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The evolution of metamorphosis

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Summary

Linear growth in *Pararge aegeria* (LINNAEUS, 1758), suggests an archetypal dynamic able to encompass hemi- and holometabolous metamorphosis within a unifying conceptual scheme.

a) THE LINEAR GROWTH DYNAMIC

Linear dimension was plotted against time at each stage in the life cycle of the butterfly *Pararge aegeria* (LINNAEUS, 1758). The study sample was as described and reared by WINOKUR (1988) ; sixty successfully pupating individuals were analysed.

Overall growth described a sigmoid curve with a pre-pupational deviation (PPD) towards maximum length ; the larva then contracts to form the prepupa when growth returns to sigmoid (Fig. 1a-d). The size and form of the curve were similar for 4-instar and 5-instar larvae and both sexes, although there is no one-to-one mapping between 'corresponding' moults. The form of the curve will be termed the LINEAR GROWTH DYNAMIC (LGD) : it appears to be very constant and may be species specific.

The following model is proposed. Moults are superimposed on the LGD. The nature of a moult depends only on its position within the LGD. Changes and differences in the number of moults do not involve the loss or gain of any particular moult : rather they shift in relation to one another. The constancy of the LGD however precludes rearrangement of the sequence in which the different kinds of moult occur.

Hypothetical manipulations of moult positions along the LGD were performed (Fig. 2a-j). Additional or deleted moults are possible (b-c). A metamorphic moult may be missed (NIJHOUT & WHEELER, 1982) but its hemi-/holometabolous nature remains unaltered ; similarly for transformations along the LGD not breaching the PPD (d-e). Transformations breaching the PPD into

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pupation introduce additional putative moult(s) between pupation and eclosion but whose occurrence is precluded by the continuum of adult development within the pupa (f). Transformations breaching the PPD towards the initiation of embryogenesis (t_0) pull the LGD in this direction. The PPD becomes truncated and eventually disappears (g-j). Indeed, the pupal moult apart, hemi- and holometabolous alternatives share virtually identical processes :

- (1) The corpora allata cease production of juvenile hormone (JH) in the final instar (NIJHOUT, 1975).
- (2) Larvae have three metamorphic options dependent on JH concentration (NIJHOUT & WHEELER, 1982).
- (3) Cuticular stretching promotes moulting (NIJHOUT, 1979).
- (4) Final instar larvae have fat reserves for adult development (NIJHOUT, 1979).

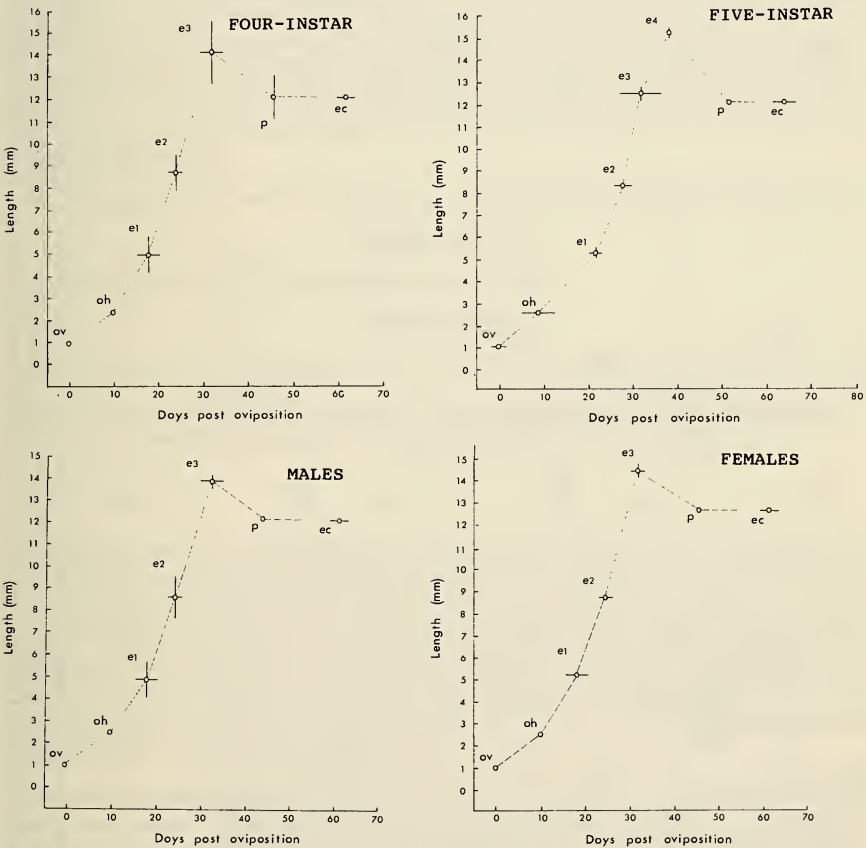


Fig. 1. Growth plots of (a) four-instar individuals, (b) five-instar individuals, (c) males, and (d) females. Vertical and horizontal bars give \pm SD for each correlate. Life cycle stages : ov = oviposition, oh = hatching, e1 to e4 = 1st to 4th ecdyses, p = pupation, ec = eclosion.

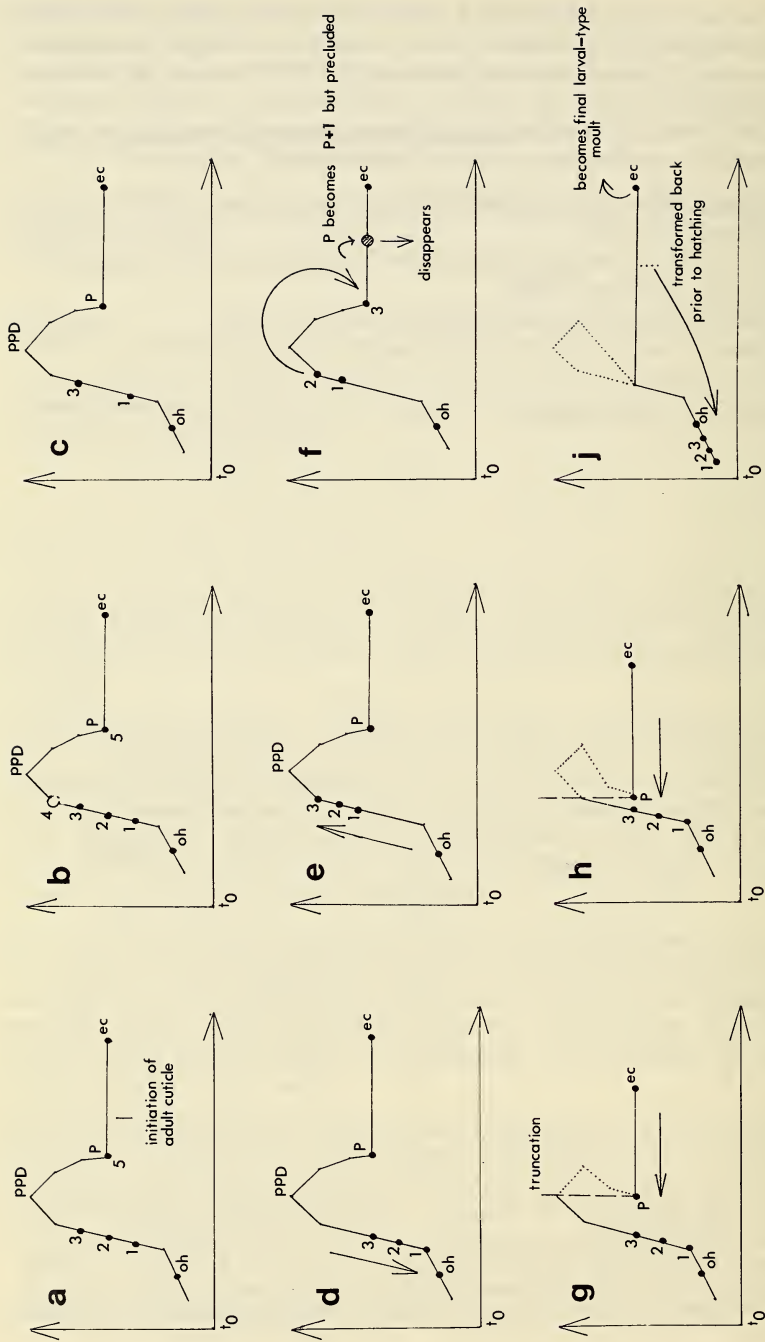


Fig. 2. Transformation along the Linear Growth Dynamic. (a) Salient features of the dynamic. Moults numeration shown only to denote temporal ordering and aid interpretation; oh = hatching, p = pupation, ec = eclosion, open circles give additional moults. Prepropupal deviation (PPD) depicted: dotted line gives putative location. Further explanation see text.

If all moults are transformed towards t_0 , the initiation of the development of adult integument within the pupa can be traced back prior to hatching from the ovum so regenerating the hemimetabolous condition (j) : hemimetabolous insect nymphs hatch with sclerotised cuticle already formed (NIJHOUT & WHEELER, 1982). This suggests that the holometabolous larval stage arose through an extension, to the pupal stage, of early within-egg nymph development. Indeed in both hemi- and holometabolous insects,

(5) Wings appear only at the imaginal moult (NIJHOUT & WHEELER, 1982).

b) COMPLEXITY

SAUNDERS & HO (1976) define complexity in terms of the number of kinds of component rather than their individual number, and the less the degree of change in complexity involved, the greater the likelihood of the change occurring (SAUNDERS & HO, 1981). Changes in life cycle duration or in mature size involve the LGD itself which comprises linear and temporal dimensions (Fig. 3a-d). Shifts in moults along it involve just one dimension. Hence the hemi-/holometabolous dichotomy would be expected to be prior to distinctions within these groups.

The two strategies can be reduced to the following minimum algorithms :

Hemimetabolous

DIFFERENTIATION (1 + 2) GROWTH WINGS (1 + 2)

Holometabolous

DIFFERENTIATION (1) GROWTH (1) DIFFERENTIATION (2) GROWTH (2) WINGS

Since both involve similar overall complexity changes, transformations between them could be expected to have been easily accomplished.

c) PUPATION

It is proposed that in the final larval instar the elastic limit of integument mechanically precludes food uptake : it may be this imposed nutritional stress which forces the breakdown of all but the vital organs for metabolic energy. This breakdown increases the Gibbs free energy (G) so destabilising development, when (G) gets dissipated through an increase in complexity (cf. SAUNDERS & HO, 1976) — here the development of adult structures. The developmental instability might also explain why young pupae are especially susceptible to 'shock' (WINOKUR, 1989).

Lepidopteran larvae produce two pulses of ecdysone and prothoracicotrophic hormone before pupation (NIJHOUT, 1974). Yet the second is not even a physiological necessity albeit eight times the titre of the first (NIJHOUT, 1976) ; this redundancy and apparent excess might now be understood as the superposition of the PPD upon an already established (hence more primitive) hemimetabolous pattern of hormone secretion.

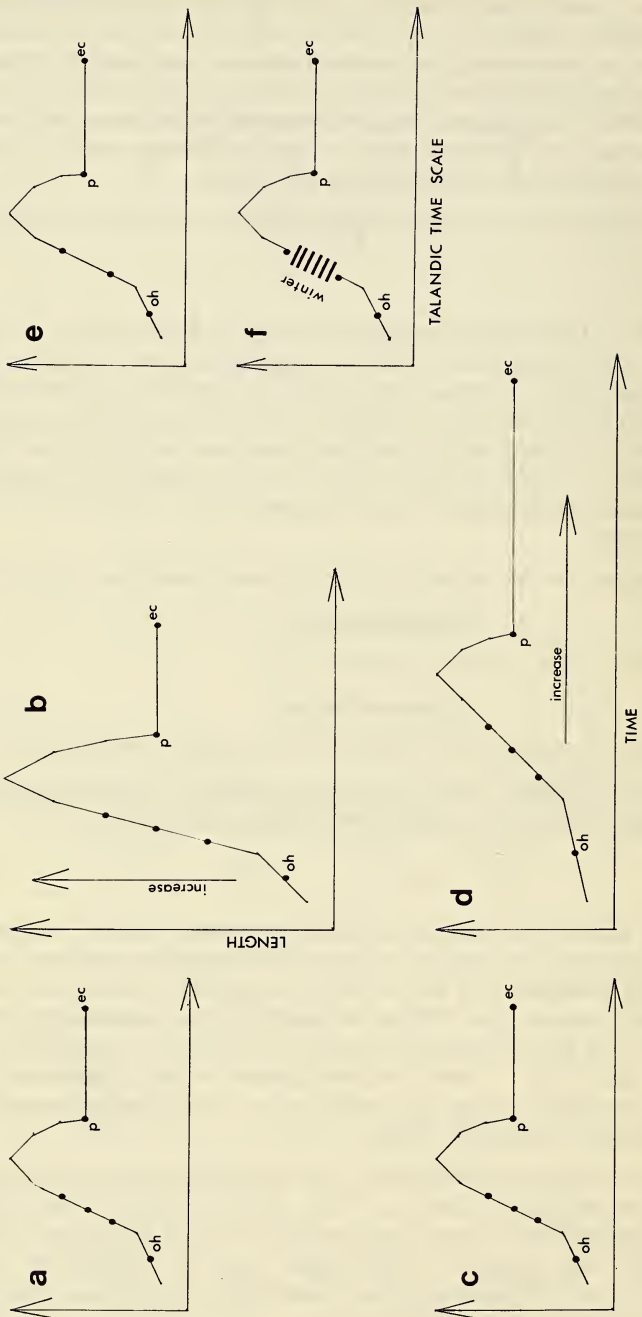


Fig. 3. Changes in size and form of the Linear Growth Dynamic: (a) and (b), increase in adult size; (c) and (d) prolongation of life cycle; (e) and (f) prolongation of life cycle with respect to seasonal but not talandic time-base, as in diapause. Moults: oh = hatching, p = pupation, ec = eclosion. Further explanation see text.

d) CONTINUITY AND PUNCTUATION

Lepidopteran pupal integument hardens into sclerotised cuticle shortly post-pupation. In certain species, local sclerotisation occurs in the larva following injury (NIJHOUT, 1976) while in others bits of ligated pupa that are still larval integument become pupal when the rest of the insect develops into the adult (NIJHOUT & WHEELER, 1982). It is postulated that pupal cuticle formation arose from a unit copying response to local integumental tearing, whose efficacy would be delimited by cuticular composition and hence certain structural genes : these would be available a priori as a heritage from their evolutionary history as a pre-hatch nymph. Hence pupation could have arisen without recourse to any de novo mutation.

The deployment of moults along the LGD need not respect the distinct metamorphic stadia : larval-pupal intermediates do occur. But as such intermediates fail to develop further, there is discontinuity in the kinds that can contribute to a viable life cycle. The phenomenon also shows how a continuum of change in the underlying metamorphic parameter (the LGD) leads to punctuated changes in outward form.

That in hemimetabolous life cycles the final moult breaches the PPD ought imply they are shorter than holometabolous ones ; yet both share comparable durations. This paradox is resolved by invoking developmental or 'talantic' (cf. GOODWIN, 1969) time-bases marked by stability and complexity changes (just as time in the familiar sense is marked by entropy increase) being matched to a common reference time base.

Talantic time bases also allow for the origin of diapause since the total complexity change between its bounding moults is unaltered (Fig. 3e-f).

e) IMPLICATIONS AND SIMPLIFICATIONS

P. aegeria larval duration correlated more strongly with oval and first instar duration combined than with either alone (WINOKUR, 1989). Consideration of this region of the LGD reveals hatching to mark simply a change in nutritional status : the differentiation of essential physiological systems starts at fertilisation with growth continuing through to the adult. Pupation recreates an effectively oval environment for the outstanding differentiation of adult structures : eclosion marks simply a change in nutritional status. The functional homologies are shown in Fig. 4.

One larva was accidentally 'clipped' in its second instar and the integument healed with two supernumerary projections to the long dorsal stripe : these were still present in the final instar (Fig. 5). Larval segmentation abnormalities in other species are known to have persisted to the adult (OLIVER, 1979 ; AINDOW, 1988). Thus integumental (pattern) parameters also appear to be conserved throughout.

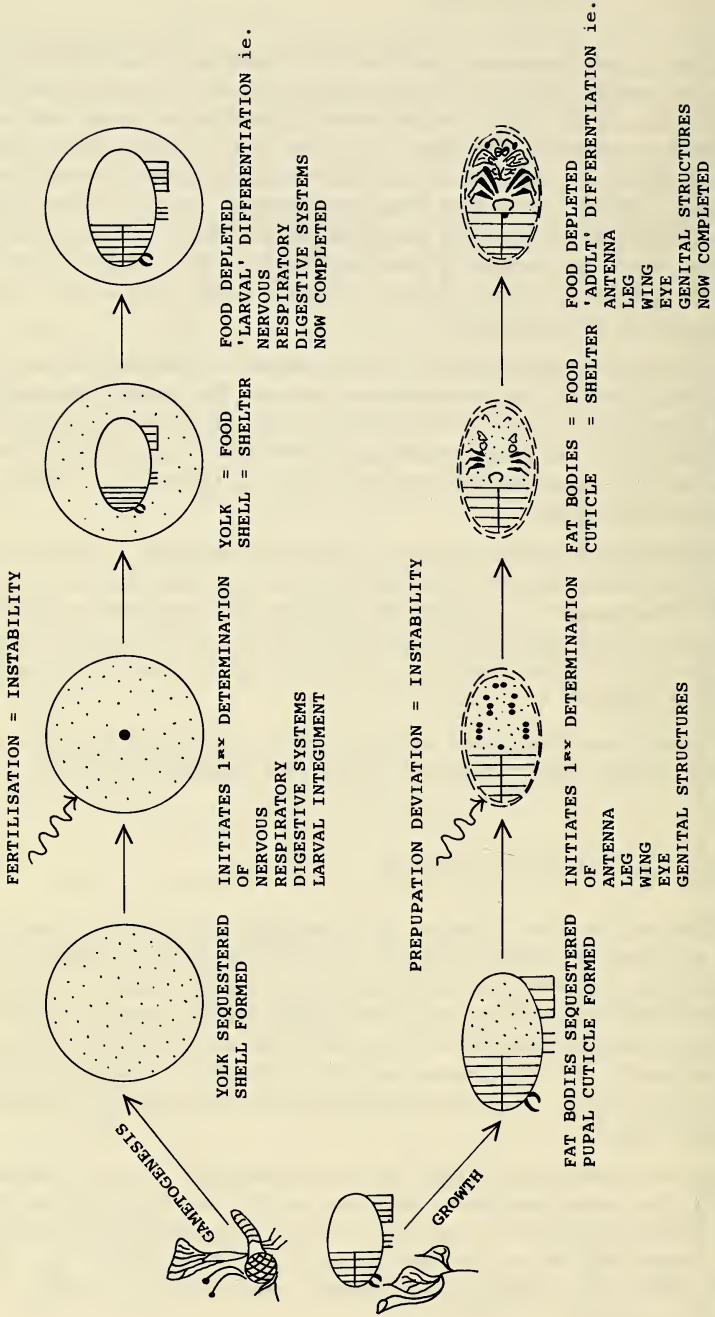


Fig. 4. Structural and functional homologies among the metamorphic stages. Development from gametogenesis to hatching parallels development from post-hatch larva to eclosion



Fig. 5. Larva showing post-traumatic extensions to longitudinal stripe.

Thus holometabolous development, though often dubbed 'miraculous', is in reality a continuum of differentiation whose only 'drastic' changes are in the visibly outward manifestation of its simple underlying process.

f) THE LGD AS AN ARCHETYPE

We have seen that the hemi-/holometabolous dichotomy might be better understood as having arisen through transformations to the LGD as an integrated system rather than through the piecemeal loss or gain of particular processes. In this sense it exemplifies an archetype or type of which the two strategies can be regarded alternative forms (cf. WEBSTER, 1984). The type involves the temporal dimension and so occupies the diachronic realm (WADDINGTON, 1962). It is suggested that each of the moults be regarded as elements of which there are four main kinds: oval hatching; ecdysal; pupational; and eclosal. Thus understood, the evolution of metamorphic strategies exemplifies the principles of Structuralism (PIAGET, 1970): elements function in relation to one another, each element is constrained by its position within the whole though they do have some degree of autonomy, and the system displays powers of self-correction.

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