Smallness and Bigness: Relation of Underlying Cell Size and Number to Lepidopteran Body Size

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SMALLNESS AND BIGNESS: RELATION OF UNDERLYING CELL SIZE AND NUMBER TO LEPIDOPTERAN BODY SIZE

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Adult body size is a key trait in Lepidoptera as in other insects because it governs or interacts with many physiological, life history, and ecological processes (Chown & Gaston 2010). Variation in adult body size, within or among species, normal or extreme, invites a fundamental developmental question, namely, how are differences in body size manifested—by different numbers of cells (**hyperplasia**), by different sized cells (**hypertrophy**), or by a combination of these? Counting and measuring all adult body cells is difficult if not impossible. An alternative is to compare samples of representative body cells among different sized individuals. Such cells in Lepidoptera include wing scale follicles, facets of the compound eye, fat body, epidermis, and doubtless other as yet unexplored tissues. Although hyperplasia and hypertrophy usually have been studied independently of one another, and not necessarily in the context of body size, previous work on each is informative. Some of the available data are intraspecific, each data point referring to one individual in a one-species dataset; most, however, are interspecific, each point referring to one individual in a multi-species dataset. Previously reported investigations mostly used wing length or span as a body-size surrogate, and surrogates and body size are used interchangeably in what follows.

Hyperplasia. Density of wing scales or their follicles reflects number of cells in wing surfaces. Köhler (1940) examined intraspecific scale-follicle density in a precisely defined forewing area of different sized adults of a strain of *Ephestia kuehniella* Zeller (Pyralidae). The differing body sizes were laboratory-induced by varying larval food availability. Using forewing length as a surrogate for body size, Köhler reported a statistically significant positive relation between follicle density and forewing length. In a sample of 1,700 individuals of many species, genera, and families, Schilder (1950) examined scale density as number of scale rows in a defined forewing area. He found scale density and forewing length positively related in this unusually large interspecific sample.

In passing, egg number—fecundity—is also positively related to female body size, most notably in capital breeding Lepidoptera (Miller 2005). Reproductive cells may or may not be equivalent to body cells in the sense of the present discussion, but in any case fecundity illustrates an important life history effect of body size.

Facets of the compound eye represent cells nearer the body core than those of the outlying wings. Facets typically appear as hexagonal imprints in the hard surface of the eye (Yagi & Koyama 1963). In data of Yagi and Koyama analyzed and discussed further on here, facet numbers proved highly positively associated with forewing span interspecifically across 10 families.

Hypertrophy. Köhler (1940) examined cell size as well as cell number in his strain of *E. kuehniella* and found it likewise positively related to forewing length. Goldschmidt (1932) similarly found scale size positively associated with forewing length within as well as among populations of *Lymantria dispar* (L.) (Erebidae: Lymantriinae) that differed naturally in body size. Finck (1938) reported a similar finding among several different strains of *Ephestia kuehniella*. Interestingly, in parallel with fecundity, Goldschmidt, using a novel measuring method, reported that size of *Lymantria dispar* spermatocytes was positively correlated with male body size. In a 150-species sample, Yagi and Koyama (1963) showed that facet diameter was positively correlated with forewing span. Remarkably, Simonsen and Kristensen (2003) found scale size to be positively correlated with forewing length inter-specifically in small- to large-bodied species across more than 20 families.

Wyatt and Linzen (1965) measured cell size of fat body and abdominal epidermis in different sized pupae of *Hyalophora cecropia* (L.) (Saturniidae). The use of pupae afforded a glimpse of cellular body-size development. Size of fat-body cells was positively associated with body size, but size of epidermal cells proved independent of body size. The authors concluded that such results were consistent with an existing hypothesis that cells destined mainly to fuel growth and development—a likely role of fat body—are correlated with body size, implying hypertrophy, whereas cells destined to persist to adult eclosion, such as epidermal cells, tend to be fixed in number, implying hyperplasia. A further generalization holds that number of body cells is fixed until their size reaches a certain limit, at which point their number increases (Yagi & Koyama 1963, Wyatt & Linzen 1965). This generalization is plausible in that cell size does not increase indefinitely, but the idea needs further research.

Two original analyses are presented in this report. The first uses scattered data gleaned from Yagi and Koyama (1963) concerning facet numbers and forewing spans (Appendix). The second uses original measurements of facet size relative to fresh female mass in *Malacosoma disstria* (Hbn.) (Lasiocampidae).

Methods and Results. The analysis of Yagi and Koyama data here uses the wingspan surrogate. Mass, or weight, is a more direct and accurate measure of body size (Miller 1977 and references in Yagi & Koyama 1963), and its use for that purpose here in *Malacosoma disstria* is a rare departure.

In both analyses, straight lines through data points were fitted to minimize the sum of squares of the vertical differences between the lines and data points, as in typical regressions, but no regressions are implied here. The lines merely describe association. In this report the main interest is whether two variables are associated, as when both co-vary in response to other factors. Olmstead and Tukey's corner test (Sokal & Rohlf 1995), a simple correlation-like graphical method, was used to evaluate association. It does not measure magnitude of association, only probability of association. The method produces an algebraic sum, S, which is compared with tabulated values to ascertain statistical significance.

Before analysis, the Yagi and Koyama data were transformed to natural logarithms (ln) to tighten point scatter. The resulting least squares line is positive and described as (ln No. facets) = 3.64 + 1.236 × (ln wing span (mm) (15 n)) (graph not shown). The resulting S-value, 13, indicates the association is significant at the 0.02 level, and that it is unlikely due to sampling error. Thus facet numbers and body size in this sample are associated inter-specifically across 10 families. Interspecific associations in particular show that cell and body-size variables are generally similar for lepidopterans irrespective of taxa or body size.

In the original examination of facet diameter relative to female adult body mass in *Malacosoma disstria*, study insects were collected as pupae in Ontario. Upon eclosion, females were freeze-killed and weighed. The length of a row of 10 contiguous facets near the center of the eye of each female was measured and divided by 10 for an estimate of single-facet diameter. With an S-value of 13, coincidentally the same as in the preceding analysis, and significant at 0.02, facet diameter and body mass are clearly and positively associated (Fig. 1). This intraspecific outcome is hardly surprising.

In contrast to linear associations in both of the foregoing analyses, curvilinear relations were the rule in published sources cited earlier, as would be expected for allometry, and mixed relations of volumetric and one- or two-dimensional body-size variables like wing length. In any case, such curvilinearity has little importance here where the main interest is association.

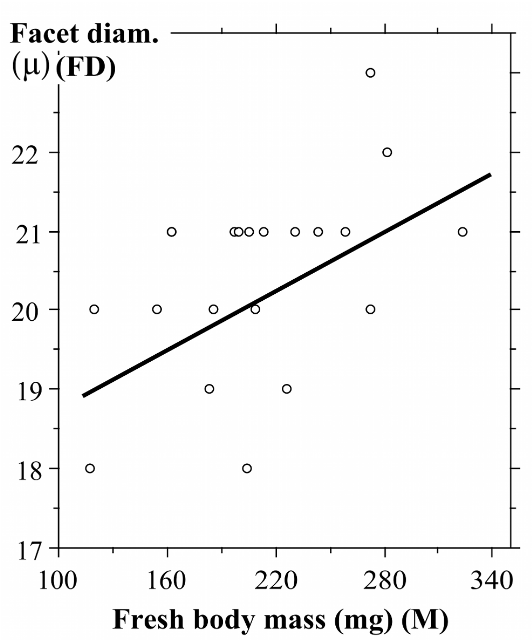

FIG. 1. Eye facet diameter (FD) as related to fresh body mass (M) in female *Malacosoma disstria* (FD = 18.07 + 0.0112 M, 21 n, S-value = 13, association of FD and M significant at 0.02 level).

Finally, all data sources were surveyed to count the number of species in which both hyperplasia and hypertrophy have been documented. Only three were found, but this paucity detracts little from implications of so much other evidence.

In conclusion, the cellular structure of all lepidopteran body sizes appears to consist of both hyperplasia and hypertrophy. Greater understanding of lepidopteran body-size differences will be advanced if future research examines additional body tissues, considers interrelations of cell size and number during ontogeny, and employs strong inference.

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Appendix. Species from Yagi and Koyama (1963) with sufficient data for analysis here. Ten families are represented.

P. xuthus	*A. preyeri*	*P. glacialis*
C. e. poliographus	*H. convolvuli*	*O. cerodelta*
P. rapae	*D. japonica*	*S. sp.*
L. p. daimio	*B. mori*	*L. ringoliella*
T. hamada	*T. a. kaguya*	*P. semifasciella*