

Allomorphosis of the Wing-Veins vs. Wing-Membranes in Insects

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Introduction

Since the concept of allometry (Huxley and Teissier, 1936), which is, according to Huxley, Needham and Lerner (1941), a covering term of heterauxesis (Needham and Lerner, 1940) and allomorphosis (Huxley, Needham and Lerner, 1941), was established by Huxley and others for the phenomena of either the relative growth or the relative proportion of the certain two organs or parts of organs, it has become frequently applied to various kinds of organisms for the sequence of ontogeny, phylogeny and systematics in terms of heterauxesis, lineage allomorphosis and species-form (or genera-form etc.) allomorphosis (Westol, 1950) respectively. To avoid confusion between negative allometry (Huxley and Teissier, 1936) and negative growth (=enantiometry, Huxley and Teissier, 1936), the term bradymetry is proposed here in place of negative allometry. Likewise, the term tachymetry is chosen for positive allometry. These new terminology may, moreover, be advantageous in coordinating to the terms bradyauxesis and tachyauxesis (Needham and Lerner, 1940). Further, if it is needed to distinguish the relative growth and relative proportion, the terms bradymorphosis tachymorphosis and also isomorphosis and enantiomorphosis may be adequately applied for the latter phenomenon. Thus the terminology can be arranged as follows.

Allometry (tachymetry, isometry, bradymetry, enantiometry)

{ Heterauxesis (tachyauxesis, isauxesis, bradyauxesis, enantiauxesis)
Allomorphosis (tachymorphosis, isomorphosis, bradymorphosis,
enantiomorphosis)

The so-called rule (or phenomenon) of Lameere and Geoffrey Smith, laid down by Huxley (1927) to refer to, according to him and to de Beer (1940), that if a number of related species have the same organs allomorphic among different individuals (individual allomorphosis, Simpson, 1953) the similar pattern of allomorphosis is apt to be found among these related species at a definite developing stage, may be especially suggestive in showing interrelations between the different systematic categories higher and lower than the species level. Partially based on this rule, indeed, Mayr (1942) intended to interpret the factors of

macroevolution of the higher categories by the experimentally analysable factors of microevolution within a species.

The wing of insects which is one of the best systematic characters having been adopted since as early as Aristotle's day is composed of two elements of different origin, the veins and the membranes. They have at various occasions been ascertained to develop independently (Oka and Furukawa, 1935) and are consequently the allometrically analysable organs not contradict to the logic of Reeve and Murray (1942) referring to that one of a paired allometrical traits should not be a part of another. In relation to the independent development or relative proportion of the veins and the membranes among various species of the genus *Drosophila*, Sturtevant (1942) found that if the second longitudinal veins end nearer the wing-tip (higher *C*-index*) the posterior crossveins are also likely to be distally placed (lower *4v*-index**), Burla (1956) referred, moreover, to a positive correlation between the *C*-index and the wing-length and a negative one between the *4v*-index and the wing-length. The former relation was called Sturtevant's rule and the latter Burla's rule by the author (1959), who statistically proved these rules to be acceptable by not only the infraspecific but also the supra-specific hierarchies in the genus *Drosophila*.

The present study is at first intended to analyse the Burla's rule, which eventually includes the Sturtevant's rule, with the concept of allomorphosis, and further to find general patterns of the allomorphosis, including the phenomenon of Lameere-Smith, between the wing-veins and wing-membranes with special regards to the systematics using materials of various insects belonging to the family Drosophilidae, order Odonata, superfamilies Hesperioidea and Papilionoidea of Rhopalocera, and the family Cicadidae.

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Material and Methods

The materials used in the present study consist of 50 species of the

* The length of the 2nd costal section divided by the length of the 3rd costal section.

** The length of the distal section of *M* divided by the length of the middle section of *M* between the anterior and posterior crossveins.

family Drosophilidae, 150 species of the division Rhopalocera, 27 species of the order Odonata and 8 species of the family Cicadidae. These are mostly Japanese species, though some of the Rhopalocera are Formosan or New-Guinean.

To determine the allomorphic patterns between the length of a wing-vein (A) and the length of the fore wing (L), the variants are plotted on the double logarithmic grid taking the former on the ordinate and the latter on the abscissa, where the value A is measured from the wing-base to the nodus in Odonata, to the end of R -cell in Cicadidae, and to the point of insertion of R_5 to the discoidal cell in Rhopalocera. A ratio A/B , in which B is taken as the length from the end of the section A to the tip of the wing, is determined as the C -index. In Drosophilidae, however, the values A and B are measured as the lengths of the 2nd and 3rd costal sections respectively.

Results of Observation

Regarding the species-form allomorphosis between the wing-veins (A) and wing-membrane (L), the genus *Drosophila* is found to compose a diphasic allomorphic tribe, having a critical point (Fig. 1). The subgenera *Sophophora* and *Paradrosophila* and *D. (D.) subtilis* are the components below this critical point and are showing the phylogenetic constant (α_1^*) 1.59, while the subgenus *Drosophila* exclusive of *subtilis* comes above the critical point and shows the α_1 0.98. The subgenera *Hirtodrosophila* and *Dorsilopha* are located close to the critical point. The similar diphasic pattern is obtained in a number of different genera of the Drosophilidae, i.e., *Mycodrosophila* and *Dettopsomyia* which compose a group below the critical point and *Leucophenga* and *Microdrosophila* which compose another group above it, showing α_1 1.52 and 1.16 respectively (Fig. 2). It is found in these allomorphic tribes that the C -index is positively correlated with L and negatively correlated with α_1 (Figs. 3-6). In the genus *Drosophila*, moreover, the constant of the individual allomorphosis or the ontogenetic constant (α_2^*) determined with 10 males per each species is found to be positively correlated with α_1 (Figs. 3, 6).

As for the Rhopalocera, each family is proved to constitute a simple or monophasic allomorphic tribe of its own, showing the specific value of α_1 which is smallest in Papilionidae (0.84), largest in Hesperidae (1.22), intermediate in Lycaenidae (0.92), Nymphalidae (0.94), Danaidae (1.03), Satyridae (1.00) and Pieridae (1.12) (Figs. 7-13). *Leptidea amurensis* which represents the subfamily Dismorphiinae of the family Pieridae is, however, strikingly deviated in its position on the graph from the main

* To distinguish the phylogenetic constant from the ontogenetic constant, the sign α_1 is given to the former and α_2 to the latter.

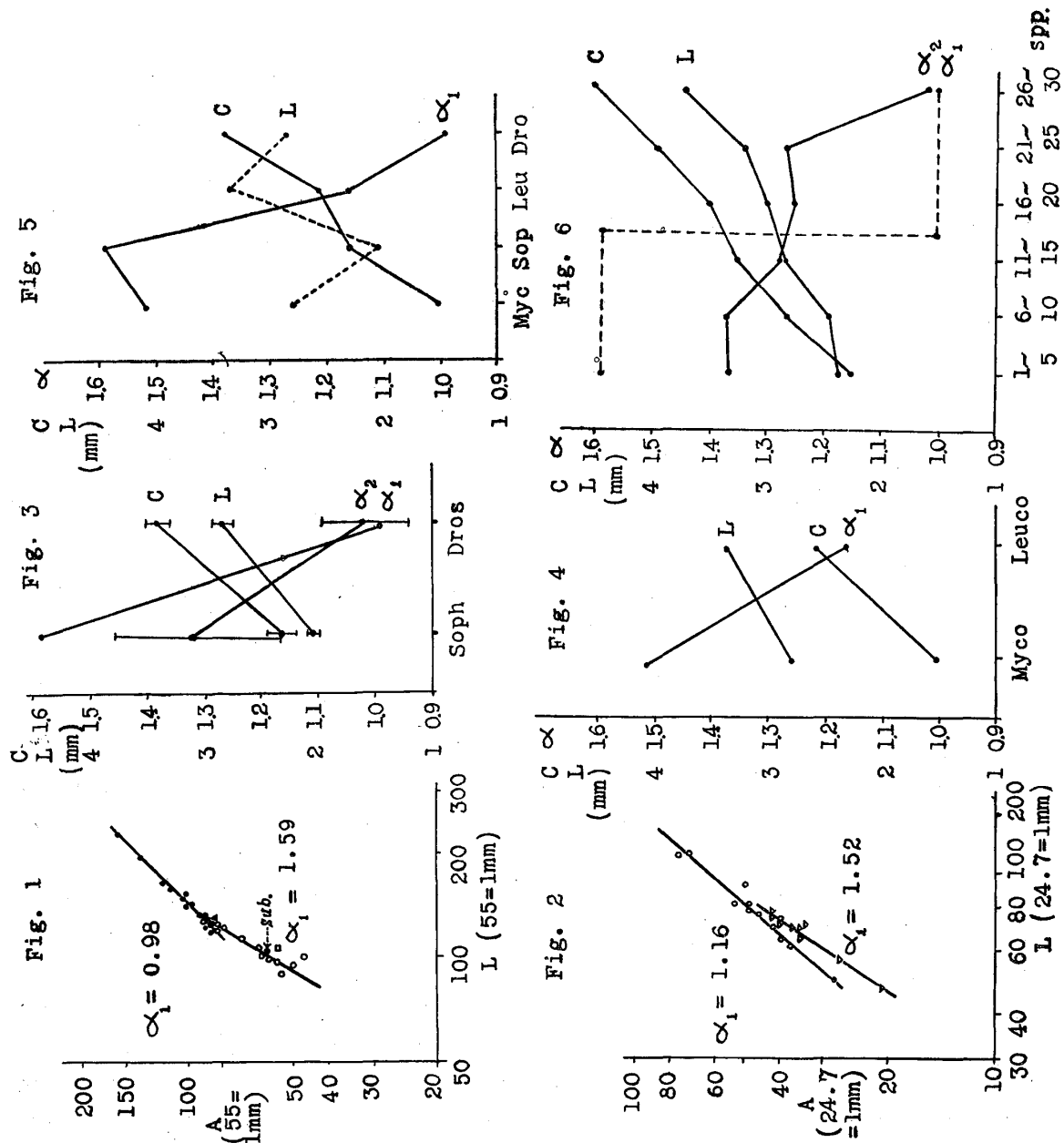


Fig. 1. The species-form allomorphosis of the wing-veins (A) and the wing-length (L) in the genus *Drosophila*. The co-ordinates are taken as the means of 10 males for each species of the subgenera *Sophophora* (○), *Paradrosophila* (□), *Hirtodrosophila* (▲), *Dorsilopha* (■) and *Drosophila* (●); *sub. subtilis*. **Fig. 2.** Ibid., in the family Drosophilidae. The co-ordinates represent a male of each species of the genera *Dettopsomyia* (▼), *Mycodrosophila* (▽), *Microdrosophila* (●) and *Leucophenga* (○). **Fig. 3.** Interrelations of the phylogenetic constant (α_1), ontogenetic constant (α_2), C-index (C) and the wing-length (L) as compared between the subgenera *Sophophora* (Soph) and *Drosophila* (Dros) of the genus *Drosophila*. **Fig. 4.** Ibid., between the genera *Mycodrosophila* (Myco) and *Leucophenga* (Leuco). **Fig. 5.** Ibid., of *Mycodrosophila* (Myc), *Sophophora* (Sop), *Leucophenga* (Leu) and *Drosophila* s. str. (Dro). **Fig. 6.** Interrelations of the phylogenetic constant (α_1), ontogenetic constant (α_2), C-index (C) and the wing-length (L) within the genus *Drosophila*. The co-ordinates show the means of every 5 species which are grouped according to the values of C-index. 10 males are calculated for each species.

tribe composed of the subfamily Pierinae (Fig. 9). The Nymphalidae does not show a clearcut tribe except the members of the genera *Argynnis*, *Melitaea*, *Calinaga* and *Pareva* which show a rather distinct tribe separable from the other members of the family (Fig. 13). If the allomorphic tribes of these families are put together, it will be proved that the Rhopalocera is divisible into two major tribes which represent two superfamilies, Hesperioidea and Papilionoidea respectively, the latter major tribe being triphasic as a whole with the lower critical point between Lycaenidae and Satyridae and the upper between Danaidae and Papilionidae (Fig. 14). Riodinidae and Libytheidae are located nearly at the lower critical point, and Nymphalidae is exceptionally much deviated from the major tribe of Papilionoidea and is occupying a special position shared in common by Amathusiidae (Fig. 14). The triphasic major tribe of Papilionoidea is bradymetric ($0 < \alpha_1 < 1.0$) below the lower critical point as well as above the upper critical point and tachymetric ($\alpha_1 > 1.0$) between the two. In this major tribe, moreover, the families except Nymphalidae show a positive correlation between C-index and L (Fig. 15). Concerning the relation between α_1 and L , it will be said that they are positively correlated when C-index is less than or subequal to 1.0 and negatively correlated in turn when C-index is more than 1.0 (Fig. 15).

If the mean values of C-index and L of every 5 species showing successive values of L of each family of Rhopalocera are plotted on a graph taking L on the abscissa and C-index on the ordinate, it will be resulted that these two traits are positively correlated in those families having α_1 more than 1.0 (Hesperiidae, Danaidae, Pieridae) and negatively correlated in those having α_1 less than or equal to 1.0 (Papilionidae, Satyridae, Lycaenidae, and also Nymphalidae exclusive of the *Argynnis*-tribe—*Argynnis*, *Melitaea*, *Calinaga*, *Pareva*) (Fig. 16).

In the Odonata, the values of α_1 are 0.89 and 1.27 in the superfamilies Aeschnoidea and Libelluloidea of the Suborder Anisoptera respectively, while they are 0.79 and 1.22 in the superfamily Coenagrioidae and the two superfamilies (Coenagrioidae and Callopterygina) taken together respectively in the Suborder Zygoptera (Figs. 17–19). The α_1 of the Callopterygina could not be determined due to poor materials. If these allometric tribes are put on a graph, it will be found that they may be divisible into two diphasic major tribes, the one representing the suborder Anisoptera and being tachymetric and bradymetric below and above the critical point respectively, the other representing the suborder Zygoptera and being bradymetric and tachymetric below and above the critical point respectively (Fig. 20). The Anisozygoptera is situated nearly at the critical point of the former major tribe, in other word, between Libelluloidea and Aeschnoidea. Furthermore, these

Fig. 7

Hesperiidae

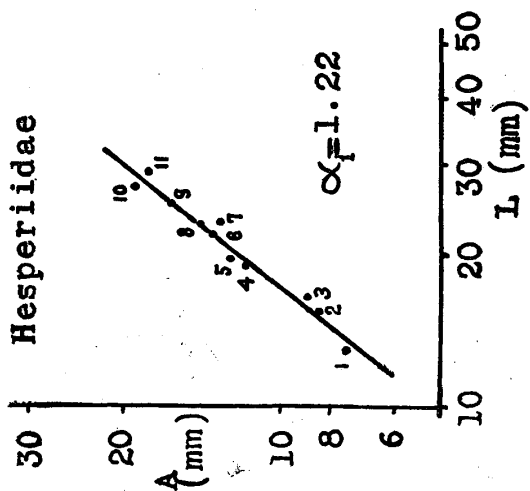


Fig. 8

Papilionidae

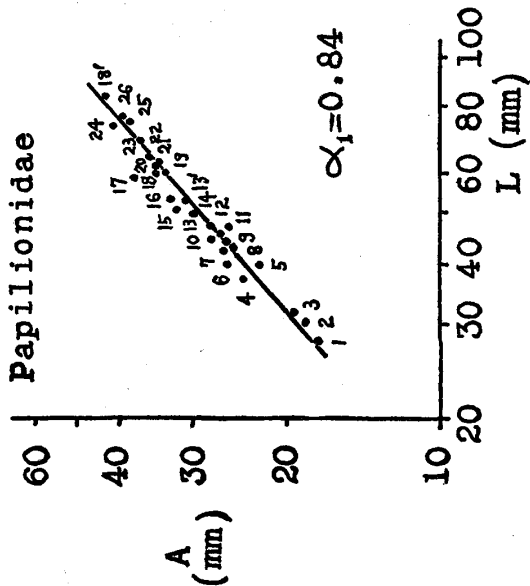


Fig. 9

Pieridae

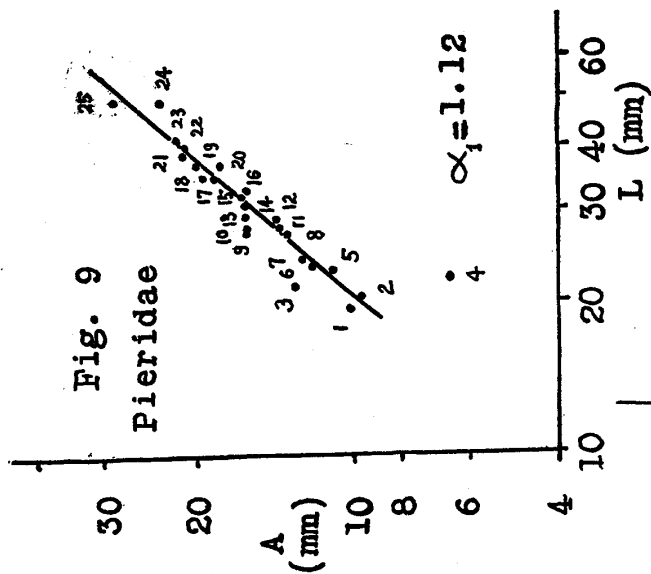


Fig. 10

Danaidae

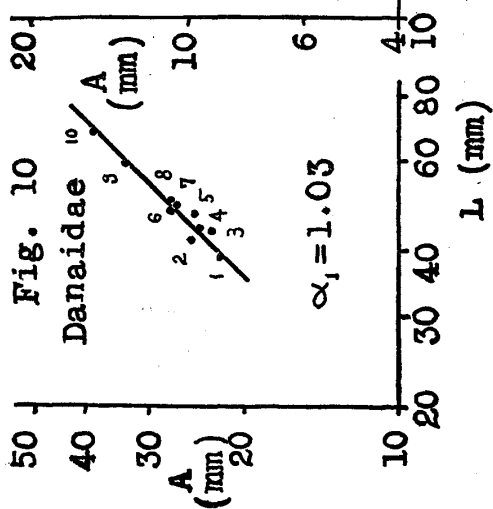


Fig. 11

Lycaenidae

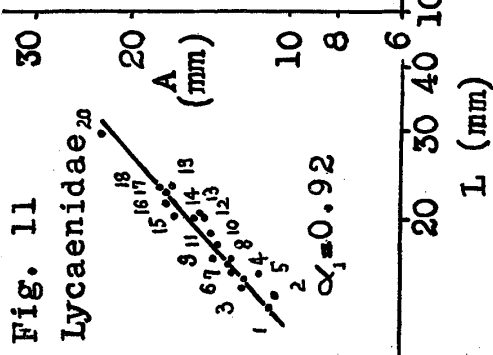


Fig. 12

Satyridae

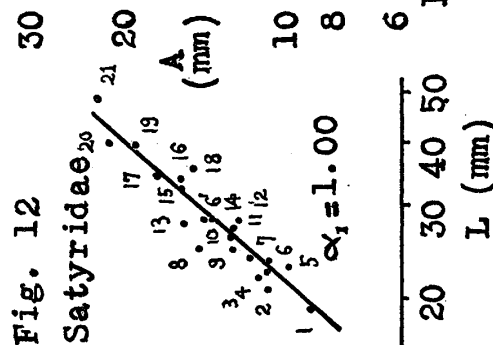
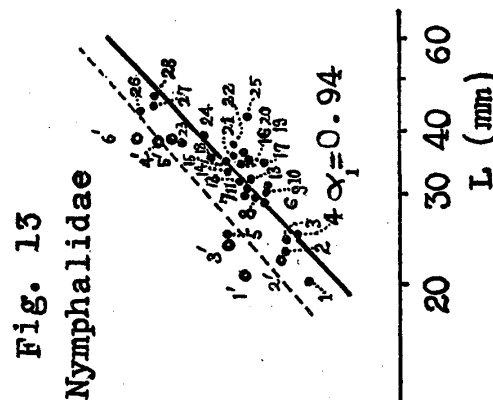


Fig. 13

Nymphalidae



two superfamilies as well as Coenagriodea and Zygoptera as a whole are so interrelated that C -index is positively correlated with L , while α_1 is positively correlated with L in those forms having C -index less than 1.0 and negatively correlated with L in those showing C -index subequal to or more than 1.0 (Fig. 21).

The phylogenetic constant of 8 species of Cicadidae is 0.89, while the ontogenetic constant of 14 specimens of *Graptopsaltria nigrofusca* shows 1.00. The similar relation between the two constants, that is, the former being smaller than the latter, is obtained in the subgenus *Drosophila* in which the α_1 is 0.98 and the α_2 at the mean of 12 species is 1.02 ± 0.031 . While the reverse relation, the α_1 being larger than α_2 , is found in some other cases, e.g., between Pieridae ($\alpha_1=1.12$) and *Pieris rapae crucivora* ($\alpha_2=0.86$ in 70 males, 0.89 in 21 females) as well as *Aporia hippia japonica* ($\alpha_2=1.06$ in 15 mostly male specimens), between Libelluloidea ($\alpha_1=1.27$) and *Sympetrum frequens* ($\alpha_2=0.26$ in 2 males and 9 females) and between the subgenus *Sophophora* ($\alpha_1=1.59$) and 12 species of this subgenus ($\alpha_2=1.31 \pm 0.066$ at mean) (Fig. 23).

Discussions

A. The characteristics of the Species-form allomorphosis

One of the specific patterns of the species-form allomorphosis of the morphological traits in question is that the constant of allomorphosis (α_1) decreases above the critical point of the diphasic tribe as in the genus *Drosophila*, the family Drosophilidae and the suborder Anisoptera (Figs. 1, 2, 20) and also above the upper critical point of the triphasic

Fig. 7. The species-form allomorphosis of the wing-veins (A) and the wing-length (L) in the family Hesperidae. The co-ordinates show the values of a specimen (usually a male) for each species designated by an ordinal number. 1. *Ochlodes*, 2. *Thoressa*, 3. *Lepetalina*, 4. *Daimio*, 5. *Erynnis*, 6. *Celaorrhinus*, 7. *Bibalis*, 8. *Seseria*, 9. *Choaspes*, 10. *Badamiä*, 11. *Satarupa*. **Fig. 8.** Ibid., in the family Papilionidae. 1, 2. *Lühdorfia*, 3. *Parnassius*, 4-6, 8. *Graphium*, 7, 9-12, 14, 16-21, 23, 24, 26, 18'. *Papilio*, 13, 13'. *Byasa*, 15. *Chilasa*, 22, 25. *Troides*. **Fig. 9.** Ibid., in the family Pieridae. 1, 2, 5-7, 12. *Eurema*, 3. *Leptosia*, 4. *Leptidea*, 8. *Colias*, 9-11, 17. *Pieris*, 13. *Cepora*, 14. *Ixias*, 15. *Gonepteryx*, 16, 20. *Catopsilia*, 18. *Appias*, 19, 22. *Aporia*, 21, 23. *Delias*, 24. *Prioneris*, 25. *Hebomoia*. **Fig. 10.** Ibid., in the family Danaidae. 1, 5, 6. *Euploea*, 2-4, 7-9. *Danaus*, 10. *Hestia*. **Fig. 11.** Ibid., in the family Lycaenidae. 1. *Plebejus*, 2. *Everes*, 3. *Heliophorus*, 4. *Lycaeides*, 5. *Celastrina*, 6. *Lycaena*, 7, 10. *Lampides*, 8, 13. *Arhopala*, 9, 11. *Rapala*, 12. *Favonius*, 14, 19. *Maculinea*, 15. *Deudorix*, 16. *Chrysozephyrus*, 17. *Artopoetes*, 18. *Curetis*, 20. *Amblypodia*. **Fig. 12.** Ibid., in the family Satyridae. 1-3, 5, 10. *Ypthima*, 4, 6, 6', 9. *Mycalesis*, 7. *Erebia*, 8. *Oeneis*, 11, 16, 18. *Lethe*, 12. *Harima*, 13. *Lopinga*, 14. *Kirinia*, 15. *Minois*, 17. *Neope*, 19. *Ninsuta*, 20. *Melanitis*, 21. *Isodema*. **Fig. 13.** Ibid., in the family Nymphalidae. 1. *Araschnia*, 2, 4, 9, 16. *Neptis*, 3. *Aglais*, 4. *Pareva*, 6. *Kaniska*, 7, 8, 14. *Tacoraëa*, 10. *Cyrestis*, 11. *Polygonia*, 12. *Vanessa*, 13. *Limenitis*, 15. *Abrota*, 17, 19, 22. *Apatura*, 19. *Dichorragia*, 20. *Sephisia*, 21. *Helcyra*, 23. *Eriboea*, 24. *Nymphalis*, 25. *Hestina*, 26. *Calinaga*, 27. *Hypolimnas*, 28. *Kallima*, 1', 2'. *Melitaea*, 3'-8'. *Argynnis*.

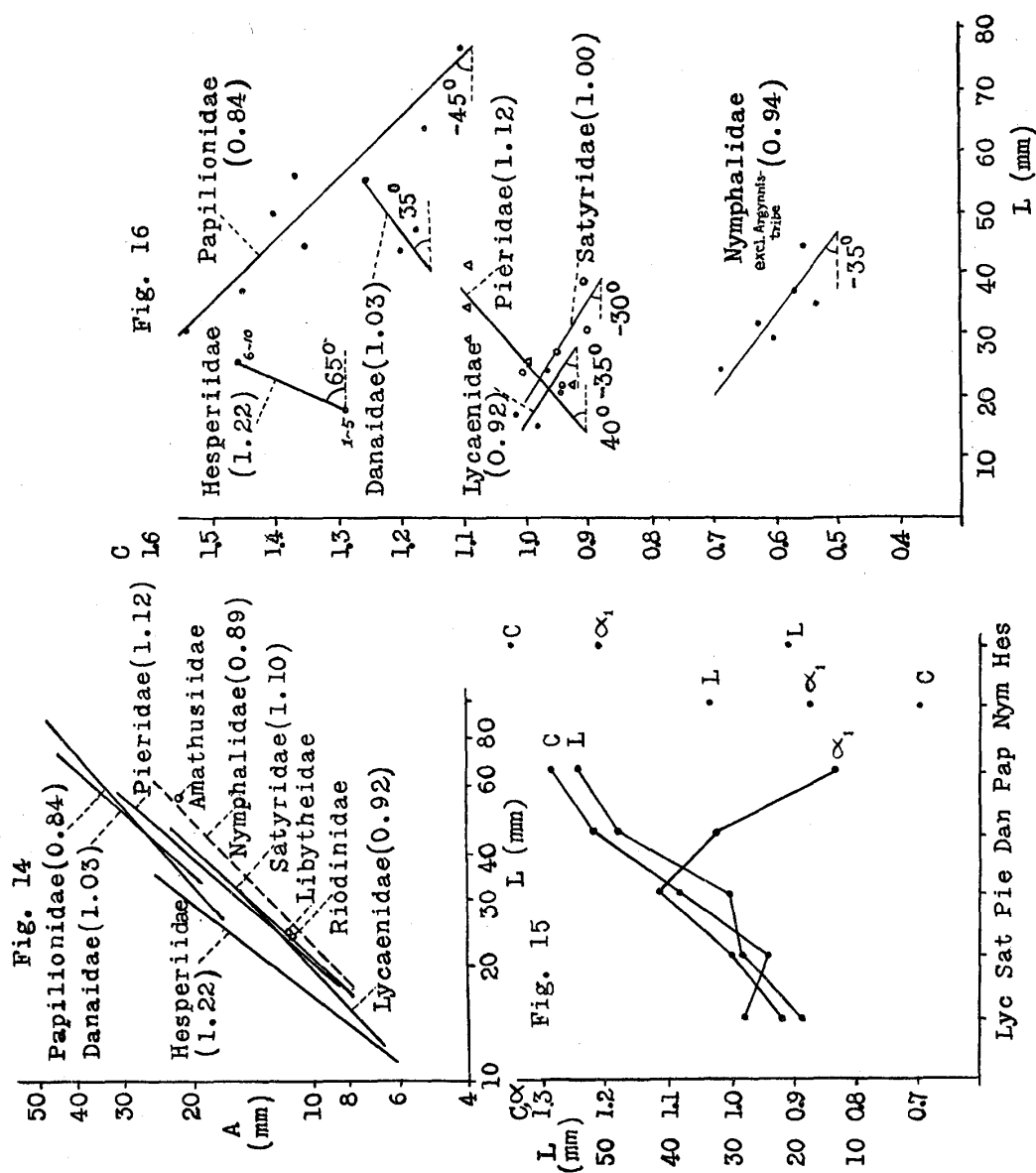


Fig. 14. Comparison of the allomorphic patterns of the families of Rhopalocera. The data given in the figures 7-13 are put together with the values of phylogenetic constant (α_1) in parentheses and the data of Libytheidae (*Libythea*), Riodinidae (*Taxila*) and Amathusiidae (*Stichophthalma*) are added. Fig. 15. Interrelations of the phylogenetic constant (α_1), C-index (C) and the wing-length (L) among the families of Rhopalocera. Fig. 16. Interrelations of C-index (C) and the wing-length (L) in each family of Rhopalocera. The ordinates are the means of every 5 or 4 species showing successive values of L. The values in parentheses indicate the phylogenetic constant (α_1).

tribe as in the superfamily Papilionoidea and the order Odonata as a whole (Figs. 14, 20). This specific pattern may show that the developments of the wing-veins and the wing-membranes are not entirely independent but mutually regulated, and consequently the hypermorphic elongation of the veins which might be disadvantageous for the organisms will be prevented. The similar regulative mutual developments of

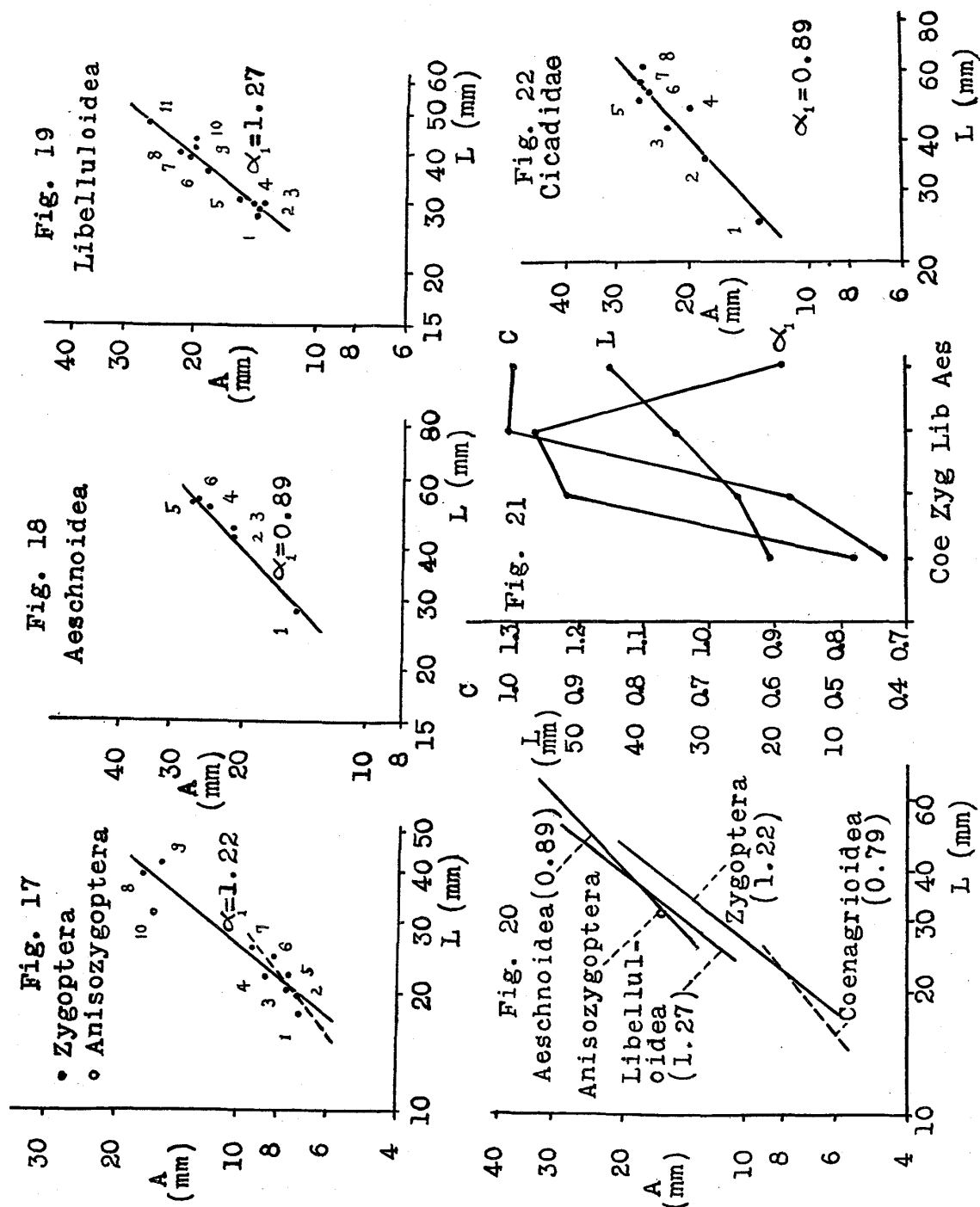


Fig. 17. The species-form allomorphosis in the suborder Zygoptera of the order Odonata. The co-ordinates show the values of a male for each species designated by an ordinal number. 1. *Cercion*, 2, 4. *Enallagma*, 3. *Sympecna*, 6. *Copera*, 5, 7. *Lestes*, 8, 9. *Calopteryx*. Fig. 18. Ibid., in the superfamily Aeschnoidea. 1. *Davidius*, 2. *Gomphus*, 3. *Gynacantha*, 4. *Anotogaster*, 5, 6. *Anax*. Fig. 19. Ibid., in the superfamily Libelluloidea. 1-4. *Sympetrum*, 5, 9, 10. *Orthetrum*, 6. *Somatochlora*, 7. *Pseudothemis*, 8. *Pantala*, 11. *Macromia*. Fig. 20. Comparison of the allomorphic patterns of the suborders and superfamilies of the order Odonata. The data given in the figures 17-19 are put together and a datum of the suborder Anisozygoptera (*Epiophlebia*) is added. Fig. 21. Interrelations of the phylogenetic constant (α_1), C-index (\bar{C}) and the wing-length (L) among Coenagrioidae, Zygoptera as a whole, Libelluloidea and Aeschnoidea. Fig. 22. The species-form allomorphosis in the family Cicadidae. The co-ordinates represent every one male of a species designated by an ordinal number. 1. *Melampsalta*, 2. *Meimuna*, 3, 7. *Tibicen*, 4. *Tanna*, 5. *Graptopsaltria*, 6. *Cryptotympana*, 8. *Oncotympana*.

allometric organs have well been known, e.g., in a lineage allomorphosis of the face-length of the horses as compared with the skull-length; the allometric constant is 1.8 (tachymetric) in the fossil-forms before Miocene, while it decreases to nearly 1.0 (isometric) thereafter up to the present horse (Reeve and Murray, 1942), and also in the individual allomorphosis of the head-width vs. thorax-length in *Zygothrica dispar* (Drosophilidae) (Burla, 1955). As Huxley (1932) and de Beer (1940) insisted, this type of lineage, species-form as well as individual allomorphosis should be biologically significant in enabling the organisms to maintain their phylogenical lineages which might otherwise be led to extinction through an extreme orthogenetic selection, e.g., overelongation of the faces in horses, of the wing-veins in insects and of the head-width of *Zygothrica*.

Another kind of characteristic feature of the species-form allomorphosis is seen in the triphasic tribes, in which the phylogenetic constant decreases below the lower critical point as well as above the upper critical point, as has been frequently observed in various animals (Figs. 14, 20). The fact suggests the usual sigmoidal growth curves possessed by the wing-veins and the wing-membranes to be different in shapes and phases in such manner as the latter curve somewhat preceding the former curve at the beginning and succeeding it at the end, as diagrammatically shown in Fig. 24.

B. The Burla's rule and the species-form allomorphosis

Among various genera of Drosophilidae (Fig. 4), families of Papilionoidea (Fig. 15) and superfamilies of Odonata (Fig. 21) the *C*-index is positively correlated with the wing-length (*L*) conforming to the Burla's rule which has been established for the genus *Drosophila* as shown in Figs. 3 and 5. This holds good also between two species of the genus *Apis*, *A. melliferae* L. and *A. cerana* Fabricius in both the fore and the hind wings, in which, according to the measurement of Akahira and Sakagami (1959), the relative length of the median vein (*M*) measured from the wing-base to the end of the 2nd discoidal cell and the wing-length (*L*) minus the length of the median vein (*M*), i.e., $M/(L-M)$, corresponding to the *C*-index, is positively correlated with *L* as shown below.

	Worker				Drone			
	fore	wing	hind	wing	fore	wing	hind	wing
	<i>L</i>	$M/(L-M)$	<i>L</i>	$M/(L-M)$	<i>L</i>	$M/(L-M)$	<i>L</i>	$M/(L-M)$
<i>melliferae</i>	8.32	0.510	5.38	0.550	10.40	0.513	6.96	0.535
<i>cerana</i>	7.53	0.505	5.36	0.530	8.60	0.509	6.16	0.503

While the negative correlation between *C*-index and *L* contradicting

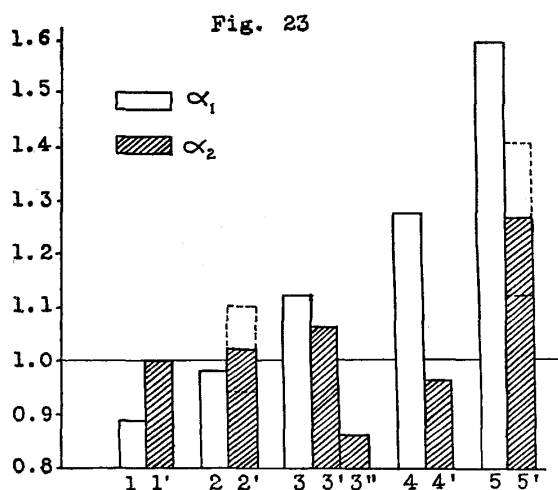
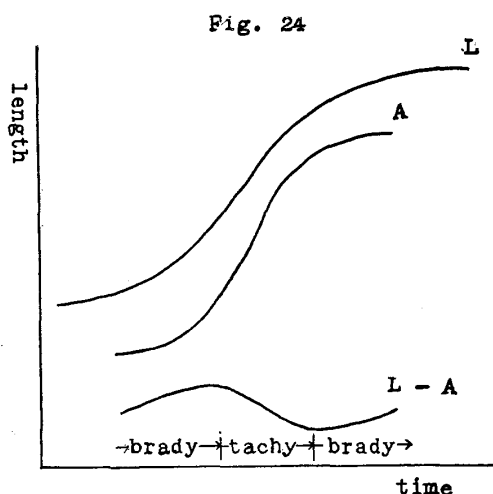


Fig. 23. The relations between the phylogenetic constant (α_1) and the ontogenetic constant (α_2). 1. *Cicadidae* (8 spp.), 1'. *Graptopsaltria nigrofuscata* (10 males and 4 females), 2. *Drosophila* s. str. (13 spp.), 2'. The mean of α_2 of 13 spp. of *Drosophila* s. str. (10 males for each sp.), 3. *Pieridae* (24 spp.), 3'. *Aporia hippia japonica* (12 mostly males), 3''. *Pieris rapae crucivora* (70 males), 4. *Libellulidae* (11 spp.), 4'. *Sympetrum frequens* (2 males, 9 females), 5. *Sophophora* (13 spp.), 5'. the mean of α_2 of 13 spp. of *Sophophora* (10 males for each sp.). The 95% confidence limits of the mean of population are shown by dotted cross-bars in 2' and 5'. Fig. 24. Schematic growth curves of the wing-length (L) and the wing-veins (A), to show a possible relation of the triphasic allomorphic pattern and the time factor.



to the Burla's rule is observed in the cases such as Papilionidae, Lycaenidae, Satyridae and also Nymphalidae (exclusive of *Argynnis*-tribe: *Argynnis*, *Melitaea*, *Calinaga*, *Pareva*) in which the α_1 is less than 1.0 or nearly 1.0 (Fig. 16). This contradiction may, however, be easily understood as a result of bradymetry which attributes the growth rate of the section A to be lower than that of the section B ($=L-A$) and consequently the C-index (A/B) to be smaller in the larger wings. The tachymetry may in turn cause the agreement to the Burla's rule and the isometry may result in the indifference to it. Indeed the degree of agreement to the Burla's rule can be expressed by the gradient of the line in the graph (Fig. 16), which turns out to be roughly correlated with the value of α_1 ; the nearer the gradient to 0° the more the value of α_1 approaches 1.0 as shown below (also in Fig. 16).

	Gradient	α_1
Hesperiidae	65°	1.22
Pieridae	40	1.12
Danaidae	35	1.03
Satyridae	-30	1.00
Nymphalidae (excl. <i>Argynnis</i> -tribe)	-35	0.94
Lycaenidae	-35	0.92
Papilionidae	-45	0.84

C. *The rule of Lameere-Smith and its biological significance*

The constant of the individual allomorphosis or the ontogenetic constant (α_2) is found to vary according to the different species or subgenera of the genus *Drosophila* to the effect that the higher value of α_2 is obtained in the forms with the shorter wings and the smaller C-index, in other words, α_2 is negatively correlated with L and C-index (Figs. 3, 6). As the constant of the species-form allomorphosis or the phylogenetic constant (α_1) is also negatively correlated with L and C-index, α_2 turns out to be positively correlated with α_1 , agreeing to the rule of Lameere-Smith. The agreement may, if not entirely, be ascribed to the monophyletic origin of the insect wings which have a basic pattern of venations as assumed by Comstock and Needham (1898-9) and also to the common fundamental function of this organ adapted for flight, to which the wing-veins concern in such way as to support and strengthen the wing-membrane. Although the common origin and function of the wings qualify the rule of Lameere-Smith, the values of α_1 and α_2 are found to fluctuate in such manner as to indicate the quantitative differences between the higher and the lower systematic categories of the evolutionary change in the allomorphic organs; α_2 tends to be nearer 1.0 or isometric as compared with α_1 , and if α_1 is smaller than 1.0 the corresponding α_2 is apt to be larger than α_1 (Cicadidae, *Drosophila* s. str.), while if α_1 is larger than 1.0 the corresponding α_2 tends to be smaller than α_1 (Pieridae, Libelluloidea, *Sophophora*) (Fig. 23). The facts indicate that the interspecific evolutionary change is broader or more diversified than the intraspecific one. The sequence agrees to what is given by Lull and Gay (1949, after Shimizu, 1959) in a schematic diagram, in which the α_2 is much larger than α_1 and is nearly isometric. This is, however, not the universally accepted principle, and there are some exceptional cases such as seen in the allomorphosis of the brain-weight vs. body-weight in the vertebrates, in which α_2 (=0.26) is much smaller than α_1 (=0.56) (Dubois, 1897, 1913; Brummelkamp, 1937, 1939, after de Beer, 1940).

D. *The species-form allomorphosis in relation to the systematics of the higher categories*

As is often recognized, the allomorphic patterns are apt to finely reflect the relationships of the systematic groups of especially the higher categories. This holds good in the present study to a considerably high extent. In the genus *Drosophila* the allomorphic patterns show that the subgenus *Paradrosophila* is included in the tribe of the subgenus *Sophophora* and that the subgenera *Hirtodrosophila* and *Dorsilopha* are placed near the critical point between *Sophophora* and *Drosophila* s. str. (Fig. 1). These relations are entirely the same as postulated by

Sturtevant (1942), Patterson and Stone (1953) and also the present author (1956) in view of various systematic characters. The situation of *Drosophila subtilis* is unique among the subgenus *Drosophila* in having close connections with *Paradrosophila* and *Sophophora* as discussed by the present author (1955 etc.) in view of the phallic organs and the other structures and equally as obtained in the present study (Fig. 1). The occurrence of the pregenital plates or sclerites in the uterus and the lack of the clasper teeth in periphallidic organs are widely observed in the genus *Microdrosophila* (Okada, 1956), which is consequently thought to be closely related to the genus *Leucophenga*. These two genera belonging to different subfamilies, Drosophilinae and Steganinae respectively, are proved, indeed, to compose a common allomorphic tribe (Fig. 2).

The Rhopalocera is divided into two superfamilies, Hesperioidea and Papilionoidea, the former shows a special type of allomorphosis distinctly separable from that of the latter (Fig. 14). The high values of α_1 as well as of C-index in the former superfamily as compared with those of the latter may be responsible for the thick thorax containing the strong muscle bundles which enable the skippers to fly swiftly. In another aspect this tachymetry may have a certain connection with the finding by Shimizu and Miyao (1954) that some of the skippers having comparatively small body show a bradymetric pattern of species-form allomorphosis of the wing-length vs. the body-length, contrary to the other members of Rhopalocera which show nearly isometric patterns within each family. In Pieridae, *Leptidea amurensis* belonging to the subfamily Dismorphiinae constitutes a monotypic tribe strikingly different from that of the subfamily Pierinae (Fig. 9). Nymphalidae is known to be one of the most polytypic families among the Rhopalocera, and is also polytypic in the allomorphic patterns (Fig. 13). Amathusiidae is located near Nymphalidae, and Riodinidae and Libytheidae are near Lycaenidae in their allomorphic tribes, finely agreeing to their systematic relationships (Fig. 14). Regarding the allomorphic patterns of the order Odonata, it should be noticed that the suborder Zygoptera is separable from the suborder Anisoptera, and that the suborder Anisozygoptera is situated just between the superfamilies Aeschnoidea and Libelluloidea, somewhat remote from Zygoptera (Fig. 20). Consequently, the wing-character in question of *Epiophlebia* seems to be one of the "specialized characters in common with that of the Anisoptera (Asahina, 1954)."

It will be concluded as a whole that although the wing-veins of the insects are radically common in their structures and functions as well as in their general allomorphic features obeying the various fundamental rules, they show considerable degree of variations or differentiations in their detailed allomorphic patterns subject to the systematic relationships of the higher categories, either morphological or functional.

E. *The heterauxesis and the allomorphosis*

Although the wing of insect is not *a priori* responsible for the heterauxetic analysis as it is an organ of adult, its development in *Drosophila* can be divisible, according to Waddington (1950), into several phases which are tempted to be subject to the heterauxetic changes: the first cell division mainly in the longitudinal direction, the first expansion and contraction, the second cell division mainly in the transverse direction, the second expansion in length, all round and in breadth according to Henke (1947), the last expansion of cells on the under side then on the upper side. Thus the ultimate size and shape of the normal wing seem to be determined by the genetic and environmental influences upon these alternative phases. It should be noticed that the larger wing is comparatively narrower and the smaller wing broader among the individuals of a species as well as among various species at least in the genus *Drosophila*, and that expansion of the wing is, according to the figures of Waddington, more prominent at the proximal half of the wing than at the distal half, and, moreover, that the degree of expansion especially at the proximal half is higher in the larger (and consequently narrower) wing than in the smaller (and broader) one. These facts may have some connections with the allomorphic sequences and the Burla's rule observed among individuals or species. In deed, a rough estimation from the photographs of the developing wings of *Drosophila melanogaster* given by Bodenstein (1950) results in the finding that the *C*-index gradually increases during development of the wing as follows and α approximates 0.65.

Stage	<i>K</i> (18 hours after pupation)	<i>L</i> (28 h.)	<i>M</i> (38 h.)
<i>L</i>	2.75	3.15	3.30
<i>A</i>	2.00	2.30	2.48
<i>B</i>	0.82	1.23	1.48
<i>C</i> -index	1.25	2.93	3.33

Summary

1. Although the wing-veins of insects have been known to undergo development independent of the wing-membranes, the allomorphic pattern of these two morphological traits shows that they are subject to phylogenetic developments mutually dependent and harmonious to some extents and characteristic in exhibiting diphasic or triphasic species-form allomorphosis in comparatively high systematic categories such as the genus *Drosophila*, the family Drosophilidae, the division Rhopalocera and the order Odonata, in which the allomorphic patterns change from tachy- to bradymetry or from brady- to tachy- and ultimately to brady- or isometry.

2. The Burla's rule established for the genus *Drosophila* to indicate that the longer wings have the more distally placed wing-veins is proved to be acceptable in the forms having tachymetric allomorphosis of the wing as Drosophilidae, Hesperidae, Pieridae and Danaidae, while a reverse relation is found in the groups showing bradymetric allomorphosis as Lycaenidae and Papilionidae. The degree of applicability of the Burla's rule as expressed by C-index, a length ratio of a vein and the wing itself, is roughly correlated with the phylogenetic constant.

3. The rule of Lameere and Geoffrey Smith referring to the occurrence of the similar patterns of allomorphosis both among the individuals of each of the related species and among these related species is recognized in Drosophilidae, Pieridae, Libellulidae and Cicadidae, in which the ontogenetic constant tends to approach 1.0 or isometric as compared with the phylogenetic constant, indicating that the interspecific evolutionary change in the wing-venation is more diversified than the intraspecific one.

4. The allomorphic patterns of the wing-veins vs. wing-membranes are found to strikingly reflect the hitherto known relationships of the various orders of the higher systematic categories of insects and sometimes to be correlated with the functions of wing and its veins responsible for the flight.

5. The sequences of allomorphosis and the Burla's rule may have some connections with the heterauxetic development of the wings at least in the genus *Drosophila*.

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