, it is not suggested that losses by disease have no genetic aspect: it may well be that different genotypes possess different resistances.

The advantage of one genotype over another, as reflected in breeding results, is always relative to the conditions obtaining during the experiment. Although selection by disease or bad management can be very severe, it is seldom as rigorous as that operating in natural conditions, where one pair produces one pair. This being so, any attempt to establish by breeding a change in the degree of some genetic advantage with the passage of years (supposedly due to gene-complex selection) is extremely hazardous, and even more difficult when results of different breeders are compared.

The present paper is concerned principally with a series of related

hybrid *Pieris* broods in which males were underrepresented, in apparent contradiction to Haldane's rule.

#### EXPERIMENTAL

In a previous publication in this journal (1958) the present author reported on the occurrence of sexual mosaics among inter-subspecific or -specific hybrids within the European *Pieris napi-bryoniae* group. These butterflies are all so closely related that in the  $F_1$  crosses Haldane effects are small. In only five or six of all the 69 broods examined for sex-mosaicism did the sex ratio depart significantly from unity. In four of these the females numbered only about half the males; in another there were 28 females to 42 males.

A brood 1952-*b* on the other hand consisted of 15 females and one almost entirely female mosaic (?). While this instance of male deficiency remained an isolated one, only conjecture was possible; at the time it was considered not unlikely that chromosomal males (XX) had been converted into mosaics in which male scaling had almost completely disappeared.

However, in 1957 a new series of crosses between the same two subspecies, the Swiss *bryoniae* Ochsenheimer (locality Engelbergertal) and British *napi* L., was begun. This experiment was designed to test the possibility of maintaining particular *napi* genes in hybrids whose *napi* component was progressively diminished by repeated backcrossing to *bryoniae*. A preliminary account of this work, up to 1959-1960, has been given (Bowden, 1962); subsequent breeding has maintained the chosen *napi* recessive gene to the time of writing, in butterflies calculated to carry in 1964 only  $\frac{3}{128}$  of *napi* autosomal material. As so often happens, an experiment designed to decide one question suggested an answer to another: this series provided no less than four broods in which females outnumbered males by between five and ten to one. Many of the few males surviving to the imaginal stage were crippled or weak. Such results imply a sex-limited lethality of variable penetrance.

The relevant figures are given in Table I. Each brood is indicated by an italic or Greek letter preceded by the year in which the eggs were laid. The notation for the subspecific makeup is as in the 1958 paper: B stands for *bryoniae*, N for *napi*, and K for *neobryoniae* Sheljuzhko (Kärnten, Austria). In addition the Greek letter beta is used as shorthand for (BN.B).(B.BN), to simplify notation for the later broods. Placing the female first, the symbols are combined pseudoalgebraically; but an  $F_3$  brood written  $(BN)^3$  would be  $(BN)^2 \times (BN)^2$ , and so differs from  $(BN)^2.BN$ . Some cultures were of necessity mixed broods from more than one female, though these were always sibs of similar pheno-

TABLE 1. Sex-differential lethality in *Pieris* Hybrids

Parentage ♀ ♂	No. of used ♀	Hybrid type	Sex chromo- somes <sup>1</sup>	Brood	No. of imagines ♀ ♂	$\chi^2$ (Yates')	Probability	Remarks
'50- $\theta$ x '50- $\omega$	1	BN	C	1951- $\gamma$	31 31	0	P>0.99	Very few losses
'51- $\beta$ x '51- $\gamma$	1	(BN) <sup>2</sup>	E	1951- $\nu$	39 43	0.11	0.8>P>0.7	Few larval losses (23 as pupae).
'51- $\nu$ x '51- $\gamma$	1	(BN) <sup>2</sup> .BN	E	1952-b	15 ♂ 1♀	11.4	P<0.001	1 mosaic? Most of ca. 80 eggs failed.
'56- $\bar{t}$ x '56- $\bar{m}$	1	BN	C	1957-a	14 13	0	P>0.99	Few losses.
'57- $\bar{c}$ x '56- $\bar{h}$	2	BN.B	D	1957-h	36 ♂ 7	18.2	P<0.001	Heavy losses in eggs and very young larvae, 5 of males crippled or weak.
'56- $\bar{h}$ x '57- $\bar{e}$	1	B.BN	B	1957-t	33 24	1.12	0.3>P>0.2	A few losses as eggs and pupae.
'57- $\bar{h}$ x '57- $\bar{t}$	3	(BN.B) (B.BN)	B	1958- $\phi^i$	26 < 48	5.96	0.02>P>0.01	At least 89 losses as eggs and young larvae.
"	2	"	B/A	$\phi^{ii}$	4 6	0.10	0.8>P>0.7	Few losses
'57- $\bar{t}$ x '57- $\bar{t}$	3	(B.BN) <sup>2</sup>	B/A	1958- $\theta^i$	22 18	0.23	0.7>P>0.5	3 mosaics. At least 34 eggs failed.
"	3	"	"	$\theta^{ii}$	2 3	-	-	At least 185 eggs failed.
'58- $\phi^i$ x '58- $\theta^i$	1	$\beta$ .(B.BN) <sup>2</sup>	B/A	1959- $\theta$	2 4	-	-	Many eggs infert. Larval and pupal losses, 101. Disease present.
'58- $\bar{t}$ x '58- $\phi^i$	2	B. $\beta$	B	1959- $\phi^i$	12 21	1.94	0.2>P>0.1	1 mosaic) Many losses among larvae
"	2	"	B	$\phi^{ii}$	13 16	0.14	0.8>P>0.7	) and pupae.
"	2	"	B/A	$\phi^{iii}$	18 14	0.28	0.7>P>0.5	Disease present.
'59- $\bar{e}^{\bar{t}}$ x '59- $\phi^{ii}$	2	B.B $\beta$	B/A	1960-d	11 7	0.50	0.5>P>0.3	5 eggs died.
'59- $\phi^i$ x '59- $\phi^i$	1	(B $\beta$ ) <sup>2</sup>	"	1960-e	1 -	-	-	16 eggs infertile or dead.
'59- $\phi^{ii}$ x '59- $\phi^i$	1	(B $\beta$ ) <sup>2</sup>	E	1960- $\eta^i$	10 ♂ 1	5.82	0.02>P>0.01	32 losses, all stages. Only male, crippled.
"	2	"	E/D	$\eta^{ii}$	41 ♂ 5	26.6	P<0.001	37 losses as eggs and young larvae.
"	1	"	B/A	$\eta^{iii}$	3 2	-	-	14 eggs infertile.
'60- $\eta^i$ x '60- $\bar{a}$	1	(B $\beta$ ) <sup>2</sup> .KN	E	1961-a	95 ♂ 19	49.4	P<0.001	158 eggs recorded; 10 of males crippled etc.
'60- $\eta^{ii}$ x '60- $\bar{h}$	1	(B $\beta$ ) <sup>2</sup> .B	A	1961- $\bar{c}^i$	12 18	0.83	0.5>P>0.3	From 140 eggs. Losses in egg and pupal stages.
"	1	"	A	$\bar{c}^{ii}$	15 19	0.26	0.6>P>0.5	Losses in egg and pupal stages.
'61- $\bar{c}^i$ x '61- $\bar{c}^{ii}$	1	[(B $\beta$ ) <sup>2</sup> .B] <sup>2</sup>	A	1962-m	8 10	0.056	0.9>P>0.8	Probably ca. 100 eggs, incl. at least 39 infert. or dead; also larval and pupal losses.
'61- $\bar{c}^{ii}$ x '61- $\bar{c}^i$	1	[(B $\beta$ ) <sup>2</sup> .B] <sup>2</sup>	A	1962- $\eta^i$	14 17	0.13	0.8>P>0.7	Many losses, chiefly eggs and larvae.
"	1	"	A	$\eta^{ii}$	35 43	0.63	0.5>P>0.3	Many larval losses.
"	3	"	A	$\eta^{iii}$	8 5	0.31	0.7>P>0.5	Many eggs infertile, few other losses.

At fertilization we may have: A XY x XX → XY, XX  
 B XY x X'X → XX, X'Y, X'X  
 C XY x X'X' → X'Y, X'X  
 D. X'Y x XX → XY, X'X  
 E X'Y x X'X → XY, X'Y, X'X, X'X'

where X' is from *napt*.

type. From the present point of view this does represent a defect in the design of the experiment, but fortunately it seems to have led to no fatal ambiguity.

The 1961-*a* brood belongs in part to yet another experiment (Bowden, 1963), concerned with the linkage of form "subtalba" with form "sulphurea."

It is thought that only 1959- $\theta$ ,  $\phi^i$ ,  $\phi^{ii}$ , and  $\phi^{iii}$  suffered heavy losses from disease irrespective of any special susceptibility. The 1962 and 1963 broods did appear to be affected by general inbreeding depression, which has since been corrected. In most broods the losses, from whatever cause, were sufficient or more than sufficient to cover the sexual imbalance; for example, from 1960- $f^{ii}$  (41 ♀ and 5 ♂) 37 eggs and young larvae were lost (the almost complete absence of males among the more mature larvae of this brood was noticeable at the time). For 1961-*a* (95 ♀ and 19 ♂) only 158 eggs are recorded as laid, but there may in fact have been a few more.

#### DISCUSSION

Stebbins (1958) points out that if any recessive or semidominant sex-linked gene exists in one species, which produces lethal or sterility effects in combination with autosomal genes of the other, these effects will be covered in the homozygous sex by the corresponding dominant allele in the second X, but will be expressed in the heterozygous sex [female in Lepidoptera] where the dominant gene is absent. Essentially the same particularized explanation of Haldane's rule was earlier given by Muller.

Disturbances of the normal sex ratio, in *Drosophila* and in other animals, have received considerable attention from geneticists. Some of the diverse mechanisms suggested for *Drosophila* species, in which the male is the heterogametic sex, would require modification to be applicable to the Lepidoptera.

Patterson and Stone (1952) mention a gene on the third chromosome of *Drosophila* which reacts to cause death in X-bearing eggs: progenies of any females receiving this gene from their male parent are all male. Another gene, on the second chromosome, is lethal, especially when in the homozygous condition, to diploid females. They also quote a case where females carrying a certain gene had only male progeny, no matter with what kind of male they mated. Again, a dominant mutant in *D. pseudoobscura* changed chromosomal females into intersexes. The original references are given by Patterson and Stone.

Watson (1960) points out that although some of the known instances of abnormal "sex-ratio" condition in *Drosophila* species are due to the action of chromosomal genes, some appear to be cytoplasmic; in the

latter case the condition is transmitted constantly through the female only, over a series of backcrosses to other strains. About 99 percent of the males die, mostly in the embryonic stage; any survivors do not transmit the "sex-ratio" character.

Genic sterility may from the developmental-physiological viewpoint be very similar to hybrid inviability; both may be due to inability to carry out specific metabolic processes—which again is the basis of lethalities due to homozygous genes or deficiencies. A type of male sterility described by Ehrman (1960) in the *D. paulistorum* agg. is therefore worth quoting here. The inter-subspecific hybrids comprise fertile females and sterile males, the sterility depending upon the possession by the male's mother of a mixture of chromosomes from different subspecies: any one foreign chromosome is sufficient and the genotype of the male parent is immaterial.

Some of these mechanisms proposed for *Drosophila* can be ruled out at once in the present case. The cytoplasm is *bryoniae* throughout, for both normal and affected broods: pure cytoplasmic inheritance cannot explain the results. It seems impossible, too, to account for an intermittent decimation of males by any simple autosomal gene that they may themselves carry. Between 1957-*h* and 1960-*f*<sup>ii</sup> lie two unaffected annual generations, yet the gene cannot be a recessive since far more than a quarter of the males are destroyed at each occurrence.

The brood 1961-*a* forced us to consider in detail the possibility that the constitution of the mother of the brood is alone responsible.

Examining the series of hybrids and backcrosses begun in 1957, we first find the F<sub>1</sub>, 1957-*e*, perfectly normal. There is not even a Haldane effect.

The backcrosses, 1957-*h* and *i*, differ. The latter, *i*, is close enough to normal, but *h* shows a deficiency of males that is certainly significant. We can probably neglect minor, chance, genetic differences and assume that the effect is due to subspecific makeup. Broods *h* and *i* are merely reciprocal, but the mother of *h* carried a complete haploid set of *napi* autosomes and a *napi* X, whereas the mother of *i* was pure *bryoniae*. Are we to attribute the sex-ratio effect to the X-chromosome or to a dominant autosomal gene of *napi* origin?

We are unable to eliminate entirely the possibility of an autosomal effect. If, however, the mother of *h* carried such a dominant autosomal gene, she must have passed it to half her daughters, and similarly the father of *i* should have passed the same gene to half his daughters. Nevertheless, the three *h* females jointly responsible for 1958- $\phi$ <sup>i</sup> and the three *i* mothers of 1958- $\theta$ <sup>i</sup> show no sign of it in their progeny. The very

small broods 1958- $\phi^{ii}$  and  $\theta^{ii}$  point in the same direction, but can be neglected.

The alternative hypothesis, that the responsible gene or genes are sex-linked, appears more probable. The mother of the affected 1957-*h* had sex chromosomes X'Y, where X' is from *napi* (we shall neglect any crossing-over between X and X'; X' is to be considered as the X carrying the relevant genes originally derived from *napi*). Her sons will have been X'X, but X'X is not itself lethal or sublethal in *bryoniae* cytoplasm, since F<sub>1</sub> hybrid sons of a *bryoniae* female are normal. The inference is that the sons of an X'Y mother are affected, irrespective of their own genotype.

The brood 1958- $\phi^i$  will not have had such a mother, but an XY. Accordingly, the sex ratio  $\delta / \varphi$  was in fact normal, or even high. The male parent could have been XX or X'X; we must assume that it was X'X and the composition of the brood was then X'Y, XY, X'X, XX.

The broods 1959- $\phi^{i, ii, iii}$  were also normal, as would be expected from the XY *bryoniae* mothers. We must again assume that (at least for 1959- $\phi^{i, ii}$ ) the males from 1958- $\phi^i$  were once more of X'Y constitution, and the brood composed as in the previous generation.

The broods 1960- $f^{i, ii, iii}$  could thus have been produced by X'Y  $\times$  XX or X'X or by XY  $\times$  XX or X'X. On our hypothesis, the results imply that the small 1960- $f^{iii}$  was produced by the second alternative, but that the three females responsible for  $f^i$  and  $f^{ii}$  were all X'Y.

The parents of the earlier mentioned (B $\beta$ )<sup>2</sup>.KN brood, 1961-*a*, were from 1960- $f^i$  and a KN brood 1960-*s*. The female parent can have been X'Y; the male was X'X'', probably very like X'X; in this case the brood is essentially similar to 1960- $f^i$ .

Reverting to the main series, the brood 1960-*d*, having a pure *bryoniae* mother, is of normal sex ratio. Broods 1961- $c^{i, ii}$  are from 1960- $f^{ii} \times$  *bryoniae*. Here the female parent can have been XY, allowing the normal ratio actually obtained. But if so, the X' is eliminated from the series, and all later broods must also be normal. The subsequent 1962-*m*, 1962- $n^{i, ii, iii}$  in fact show no deficiency of males; two other broods of that year, being from pure *bryoniae* females, would be expected normal in any event. Two 1963 broods produced only 16 butterflies altogether, but there was no relative deficiency of males.

Thus, results in the 1957 series are consistent with the supposition that females carrying a *napi* X with *bryoniae* Y and *bryoniae* cytoplasm produce the broods in which males are underrepresented. In some cases there is no certainty that a *napi* X was present, though always it may

have been. Unfortunately no "visible" sex-linked genes are yet known in *P. napi*, and the X-chromosome is necessarily unmarked.

We may now return to the earlier brood 1952-*b*, which was entirely, or almost entirely, female. Its makeup was  $(BN)^2.BN$ , and the mother, from 1951-*v*, must have been produced by  $X'Y \times X'X \rightarrow X'Y, XY, X'X, X'X'$ , but in spite of this she belonged to a brood of normal sex ratio. Four similar  $F_2$  hybrid broods from the year 1952 were listed in our 1958 paper and will not be repeated here: all had normal ratio. Unfortunately, a straight  $F_2$  pairing in the 1957 series produced only infertile eggs, so it is not possible to say whether some special circumstance always rules for  $F_2$  hybrids. If this could be granted, we could explain 1952-*b* as from  $X'Y \times X'X$ .

Seven broods  $B.(BN)^2$  in 1953, having XY mothers, would be expected normal; the male parents being  $X'X$  and  $X'X'$ , both  $X'Y$  and (in smaller numbers) XY females would be produced. The ten  $[B.(BN)^2]^2$  broods obtained by inbreeding could thus have had XY or  $X'Y$  mothers. In fact, as the previously published table shows, the three largest broods had subequal sexes, totaling 54 females plus 54 males, while seven small broods yielded 18 females plus two males; there were also a few sexual mosaics. It seems possible, then, that the female parents were of the two genotypes suggested.

Results in the 1951 series also were therefore in accordance with the  $X'Y$ -mother hypothesis, except that the  $F_2$  hybrids which were included in that series showed a normal sex ratio. It is not clear what special circumstance can rule in the  $F_2$ ; the brood 1951-*v* was too successful for the easy assumption of a compensating loss of females. We are unwilling to postulate any difference between the stocks used in 1951 and 1957 that would be relevant here. Nor does the autosomal-gene alternative remove the difficulty.

It is clear from Table I that among *napi-bryoniae* hybrid populations other lethal effects, which are not sex-limited, must at times reduce numbers drastically, and perhaps more significantly by their extension to females. A more adequate discussion of the bearing of the sex-ratio effect, as of other phenomena reducing viability and fertility, on the likelihood of successfully continued hybridization in the wild, must be reserved. The *napi*  $X'$  may be more, or less, compatible in the genetic environment provided by other *bryoniae* subspecies.

Meanwhile, it appears to be desirable to raise new broods  $BN.B$  and  $(BN)^2$  using different *napi* stocks. In most  $(BN)^2$  broods heavy losses are likely, but a further  $(BN)^2.BN$  brood might be obtainable. With the  $X'Y$  hypothesis in mind, it should be possible to avoid the improvi-

dence of the accidental elimination of the *napi* X'. Such experiments, employing Yugoslav and Corsican *napi*, were begun in 1964. Results of a reverse experiment, in which *bryoniae* provides the "foreign" X, might also be illuminating.

#### SUMMARY

Five broods of *Pieris napi-bryoniae* hybrids have been obtained with male numbers about one-fifth to one-tenth of the females, in conflict with Haldane's rule that the heterozygous sex is the more liable to the prejudicial effects of hybridity. Many of the male escapers were weak. In every case the mother of the brood may have carried *napi* X-chromosomal material with *bryoniae* Y and *bryoniae* cytoplasm, and it is suggested that the effect is purely maternal. However, females thus constituted have on occasion produced F<sub>2</sub> hybrid broods of normal sex ratio. Necessary further experiments are in progress.

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## The Lepidopterists' Society CONSTITUTION AND BY-LAWS

(As amended January 1964)

WHEREAS, The Lepidopterists' Society was formed on May 4, 1947, to promote the scientifically sound and progressive study of Lepidoptera by —

1. publishing a periodical on Lepidoptera.
2. facilitating the exchange of specimens and notes by both the professional worker and the amateur in the field,

AND WHEREAS, it is now proposed to organize said Society in a more formal manner, the following Constitution and By-Laws are hereby adopted by the duly appointed Organization Committee. [1 October 1950]

### CONSTITUTION

#### Article I. NAME

Section 1. The organization shall be known as The Lepidopterists' Society.

#### Article II. OBJECT

Section 1. It shall be the purpose of the Society to promote internationally the science of lepidopterology in all its branches; to further the scientifically sound and progressive study of Lepidoptera; to publish periodicals and other publications on Lepidoptera; to facilitate the exchange of specimens and ideas by both the professional worker and the amateur in the field; to secure cooperation in all measures tending to that end, and to facilitate personal intercourse among its members.

#### Article III. MEMBERSHIP

Section 1. All persons interested in lepidopterology shall be eligible for membership.

Section 2. All individual subscribers to the *Journal* and the *News of the Lepidopterists' Society*, who have paid their current annual dues, shall be deemed members of the Society.

Section 3. The membership of the Society shall consist of four classes — Active, Sustaining, Life, and Honorary Members. All persons who joined the Society before January 1, 1948, shall be designated Charter Members.

Section 4. Application for Active, Sustaining, and Life membership in the Society, received by the Secretary or Treasurer and accompanied by the annual dues for the current year, shall constitute formalization of membership, and no nomination or election to membership shall be necessary. The annual dues shall be fixed by the By-Laws.

Section 5. Any member may become a Life Member upon the payment, at one time, of such sum as shall be fixed by the By-Laws, and shall be exempt from further assessment. He shall receive during his life a subscription to the *Journal* and the *News of the Lepidopterists' Society*. Life Membership fees shall be placed in a permanent Publication Fund.

Section 6. Individuals who have made important contributions to the science of lepidopterology may be elected Honorary Members of the Society. There shall not be more than ten living Honorary Members.

Section 7. Members one year in arrears in the payment of dues shall be dropped from the rolls by the Secretary.

Section 8. The Executive Council may expel any member of the Society for such cause as it may deem sufficient for expulsion. This action may be taken only after unanimous approval by members of the Council. Petition for expulsion shall be presented to the Secretary for presentation to the Council. On expulsion, the departing member shall be refunded all dues paid for the current year. An expelled member may be reinstated by unanimous affirmative vote of the Council.

#### Article IV. OFFICERS

Section 1. The officers of the Society shall consist of a President, three Vice-Presidents (not more than one of whom shall reside in one country), a Secretary, and a Treasurer, but these last two offices may be filled by the same person.

*Section 2.* The business and affairs of the Society, not otherwise provided for, shall be controlled by an Executive Council, consisting of the President, three Vice-Presidents, the Secretary, the Treasurer, and six other members of the Society. Action on all amendments to the By-Laws and all appointments and elections by the Executive Council shall be obtained by a canvass by the Secretary of all members of the Council.

*Section 3.* The Executive Council may appoint one or more Assistant Secretaries or Assistant Treasurers to serve during the pleasure of the Council. The offices of Assistant Secretary and Assistant Treasurer may be filled by the same person.

*Section 4.* The Executive Council shall have power to make and adopt By-Laws for the conduct of the business and affairs of the Society and for the regulation of its procedure not inconsistent with the terms and provisions of the Constitution.

#### Article V. ELECTIONS

*Section 1.* The President shall before the first of July appoint a Nominating Committee who shall nominate one candidate for each elective office to be filled for the ensuing year, and a list thereof shall be published in one of the Society's periodicals or mailed to the members at least sixty days before ballots are mailed by the Secretary. Additional candidates may be nominated by submission to the Secretary of written nominations signed by not less than ten members. Ballots containing all nominations shall be mailed in November of each year, setting forth the officers to be elected and the names of those nominated for each office. If more than one person is nominated for any office, their names shall be arranged alphabetically on the ballot.

*Section 2.* Election of Officers. All officers shall be elected by ballot. The President and all Vice-Presidents shall be elected for the term of one year, and shall be eligible to succeed themselves once. The Secretary and Treasurer shall be elected for the term of three years and shall be eligible to succeed themselves twice. The six other elective members of the Executive Council shall be elected for the term of three years; two of them shall be replaced each year; these members shall not be eligible to succeed themselves. For each office, the nominee receiving the highest number of ballots shall be elected. Officers shall take office at the beginning of the calendar year for which they are elected.

*Section 3.* Election of Honorary Members. Honorary Members shall be nominated by the unanimous vote of the members of the Executive Council. The nominee shall be voted on by mail ballot distributed to all members of the Society and reported in one of the Society's periodicals, and must receive 80% of all ballots cast to be elected. Not more than five Honorary Members may be elected at the first annual meeting, and not more than two in any one calendar year.

#### Article VI. DUTIES OF OFFICERS

*Section 1.* The President shall preside at all meetings. He shall appoint all committees and be Chairman of the Executive Council and a member *ex officio* of all other committees, except the Editorial Board. He may appoint also delegates to other learned societies, Congresses, and conventions.

*Section 2.* The First Vice-President shall assume the duties of the President in case of his death, resignation, absence, or disability.

*Section 3.* In case the President and all Vice-Presidents are absent at a meeting, a temporary Chairman may be chosen by a majority vote; he shall be a member of the Executive Council unless none is present, in which event another member of the Society may be elected.

*Section 4.* The Secretary shall keep the minutes of the meetings of the Society and of the Executive Council; shall give notice of the meetings of the Society; shall attend to all general correspondence; shall keep all records and files of the Society; shall prepare and distribute ballots; and shall generally perform all services that may be delegated to him.

*Section 5.* The Assistant Secretary shall assume the duties of the Secretary in

case of the death, resignation, absence, or disability of the Secretary, and shall assist the Secretary as need be.

*Section 6.* The Treasurer shall receive all monies for the Society and deposit them in the name of the Society in such banking institutions as the Executive Council shall direct. He shall pay therefrom by draft or check all bills and obligations of the Society; he shall keep an account of all monetary transactions and shall exhibit a statement of them when called for by the President or the Executive Council, and shall make a full report for the preceding calendar year at the annual meeting.

*Section 7.* The Assistant Treasurer shall assume the duties of the Treasurer in case of the death, resignation, absence, or disability of the Treasurer, and shall assist the Treasurer as need be.

*Section 8.* At the expiration of his term of office, each officer shall deliver to his successor all books, papers, funds, and vouchers belonging to the Society.

*Section 9.* The Society shall not and may not make any dividend, gift, division, or bonus in money to any of its members.

#### Article VII. MEETINGS

*Section 1.* The annual meeting shall be held in affiliation with the International Congress of Entomology or the annual meeting of the American Association for the Advancement of Science, or at such other time and place as the Executive Council may determine. Notice of said meeting shall be given as provided in the By-Laws.

*Section 2.* Special meetings of the Society may be called by the Secretary upon the written request of the President or ten active members. Such request shall state the purpose for which the meeting is to be called and the time and place where it is to be held. No other business, except that specified in the call, shall be transacted, except by unanimous consent of the members present.

#### Article VIII. PUBLICATIONS

*Section 1.* The Society shall publish a periodical to be known as the "*Journal of the Lepidopterists' Society*," a continuation of *The Lepidopterists' News*. The *Journal* shall be devoted to original papers, literature abstracts, and other matter of permanent record. Each volume shall be issued for a calendar year, and shall be composed of four numbers. In it shall be published a summary of the proceedings of the annual meetings.

*Section 2.* The Society shall also issue a periodical to be known as "*News of Lepidopterists' Society*," which shall be devoted primarily to notices by members, lists of new members, announcements of nominations, committee appointments, forthcoming meetings, summaries of the recent field collecting season, and other matter of interest to members but not requiring permanent record. It shall appear at more frequent intervals than the *Journal*. A list of members of the Society shall be issued at least every second year.

*Section 3.* The Society may issue from time to time serial publications to be known as "*Memoirs of the Lepidopterists' Society*" to contain longer works than are normal for the *Journal* and the *News*. This shall be financed by special funds, not by the annual dues, and shall be sold separately to members, at a lower price than to non-members.

#### Article IX. EDITORIAL BOARD

*Section 1.* The publications of the Society shall be under the charge of an Editorial Board, consisting of a Chairman and two other at-large members, the Editor of the *Journal*, the Editor of the *News*, the Editor of the *Memoirs*, and the two Associate Editors of the *Journal*. The Chairman may also be one of the above five editors. It shall determine broad publication policies of the Society not otherwise provided for in the Constitution or the By-Laws. It shall consider potential candidates for editorships and then make recommendations to the Executive Council for appointments of the three Editors.

*Section 2.* The Chairman of the Editorial Board shall be appointed by the Executive Council for the term of three years, and he may be re-appointed. The Executive Council shall appoint, on recommendation of the Editorial Board, the

three Editors, for terms of three years each; all three Editors may succeed themselves once.

The Associate Editors and other members of the editorial committee of the *Journal* shall be appointed by the *Journal* Editor; their terms shall terminate with his term, but his successor may reappoint any of them.

Editorial committees or staff members of the *News* and the *Memoirs* shall be appointed by the respective Editors, but their terms shall terminate with those of their Editors; they may be reappointed.

#### Article X. AUDITING COMMITTEE

*Section 1.* The President shall appoint an Auditing Committee consisting of three members who shall audit the accounts of the Treasurer and render their report to the Secretary before December 31st.

#### Article XI. LIBRARIAN

*Section 1.* The Librarian shall be appointed by the Executive Council. The Librarian shall serve for the term of three years, or until his successor shall have been appointed.

*Section 2.* The Librarian shall have charge of the library of the Society, and of all books, periodicals, reprints, and historical material received by the Society. He may make all necessary rules and regulations for the use of the library, not otherwise provided for in the Constitution or the By-Laws.

#### Article XII. AMENDMENTS

*Section 1.* This Constitution may be altered, amended, or repealed by a two-thirds vote of the members voting by mail ballot. Each proposal for amendment must be signed by not less than five members of the Society and submitted to the Secretary who will promptly transmit it to the Editors of the *Journal* and *News*. Each proposed amendment shall be published in one of the Society's periodicals at least three months before the annual ballot is mailed in November.

*Section 2.* The By-Laws may be altered, amended, or repealed, by a majority vote of the members voting, at any meeting of the Executive Council or in a mail-canvass of the Council by the Secretary. All changes so validated shall be published in one of the Society's periodicals.

### BY-LAWS

#### Article I. DUES

*Section 1.* Beginning with 1961, the annual dues for active members shall be Six Dollars, U.S.A. (\$6.00). Active membership shall include a subscription to the *Journal of the Lepidopterists' Society* and the *News of the Lepidopterists' Society*.

*Section 2.* The annual dues for sustaining members shall be Fifteen Dollars, U.S.A. (\$15.00). Sustaining membership shall include a subscription to the *Journal of the Lepidopterists' Society* and the *News of the Lepidopterists' Society*.

*Section 3.* Life members shall pay the sum of One Hundred and Twenty-Five Dollars, U.S.A. (\$125.00). Each life member shall receive a subscription to the regular society publications during his life.

*Section 4.* Honorary members shall pay no annual dues, but shall receive a subscription to all publications of the Society.

*Section 5.* All dues shall be payable on January 1 of each year, and shall be deemed in arrears on March 1 of that year.

*Section 6.* Publications of the Society shall not be mailed to any member whose dues are in arrears.

*Section 7.* After 1955 the annual dues shall be waived for the Secretary, the Treasurer, and the Editor of the *Journal*, while they are in office; they shall continue to receive all publications of the Society.

#### Article II. MEETINGS

*Section 1.* Notice of all meetings of the Society shall be printed in the *News of the Lepidopterists' Society* at least two months in advance thereof.

*Section 2.* A majority of members present at an annual meeting, or represented by proxy, shall constitute a quorum for the transaction of business, not otherwise provided for.