

CLADOGENETIC DIFFERENTIATION OF DROSOPHILIDAE IN RELATION TO MATERIAL COMPENSATION

By Toyohi Okada¹

1. Introduction

Although the phylogenetic researches of an animal group should essentially be based on paleontological evidence, the neontological approaches from various branches of zoology can also build up a relationship diagram which reflects presumed phylogeny. This is because the rate of evolution differs according to taxa (Dobzhansky, 1951) and vertical relationships alone do not guarantee phylogeny (Simpson, 1961). Rensch (1960) and Sneath (1961) also put importance upon "rich material" of the recent animal groups for the finding of phylogenetic sequence, even when the fossil material is poor. Complete sets of neontological characters are often superior to an incomplete fossil evidence. The current system of the genus *Drosophila* may be an excellent example of neontological outcome by which the presumed phylogeny with sufficient evidence has been presented.

Under this consideration the present research is intended to find out bearing of the phenomenon of material compensation (Rensch, 1954), which is one of the various factors of transspecific evolution, upon the specialization phase of cladogenesis in the family Drosophilidae. As the major factors of transspecific evolution Rensch enumerated pleiotropy, allometry, and material compensation. This factor or phenomenon of material compensation, which refers to, according to him, that the strongly developing parts of an animal consume so much body material that the less strongly developing parts remain small or become more or less reduced due to deficiency of body material. It has been known since Geoffroy St. Hilaire (1822, according to Rensch) and repeatedly discussed and validated by various investigators from diverse aspects, not only ontogenetically but also phylogenetically. Mayr (1942) also enumerated this phenomenon one of the factors causing macro-evolution (transspezifische Evolution, Rensch, 1954) as well as micro-evolution (infraspezifische Evolution, Rensch, 1954).

In connection to the phenomenon of allometry, the ontogenetic and phylogenetic material compensations can sometimes be attributed to enantiometry (Huxley and

¹ Department of Biology, Faculty of Science, Tokyo Metropolitan University.

Teissier, 1936) and enantiomorphosis (Okada, 1960₂), respectively, because one organ grows in advance while the other is degenerated. Moreover, radical sources inducing enantiomorphosis may be attributed to the pleiotropic effect of genes. Therefore, these three factors or phenomena, pleiotropy, allometry and material compensation, are thought, if not entirely, merely to be the same phenomenon viewed from different angles.

As indicated by Rensch (1960), the reduction of some organs or parts of organ during phylogenetic material compensation does not always comprise regressive evolution, but rather usually means progressive rationalization to abolish superfluous organs or parts of organ. The compensatory reduction should essentially be a by-product of progressive evolutionary change and ultimately attributable to random mutation and natural selection.

2. Material and examples

The species examined in the present study are mostly Japanese and attain to about eighty. They are grouped into taxa higher than species group (Table 1). Main focus is centered around the genus *Drosophila* as the interrelations of the taxa within this genus have been extensively worked out. In comparison to the genus *Drosophila*, special attention is paid to the genus *Amiota*, a member of subfamily Steganinae, and also to the genus *Scaptomyza*, a member of subfamily Drosophilinae, as these two genera are thought closely related to the genus *Drosophila*. The genus *Diastata* representing Diastatidae is also put into consideration, as Diastatidae is one of the families most intimately associated with the family Drosophilidae.

In this research following eleven examples, 1-11, were chosen as morphological characters of adults, larvae and eggs to show phenomenon of phylogenetic material compensation, which is tentatively classified into five categories, A-E.

Category A: Compensation between different organs or parts of organ with different functions, as is known between wings and ovaries of some grasshoppers and psychid larvae (Rensch, 1960). Ex. 1. Increase of mid-intestinal convolution in compensation for the narrowing of rectal papilla (Okada, 1954₂).

Category B: Compensation between different organs or parts of organ with the same function, as known between labella (hausterum) and oesophageal pump in dipterous flies (Okada, 1936). Ex. 2. Development of aedeagus in compensation for the reduction of parameres and other accessory organs of male phallic organs (Okada, 1954₁).

Category C: Compensation between the elements of meristic organs, as seen between the number and size of shell spines of Prosobranchia (Rensch, 1954, 1960). Ex. 3. Increase in number of larval mouth hook teeth in compensation for the reduction of their size (Okada, 1963).

Category D: Compensation between different portions of one and the same organ, as known between lengths of metatarsus and femur of horses (Lull, 1948). Ex. 4. Elongation of aedeagus in compensation for the shortening of the basal apodeme (Okada, 1953). Ex. 5. Development of vertical rod of aedeagus in com-

Table 1. Taxonomic groups of Drosophilidae and Diastatidae higher than species groups treated in the present study, with abbreviated signs in parentheses used in figures.

Family Diastatidae	Subgenus <i>Lordiphosa</i> (Lo)
Genus <i>Diastata</i> (Di)	Species group <i>fenestrarum</i> (fe)
Family Drosophilidae	Subgenus <i>Dorsilopha</i> (Do)
Subfamily Steganinae	Subgenus <i>Hirtodrosophila</i> (Hi)
Genus <i>Amiota</i> (Am)	Subgenus <i>Drosophila</i> (Dr)
" <i>Stegana</i> (St)	Section <i>Virilis</i> (Vi)
" <i>Leucophenga</i> (Le)	Species group <i>subtilis</i> (su)
Subfamily Drosophilinae	" <i>virilis</i> (vi)
Genus <i>Microdrosophila</i> (Mi)	" <i>melanica</i> (mn)
" <i>Mycodrosophila</i> (My)	" <i>robusta</i> (ro)
" <i>Dettopsomyia</i> (De)	" <i>repleta</i> (re)
" <i>Liodrosophila</i> (Li)	Section <i>Quinaria</i> (Qu)
" <i>Chymomyza</i> (Ch)	Species group <i>bizonata-testacea</i>
" <i>Scaptomyza</i> (Sc)	complex (b-t)
" <i>Drosophila</i> (DR)	" <i>quinaria</i> (qu)
Subgenus <i>Paradrosophila</i> (Pa)	" <i>histrion</i> (hi)
" <i>Sophophora</i> (So)	" <i>grandis</i> (gr)
Species group <i>obscura</i> (ob)	" <i>melanderi</i> (md)
" <i>melanogaster</i> (mg)	" <i>funnebris</i> (fu)
" <i>willistoni</i> (wi)	" <i>immigrans</i> (im)

compensation for the shortening of the basal apodeme (Okada, 1956₁). Ex. 6. Development of the plate of ejaculatory apodeme in compensation for the shortening of its stalk (Okada, 1961). Ex. 7. Development of the bristles on ovipositor plate (egg-guide) in compensation for the narrowing of the plate. Ex. 8. Elongation of the common stalks of Malpighian tubules in compensation for the shortening of the branches (Okada, 1955₂).

Category E: Compensation between length and width of the same portion of an organ, as known in the indirect wing-muscle bundle of certain insects (Rensch, 1948). Ex. 9. Elongation of ejaculatory caecum in compensation for the decrease in width (Okada, 1958). Ex. 10. Elongation, or increase in convolution, of testis in compensation for the decrease in width (Throckmorton, 1962₁). Ex. 11. Elongation, or increase in folds or coils of ventral receptacle in compensation for the decrease in its width.

3. Material compensation illustrated in the relationship diagram of Drosophilidae

The sequence of the phenomenon of phylogenetic material compensation found in above-mentioned eleven examples can be illustrated in the current system of relationship diagram of Drosophilidae (Figs. 1-8). The diagram is adapted from Patterson and Stone (1952) and slightly modified by the addition of Japanese

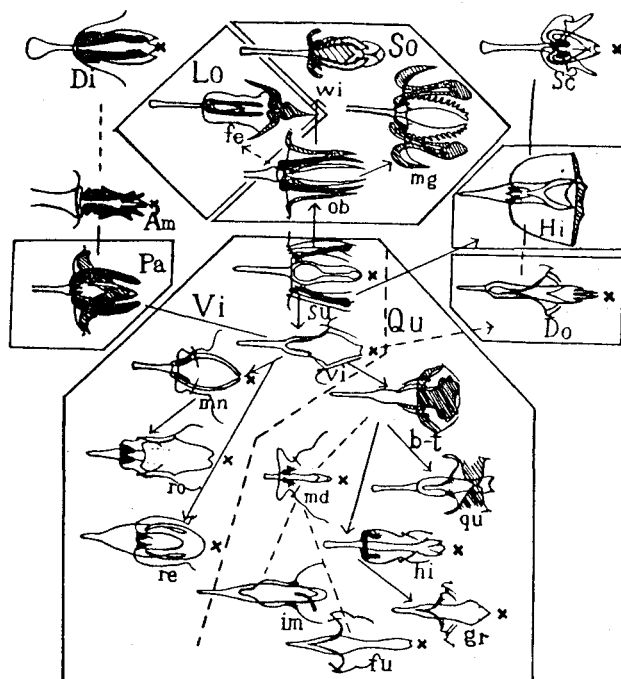


Fig. 2. Development of aedeagus in compensation for the reduction of the accessory organs, anterior parameres (tinted black), posterior parameres (obliquely striped) and hypandrium (caudal margin alone is indicated). X, posterior paramere absent. Compare Ex. 2.

rectal papilla (Fig. 1). The length of mid-intestine expressed by the number of coils is indicated at right side of each contour of rectal papilla in Figure 1. It varies from 1.9 to 3.3 on an average and is generally smaller in the basically placed taxa, larger in the more peripherally placed ones. While the width of rectal papilla expressed by a ratio relative to its length, which is shown on each contour, varies from 0.3 to 0.7 on an average and the value is generally larger in the more basically placed taxa and smaller in the more peripherally located ones, revealing a tendency of compensatorily negative correlation ($r = -0.316$) with the length of mid-intestine.

Category B: Ex. 2. Compensation between sizes of aedeagus and its accessory organs (Fig. 2). The male phallic organs of drosophilid flies are composed of aedeagus with its apodeme, anterior and posterior parameres or gonapophyses and hypandrium or novasternum. The aedeagus tends to be bifid or easily separable into lateral lobes in the basically placed forms, c. g., *Paradrosophila*, *obscura* and *subtilis* groups, *suzukii*, *takahashii* and *melanogaster* subgroups of *melanogaster*

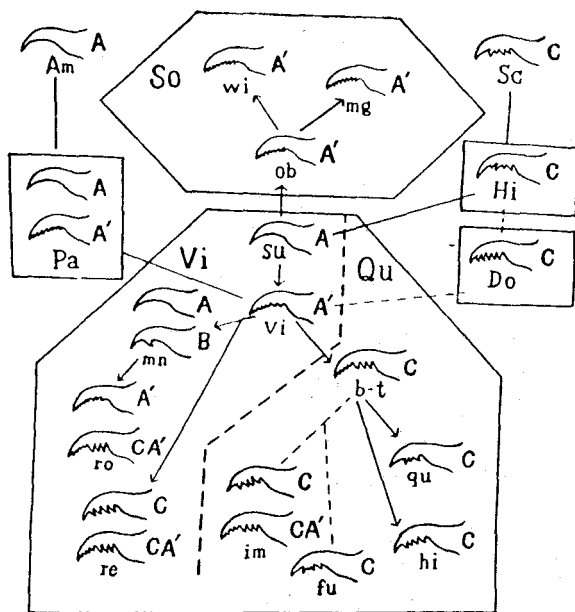


Fig. 3. Increase in the number in compensation for the reduction in the size of the last instar larval mouth hook teeth. Compare Ex. 3.

group, while it is a compact body non-separable into lateral lobes in the more peripherally located forms (Okada, 1954₁, 1955₁). The anterior paramere (tinted black in Fig. 2) is well developed in *Paradrosophila*, *subtilis*, *obscura*, *willistoni* and *melanica* groups, *suzukii* and *takahashii* subgroups, and some species of Amiotinae and Diastatidae, while it is but weakly developed or almost absent in the remaining groups which occupy comparatively peripheral positions. The posterior paramere (obliquely striped) is well developed in *Paradrosophila* and most of *Sophophora*, and weakly developed in *Hirtodrosophila* and *bizonata-testacea*, *quinaria* and *immigrans* groups, while it is absent (shown by a sign X) in the remaining representatives. The caudal margin of novasternum is not deeply notched medially in *Amiota*, *Paradrosophila*, and *obscura* and *melanogaster* groups, while it tends to be deeply notched in the more peripherally placed forms. As a whole, these accessory organs (anterior and posterior parameres, novasternum) are liable to be reduced in size in the more peripherally located taxa, in which the compensatory development of aedeagus into a compact body is pronounced.

Category C: Ex. 3. Compensation between number and size of larval mouth hook dentition (Fig. 3). The mouth hook dentition varies according to species as well as instars, indicating phyletic differentiation toward a general adaptive trend of material compensation of gradual increase in number and a gradual decrease in the size of teeth, in such way as A (without teeth) - B (one prominent tooth)-

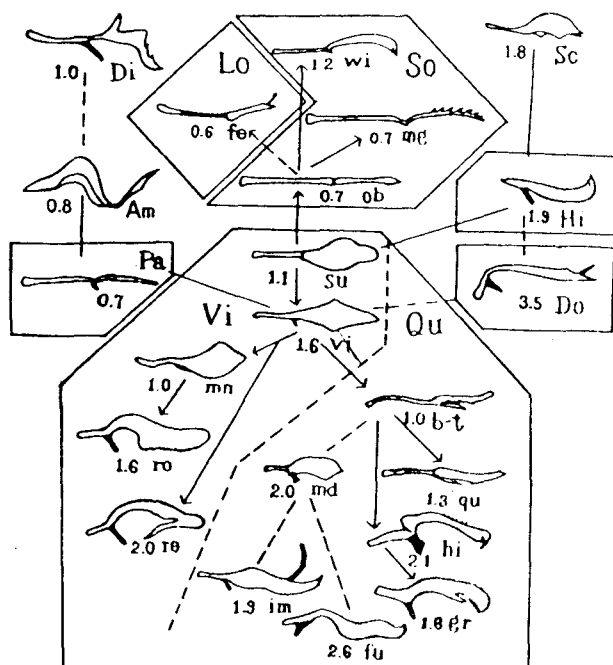


Fig. 4. Increase in the length of aedeagus and vertical rod (tinted black) in compensation for the decrease in length of the apodeme. Numerals indicate the ratio in length of aedeagus to apodeme. Compare Ex. 4 and 5. Abbreviations see Table 1.

C (several smaller teeth) - CA' (several smaller and several minute teeth) - BA' (one smaller and several minute teeth) - A' (numerous minute teeth). The general trend can be clearly traced in the relationship diagram, especially at the earlier instars, while in the later instars it is either arrested or accelerated, showing special adaptive trends in accordance with diverse food environments (Okada, 1963, also compare chapter 4).

Category D: Ex. 4. Compensation between lengths of aedeagus and its apodeme (Fig. 4). The phallosomal index (P. I.), which was proposed by the present author (Okada, 1953) for the ratio in length between aedeagus and apodeme, tends to increase in the more peripherally located groups. It is about 1.0 or less in *Paradrosophila*, *Sophophora*, *Amiota*, *Diastata*, and in some of basically placed groups of *Drosophila* s. str., about 2.0 in *Hirtodrosophila*, *Scaptomyza* and most of *Drosophila* s. str., while it is over 3.0 in *Dorsilopha*. The sequence of this serial change of both parts clearly indicate material compensation.

Ex. 5. Compensation between length of vertical rod and basal apodeme of aedeagus (Fig. 4). The vertical rod is a process ventrally projected from the junction of aedeagus and its apodeme, shown in black in Fig. 4. It is absent or, if

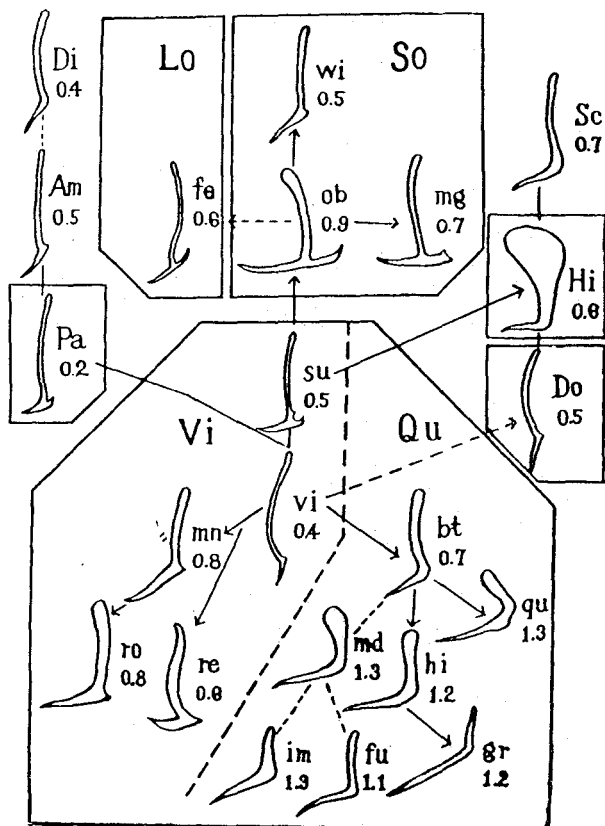


Fig. 5. Increase in the length of the plate in compensation for the decrease in length of the stalk of ejaculatory apodeme. Compare Ex. 6.

present, minute in *Paradrosophila*, *Sophophora*, *Amiota*, *Scaptomyza*, and in the more basally placed groups of *Drosophila* s. str., in which the apodeme is usually long but slender, while it is well developed in compensation for the reduction in length, but not always in width, of apodeme in the more peripherally located groups. The apodeme itself reveals another sort of compensation belonging to category E, the shorter it becomes the more broadened vertically it tends to be.

Ex. 6. Compensation in lengths between the basal plate and stalk of ejaculatory apodeme (Fig. 5). The evidence of this kind of compensation recognized by Okada (1961) will be seen in the relationship diagram (Fig. 5) as expressed by the ratio in length of plate and stalk for each group. The process of differentiation follows gradual elongation of plate and compensatory shortening of stalk, resulting in

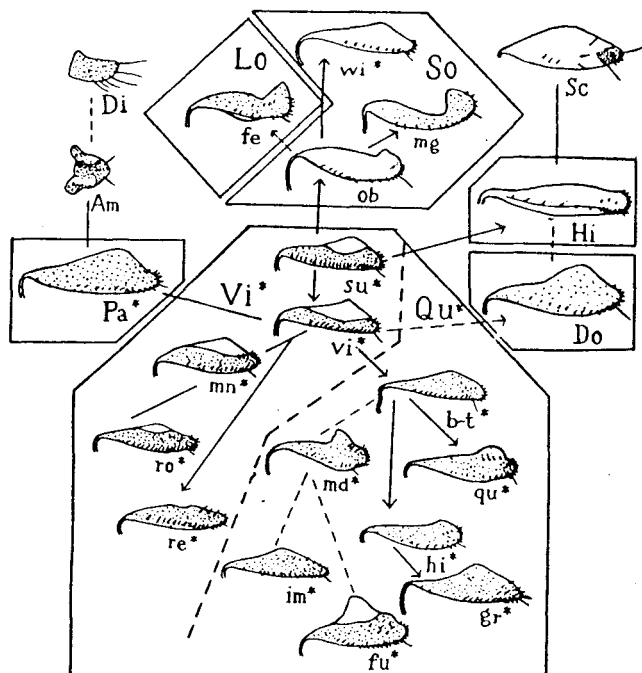


Fig. 6. Development of peg-like bristles in compensation for the narrowing of the lobe of ovipositor. Another compensatory phenomenon is shown between coloration of bristles and lobes, pale bristles (with asterisk) is usually combined with dark lobe (dotted). Compare Ex. 7.

gradual increase in the mean ratio, which is 0.5 or less in *Diastata*, *Paradrosophila*, *Dorsilopha*, and *subtilis*, *virilis* and *willistoni* groups, 0.6 to 1.0 in *Hirtodrosophila*, *Scaptomyza*, and most of *Sophophora* and *virilis* section as well as *bizonata-testacea* complex, and more than 1.0 in most of *quinaria* section. Similar sequence has been already referred to by Nater (1950) in his "morphologische Reihe der Samenpumpensklerite" which includes "Verkürzung der Platte, Verlängerung der Stiele" (from step 1 to 2) and its reciprocal (from step 6 to 8).

Ex. 7. Compensation between bristles and lobes of egg-guide (Fig. 6). The bristles on the egg-guide lobes or ovipositor are entirely undeveloped, represented only by hairs or setae, in most of Steganinae and Diastatidae, in which the lobes are broad and often fused to each other. In Drosophilinae the bristles tend to be better developed in the forms which have narrower lobes, especially well developed in most of *virilis* section, *suzukii* and *nipponica* subgroups of *melanogaster* group, and some of *grandis* group, all having narrow lobes. The relationship diagram (Fig. 6) seemingly indicates peripherally pronounced reduction or degeneration in

Table 2. Degree of compensatory development shown by eleven examples of material compensation chosen for study in each of the drosophilid taxa. S, sum of degrees of compensatory development; N, number of species examined. Further explanation see in the text.

Example Taxon	1	2	3	4	5	6	7	8	9	10	11	S	N	S/N ×100
<i>Diastata</i>	0.5	0	—	0	0.5	0	0	0	0	0	0	1.0	10	10
<i>Amiota</i>	0.5	0	0	0	0	0	0	0	0	0	0	0.5	11	5
<i>Paradrosophila</i>	0.5	0	0.5	0	0.5	0	0.5	0.5	0	0	0	2.5	11	23
<i>subtilis</i> gr.	0	0	0	0.5	0.5	0	1	0	0	0	0	2.0	11	18
<i>virilis</i> gr.	0	1	1	1	0.5	0	1	0	0	0.5	1	6.0	11	55
<i>melanica</i> gr.	0.5	0.5	0	0	0	0.5	1	0	0.5	0.5	1	4.5	11	41
<i>robusta</i> gr.	0	1	1	1	1	0.5	1	1	0.5	0.5	1	8.5	11	77
<i>repleta</i> gr.	0.5	1	1	1	1	0	1	0	0.5	1	1	8.0	11	73
<i>bizonata-</i> <i>testacea</i> gr.	1	0.5	1	0	0	0.5	0	0	1	0.5	0.5	5.0	11	45
<i>quinaria</i> gr.	1	0.5	1	0.5	0	1	0	0	1	1	1	7.0	11	64
<i>histris</i> gr.	1	1	1	1	1	1	0	0	1	1	1	9.0	11	82
<i>grandis</i> gr.	0.5	1	—	1	1	1	1	0.5	0.5	0.5	0.5	7.5	10	75
<i>melanderi</i> gr.	0.5	1	—	1	1	1	0	0	0	1	0.5	6.0	10	60
<i>funbris</i> gr.	1	1	1	1	1	1	0	0	1	1	1	9.0	11	82
<i>immigrans</i> gr.	0.5	1	1	1	1	1	0.5	0	1	1	1	9.0	11	82
<i>obscura</i> gr.	0	0	1	0	0	0.5	0	0	0	0	0	1.5	11	14
<i>melanogaster</i> gr.	0	0	1	0	0	0.5	0	0.5	0	0.5	0.5	3.0	11	27
<i>willistoni</i> gr.	1	0	1	0.5	0	0	0	0	0.5	0.5	1	4.5	11	41
<i>fenestrarum</i> gr. (<i>Lordiphosa</i>)	0	0	—	0	0	0	0	1	0	1	0.5	2.5	10	25
<i>Dorsilopha</i>	0	1	1	1	1	0	0	0	0	0	0	4.0	11	36
<i>Hirtodrosophila</i>	0.5	1	1	1	1	0	0.5	0	0	0.5	1	6.5	11	59
<i>Scaptomyza</i>	0.5	1	1	1	0.5	0.5	0	0	1	0	0.5	6.0	11	55

bristle size, which, however, may be a secondary phenomenon, and the tendency as a whole in Drosophilidae should be a peripheral development.

The egg-guide shows another kind of compensation, that in case the lobe is dark (dotted in Figure 6) the bristles are apt to be pale (shown by asterisks in Figure 6), and vice versa. All the examined species of *Paradrosophila* and *Drosophila* s. str. have dark lobes and pale bristles, while most of *Sophophora* and *Hirtodrosophila* show pale lobes and dark bristles.

Ex. 8. Compensation between branches and common stalks of Malpighian tubules

(Fig. 7). In *Drosophilidae* generally the common stalks of Malpighian tubules are rather short and their branches rather long, while a tendency of elongation of common stalks in compensation for the shortening of branches can be recognized to occur parallelly in scattered lines of the relationship diagram, e.g., in *Paradrosophila*, *Lordiphosa*, *robusta* and *grandis* groups (Okada, 1955₂), as well as *Microdrosophila* (Okada, 1960₁). These groups, except *Paradrosophila*, occupy rather peripheral positions in the diagram. According to Sturtevant (1942), the Malpighian tubules of *Drosophilidae* can be divided into three types on the basis of the feature of the posterior branches, which are, 1), ending free, 2) closely apposed at tips, and 3) fused at tips to make a complete loop. Throckmorton (1962₁) summarized the type distribution in the family *Drosophilidae*. All the three types are found in the above-mentioned groups showing compensatory shortening of branches, type 1 in the *melanogaster* group (especially *takahashii* and *ananassae* subgroups), type 2 in *Paradrosophila* and *Lordiphosa*, and type 3 in the *robusta* and *grandis* groups (type 2 or 3 also in the *cardini*, *guarani*, and *rubrifrons* groups, according to Throckmorton, 1962₁).

Category E: Ex. 9. Compensation between length and width of the ejaculatory caeca (Fig. 8). The comparative study of this organ in *Drosophilidae* has been made by Rosenblad (1941), Okada (1958) and, in more detail, by Throckmorton (1962₁). Six types of the caeca have been recognized, four by Rosenblad and additional two by Okada; they are, A), without definite caeca, B), with one simple posterior caecum, C) with a pair of simple posterior caeca, D), with a pair of branched posterior caeca, E), with a pair of anterior and a pair of posterior simple caeca, and F), with three simple anterior caeca and one posterior simple caecum. The types with the more elongate or complicately branched caeca in compensation for the reduction in their width are apt to be found in the more peripherally placed taxa (Fig. 8).

Ex. 10. Compensation between length and width of testis. The systematic importance of the morphological features of testis in *Drosophilidae* was recognized for the first time by Sturtevant (1942), and most of the succeeding authors have been adopting the features as criteria in describing new species. Throckmorton (1962₁) referred to the compensation of this organ in the genus *Drosophila* between its thickness and the number of coils. As shown in Figure 9, the more basically located groups, such as *Diastata*, *Amiota*, *Paradrosophila*, and *subtilis* and *obscura* groups, tend to have thicker and compensatorily shorter testes, while *quinaria*, *repleta* and *fenestrarum* groups, which are located peripherally, include species having exceedingly long and tightly coiled testes.

Ex. 11. Compensation between length and width of the ventral receptacle. The morphological feature of the ventral receptacle in *Drosophilidae* has also been thought systematically important since Sturtevant (1942) who recognized a positive correlation in structural complication between testis and this organ. It is short and only weakly folded in *Diastata*, *Amiota*, *Paradrosophila*, and *subtilis* and *obscura* groups, while it is usually long and kinkily coiled in the more peripherally located groups.

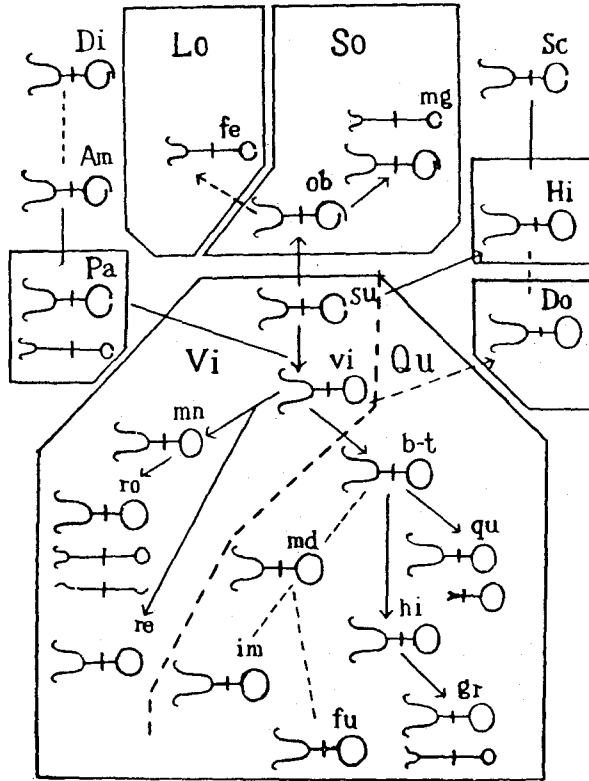


Fig. 7. Lengthening of the common stalks in compensation for the shortening of the branches of the adult Malpighian tubules. Left-hand: anterior. Compare Ex. 8.

4. Adaptive significance of the phenomenon of material compensation

The compensation between mid-intestine and rectal papillae (Ex. 1) seems to be merely mechanical, suggesting "phyletic endogenous correlation" (Eggers, 1939, after Rensch, 1960), which signifies that the size reduction of an internal organ gives more space in the interior of the body and enables the other organs to enlarge. This kind of mechanical compensation can be compared to an ecological phenomenon, the altruistic adaptation (Haldane, 1932), observable in social bees in which the majority of drones and walkers die out before winter, enabling the remaining small population involving queen to overwinter under limited food supply.

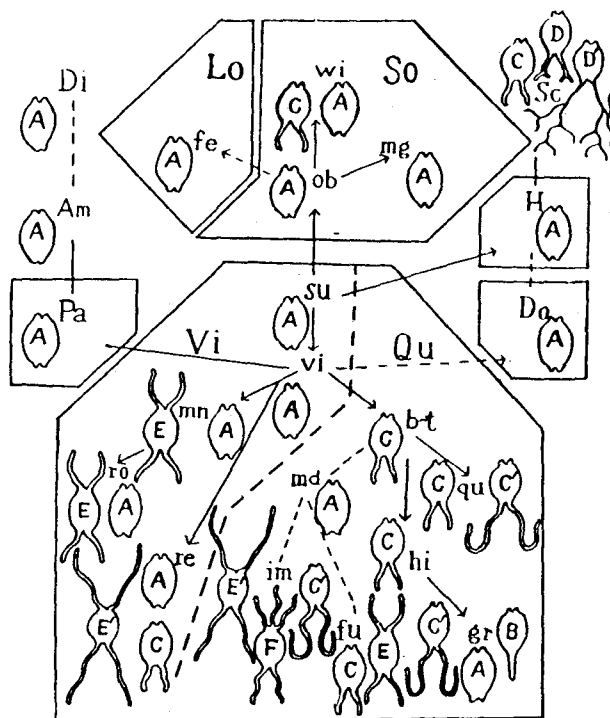


Fig. 8. Lengthening of ejaculatory caeca in compensation for the decrease in width. Alphabetical signs on the contours indicate the types of rectal papillae. Compare Ex. 9. Abbreviations see Table 1.

The case of compensation between the common stalk and the branches of Malpighian tubules (Ex. 8) also seems to be merely mechanical and to reflect a process of unknown adaptation; an extreme elongation of the common stalk often results in the reduction in the number of tubules, which is a general tendency among Diptera. In this order of insects the number of tubules is traced back to six in a hypothetical ancestor (Wheeler, 1893).

The other examples of material compensation can be interpreted as expressing more or less evident "double" adaptation in favour of both the *developing* organ or part of organ and the compensatorily *reducing* organ or part of organ. The reduction in length of the apodeme of aedeagus (Ex. 4, 5) and of the stalk of the ejaculatory apodeme (Ex. 6) in compensation for the development of the aedeagus or the vertical rod (Ex. 4, 5) and of the plate of the ejaculatory apodeme renders the muscle contraction effective due to diminution of its distance. This interpretation agrees with the "Rule of Speed Index" or "Speed Ratio" established by Lull

(1948) for the phenomenon of reduction in ratio of the length of femur to that of metatarsus III in speedy ungulates. The reduction in width in compensation for the increase in length (Category E) shown by ejaculatory caeca (Ex. 9), testis (Ex. 10) and ventral receptacle (Ex. 11), is also considered to be the double adaptation to internal environment, giving the organ an effective supply of body fluid and tracheal innervation. The compensatory differentiation of the mouth hook dentition (Ex. 3) shows a striking adaptation to diverse food environments especially in the third instar larvae. Those larvae which take harder food material tend to have better developed mouth hook teeth (Okada, 1963).

High adaptive significance involved in these examples of material compensation should have been induced by selection of internal or external environments which has made the morphological changes directed to definite specialization trends. The directed changes may *pseudo-orthogenetically* (Emerson, in Alle et al., 1949) continue until the adaptive significance becomes lost (Rensch, 1954, 1960) or until further morphological change becomes mechanically impossible (Rensch, 1948). It may thus be noted that "there is no reason to assume directed transformation processes of an autonomous nature (Rensch, 1960)."

5. Quantitative aspect of specialization in relation to material compensation

In order to facilitate description, the usually vigorously developing organ or its part, first-mentioned in each example of material compensation, is named the *primary organ*, and the last-mentioned compensatorily reducing one the *secondary organ*. Furthermore, the difference in developmental level of primary and secondary organs or net-developmental degree of the primary organ, is named the *degree of compensatory development*. Adopting a kind of equal weighting methods the development of each organ is classified into three levels, weak, moderate and strong. The number of characters considered here is only twenty-two, and this number is not sufficient to make the difference between weighting and equal weighting methods insignificant (Michener and Sokal, 1957; Sneath, 1962). The degree of compensatory development is denoted as 0 when the primary organ is strong and the secondary organ is weak in developmental level, as 1 when the former organ is weak and the latter organ is strong, and as 0.5 when both organs are subequal in developmental level. The degree of compensatory development of certain organ in a taxon higher than species is determined as an average of the degrees shown by species involved, and it is assigned also to 0, 0.5 or 1.

The degree of compensatory development should be significant in expressing real features of evolutionary processes which inevitably involve not only development but also reduction. The followings are the degrees 0 and 1, determined as standards for paired organs in each example.

Ex. 1. 0: Convolution of mid-intestine less than 2.4; ratio of width to length of rectal papilla more than 0.4. 1: Convolution of mid-intestine 2.4 or more; ratio of rectal papilla 0.4 or less. Ex. 2. 0: Aedeagus apparently bifid or horizontally flattened; anterior and/or posterior parameres large and ventral fragma not deeply

notched. 1: Aedeagus composes solid body and anterior and posterior parameres minute or absent; ventral fragma deeply notched. Ex. 3. 0: Mouth hook teeth absent or single and large (type A or B). 1: Mouth hook teeth several to numerous and small (other than types A and B). Ex. 4. 0: Phallosomal index (P.I.) 1.0 or less. 1: P.I. 1.5 or more. Ex. 5. 0: Vertical rod absent; apodeme of aedeagus long. 1: Vertical rod present, usually large; apodeme of aedeagus short. Ex. 6. 0: Stalk of ejaculatory apodeme long, plate short; ratio in length of plate to stalk 0.6 or less. 1: Stalk short, plate long; ratio more than 1.0. Ex. 7. 0: Egg-guide lobe broad at tip; bristles short or absent (only hairy). 1: Lobe narrow at tip, bristles strong. Ex. 8. 0: Common stalk of Malpighian tubule short, branches long. 1: Common stalk long, branches short. Ex. 9. 0: Ejaculatory caeca absent (type A). 1: Caeca present (exclusive of type A). Ex. 10. 0: Testis short and thick, not or but weakly coiled. 1: Testis long and slender, densely coiled more than several times. Ex. 11. 0: Ventral receptacle short and thick, folded not more than a few times. 1: Ventral receptacle long and slender, with numerous kinky coils.

Table 2 shows the degree of compensatory development determined for each example. The sum of degrees of all examples (S) for a taxon divided by total number of examples (N) may be a quantitative value to show degree of compensatory development of the given taxon, which is illustrated by a circular diagram (Fig. 9). The size of circle indicates mean body size of the examined species belonging to the taxon; small, median and large circles denote the means to be about 1.5, 2.5 and 3.5 mm, respectively. The evolutionary lineages of Drosophilidae may be divided into three presumed phylogenetic trends (fig. 10) which differ in the sequences of body size increase, structural complexity and compensatory development: 1), body size increase not combined with structural complexity and compensatory development, 2) body size increase combined with structural complexity and usually with compensatory development; and 3), structural complexity not combined with body size increase, but followed by compensatory development. The first trend is observed along a line, *Amiota* (*Amiota*)-*Amiota* (*Phortica*) or *Diastata*. As these taxa are generally considered to be primitive or archaic, having simple structures, this trend may be assorted to bradytely of Simpson (1953). The second trend is seen along a line, *Paradrosophila*-*Drosophila* s. str., the latter taxon starting from *subtilis* group and divided into two parallel sublines, the *virilis* and *quinaria* sections. Involving primitive as well as serially advancing taxa, this trend can be assorted to holotely of Simpson. It also agrees with the Cope's Rule established by Rensch (1948) for the phenomena of phyletic size increase combined with structural complexity; the former phenomenon was primarily found by Cope (1884) and proved by Dépérét (1907) and others, and the latter was discussed in combination with the former by Haldane and Huxley (1927), Rensch (1948), Newell (1949) and others. Rensch (1954) stated that the Cope's Rule can not be applied to flying insects due to the upper limitation of body size fitted for flying mechanism. This may not preclude, however, the possibility of specialization toward phyletic size increase within a limited range. The third trend is found in lines, *Paradrosophila*-*subtilis*-*Sophophora*, and *Paradrosophila*-*subtilis*-*Dorsilo-*

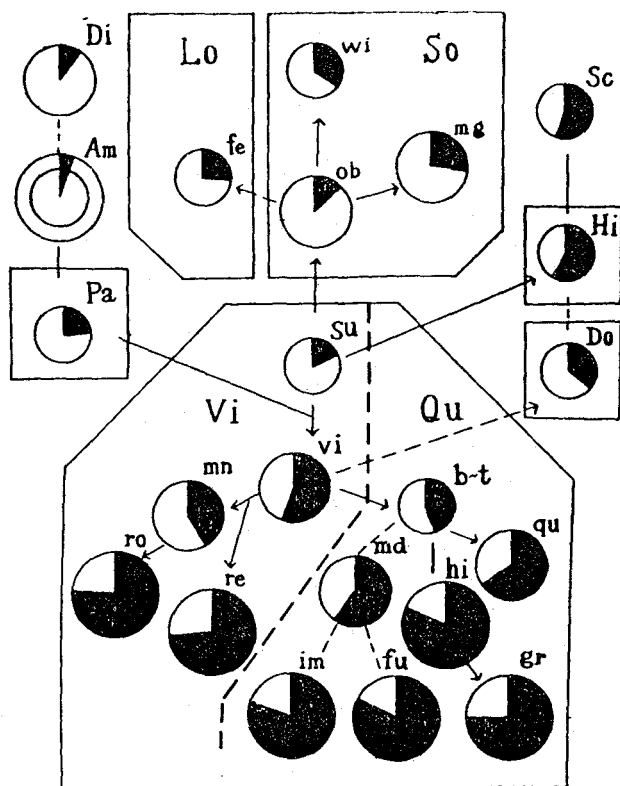


Fig. 9. Cladogenetic differentiation of Drosophilidae, to show interrelation of the degrees of compensatory development (shown black) and body sizes (shown by the size of circle: about 1.5, 2.5 and 3.5 mm in length by the small, median and large circles, respectively). In the genus *Amiota* (Am), a large circle indicates the subgenus *Phortica* and a small one the subgenus *Amiota*. Abbreviations see Table 1.

pha, *Hirtodrosophila* or *Scaptomyza*. This trend can be ascribed to tachytely of Simpson. Retention of comparatively small body size in spite of high structural complexity in this trend suggests the occurrence of *acceleration* in the early developmental stages during ontogeny, as this is thought by Newell (1949) to be a reverse phenomenon of *size increase*. Actually even the first instar larvae of the advanced forms in these lines are often possessed by highly developed mouth hook dentitions, presumably preadapted to the hard food media, toadstools (Okada, 1963).

The subgenus *Paradrosophila* has been thought to be the most unspecialized and primitive taxon among the genus *Drosophila* (Okada, 1956; Throckmorton, 1962_{1,2}),

being simple in various morphological and biochemical features and small in body size. It shows, moreover, extensive plasticity in some characters as the number of egg filaments (0, 1, 3, 6 to 10 according to species or to individuals. Kikkawa and Peng, 1938; Sturtevant, 1942; Patterson 1943; Wheeler, 1949; Burla, 1954). It has also some features common to Steganinae, e. g., larval skipping nature, pre-scutellar bristles, and well developed first abdominal sternite of male in some species (Wheeler, 1960). Occurrence of these features suggests *Paradrosophila* to be archaic or common ancestral between Drosophilinae and Steganinae, and possession of simple and plastic structures as well as small body size indicates high potentiality of evolution, as explained by Cope's Rule of Unspecialized and by the principle of heterozygosity (Throckmorton, 1962₁). Again the present state of subgeneric splitting of the genus *Drosophila* should have originated from the ancestor, like *Paradrosophila*.

The phyletic structural complexity may fundamentally include two different processes, the one is complication due to material increase and the other is complication due to material compensation. The structural complexity can be attained without compensation if the body size shows phyletic increase (the second trend), while the process of compensation is inevitable for the structural complexity in case the body size remains unchanged (the third trend). Furthermore, neither

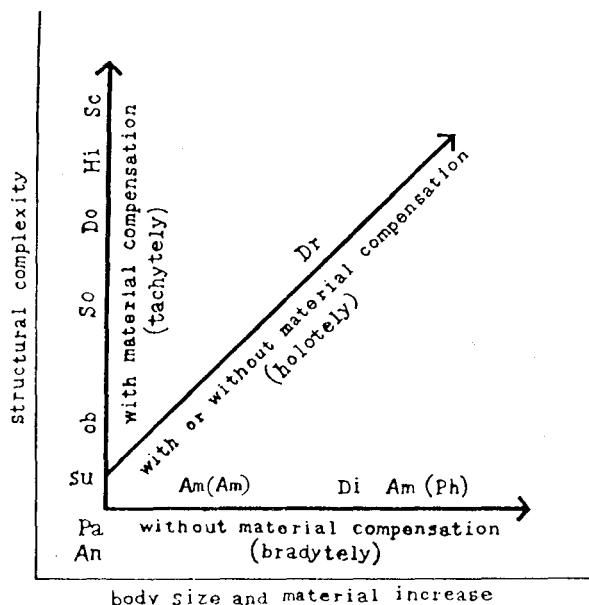
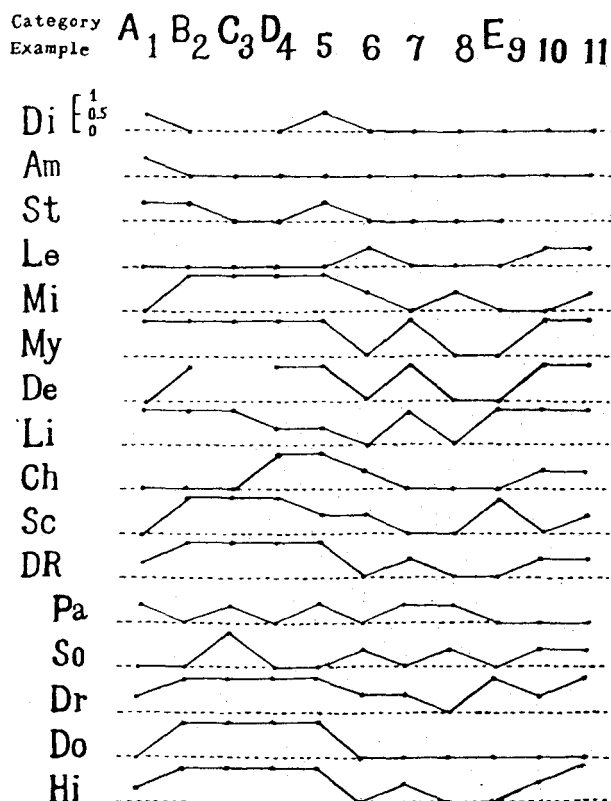


Fig. 10. Three trends of cladogenetic differentiation of Drosophilidae in relation to structural complexity, body size and material increase, and quantitative compensatory development. An. Presumed ancestral form. Other abbreviations see Table 1.



Figs. 11 Qualitative compensatory development of Drosophilidae, to show interrelation of genera and subgenera. The degree of compensatory development in the examples (1-11) of five categories (A-E) of material compensation are expressed by the height of graphs (low, median and high in accordance with 0, 0.5 and 1 in the degrees, respectively). Abbreviations see Table 1.

the phyletic size increase nor the material increase does necessarily follow structural complexity (the first trend). The Figure 10 shows cladogenetic sequences of these three presumed phylogenetic trends in view of body size and material increase, structural complexity and material compensation.

6. Qualitative aspect of specialization in relation to material compensation

Quantitative analysis does not always explain real interrelationships of the taxa,

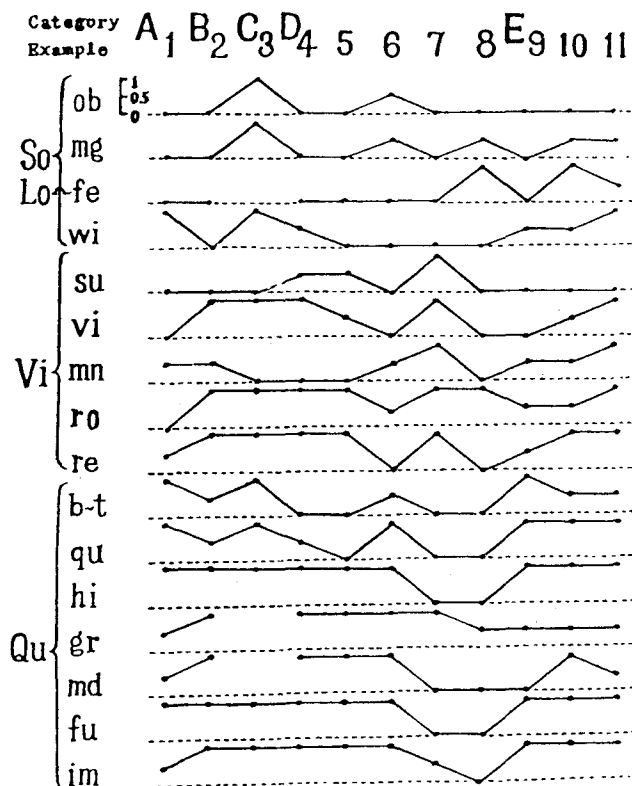


Fig. 12. Qualitative compensatory development of *Drosophilidae*, to show interrelation of species groups. Further explanation see Fig. 11.

as often much diverged taxonomic groups may take very similar total quantitative values. In such cases every character should qualitatively be examined and compared.

The degree of compensatory development differs according to the characters adopted as examples as well as to different taxa among *Drosophilidae*, in such way that each taxon takes characteristic combination of degrees. Comparison of the combination of degrees renders it possible to find qualitative relationships between taxa, and for this purpose the degrees determined, as shown in Table 2, are diagrammatically illustrated in Figures 11 and 12. The data for some genera, not referred to in this table but obtained by similar analysis, are also given in the former figure. The cladogenetic differentiation of the taxa into various combinations of degrees indicated by these figures will be found well coordinated with the current systematic grouping of the taxa, as briefly explained below.

In the subgenus *Sophophora*, the *obscura* group is directly connected with the *melanogaster* group, while the *willistoni* group is somewhat different from the former two. The subgenus *Lordiphosa* is best placed near *Sophophora*, but is somewhat different from any group of the latter subgenus. In the subgenus *Drosophila*, the *virilis* and *quinaria* sections belong to different alleys; the difference may be clearly seen in the diagram especially at the portion corresponding to the examples 6, 7 and 8. In the *virilis* section the *subtilis* group seems to be closely connected with the *robusta-repleta* line. In the *quinaria* section the *bizonata-testacea* complex is directly connected with the *quinaria* group, just as the *histrion* with the *funeraria* group; *grandis* group is shown to occupy unique post in this section. As suggested by the present author (Okada, 1956), the genus *Drosophila* is divisible into two groups, the subgenera *Paradrosophila*, *Sophophora* and *Lordiphosa* in one group and the subgenera *Dorsilopha*, *Hirtodrosophila* and *Drosophila* s. str. in the other. In the subfamily Steganinae, *Aniota* resembles *Stegana*, which in turn, is related to *Leucophenga*. In the subfamily Drosophilinae, *Microdrosophila* is considerably apart from the other genera; *Mycodrosophila*, *Dettopsomyia* and *Liodrosophila* are mutually related and are connected also with the *virilis* section; *Chymomyza* shows some resemblance to *Scaptomyza*, and these two genera seem to be related to the *quinaria* section.

The author wishes to acknowledge his thanks to Dr. Daigoro Moriwaki, Dean of the Faculty of Science, Tokyo Metropolitan University, for his kind suggestions given in the present work. His sincere thanks are also due to Dr. Ichiro Iiyasaka, former President of Shimane University, who has been taking trouble of reading the manuscript.

Summary

Bearing of the phenomenon of the compensation of body material upon the specialization phase of cladogenetic differentiation is discussed on the basis of various morphological characters possessed by the different taxa of Drosophilidae. The examples of the phenomenon revealed by these morphological characters are grouped into five categories (A-E). A. Compensation between different organs or parts of organ with different functions. B. Between different organs or parts of organs with the same function. C. Between the elements of meristic organs. D. Between different portions of one and the same organ. E. Between length and width of the same portion of an organ. The examples chosen are proved mostly to have adaptive significance, which must be a factor to lead the cladogenetic changes of the taxa canalized into three different trends in view of the sequences of body size increase, structural complexity and material compensation.

The first trend. Body size increase not combined with structural complexity and compensatory development (bradytely).

The second trend. Body size increase combined with structural complexity and, if not always, with compensatory development (holotely).

The third trend. Structural complexity not combined with body size increase, but inevitably combined with compensatory development (tachytely).

Qualitative combination of the degrees of compensatory development in the examples chosen provides the taxa with phylogenetic interrelation, which agrees fairly well with the current systematic relationships. The subgenus *Paradrosophila* is thought to be located at the base of these three trends and nearest the presumed ancestral stock, as the components of this subgenus are small in body size, simple in structural types, low in the degree of material compensation, and, moreover, possessed by some features intermediate between Steganinae and Drosophilinae of the family Drosophilidae.

References

- Allee, W. C., A. E. Emerson, Th. Park and K. P. Schmidt 1949. Principles of animal ecology. Saunders, Philadelphia.
- Basden, E. B. 1961. Type collections of Drosophilidae. 1. The Strobl collection. Beiträge zur Entom., 11: 160-224.
- Burla, H. 1954. Zur Kenntnis der Drosophiliden der Elfenbeinküste (Französisch West-Africa). Rev. Suis. Zool., 61 (Suppl.): 1-218.
- Dobzhansky, Th. 1951. Genetics and the origin of species. 3d ed. Columbia Univ. Press, New York.
- Eggers, R. 1939. Phyletische Korrelation bei der Flügenderreduktion von Lepidopteren. 7th Internation. Kongr. Entom., Berlin (1938): 694-711.
- Haldane, J. B. S. 1932. The causes of evolution. Harper, New York and London.
- Haldane, J. B. S. and J. Huxley 1927. Animal biology. Clarendon, Oxford.
- Hsu, T. C. 1949. The external genital apparatus of male Drosophilidae in relation to systematics. Univ. Texas Publ., 4920: 80-142.
- Huxley, J. S. and G. Teissier 1936. Terminology of relative growth. Nature, 137: 780-781.
- Kikkawa, H. and F. T. Peng 1938. *Drosophila* species of Japan and adjacent localities. Japan. Journ. Zool., 7: 507-552.
- Lull, R. S. 1948. Organic evolution (rev. ed.), MacMillan, New York.
- Mather, W. B. 1955. The genus *Drosophila* (Diptera) in Eastern Queensland. I. Taxonomy. Austral. Journ. Zool., 3: 545-582.
- Mayr, E. 1942. Systematics and the origin of species from the viewpoint of a zoologist. Columbia Univ. Press, New York.
- Michener, C. D. and R. Sokal 1957. A quantitative approach to a problem in classification. Evolution, 11: 130-162.
- Nater, H. 1950. Der Samenpumpen-Sklerit von *Drosophila* als taxonomisches Merkmal. Arch. Jul. Klaus-Stift. Vererbungsforch., 25: 623-625.
- Newell, N. D. 1949. Phyletic size increase, an important trend illustrated by fossil invertebrates. Evolution, 3: 103-124.
- Okada, T. 1953. Comparative morphology of the drosophilid flies III. The "Phallosomal index" and its relation with systematics. Zool. Mag., 62: 278-283.
- 1954₁. Ibid. I. Phallic organs of the *melanogaster* group. Kontyû, 22: 26-46.
- 1954₂. Ibid. VI. Rectal papillae, their number, arrangement and shape. Zool. Mag., 63: 257-265.

- 1935₁. Ibid. II. Phallic organs of the subgenus *Drosophila*. Kontyû, 23: 97-104.
- 1955₂. Ibid. VII. The Malpighian tubes of the adult flies. Zool. Mag., 64: 108-112.
1958. Ibid. VIII. Ejaculatory caeca of the adult flies. Ibid., 67: 264-271.
1961. Ibid. IX. Differentiation of the ejaculatory apodeme in view of systematic relationships. Ibid., 70: 253-258.
1956. Systematic study of Drosophilidae and allied families of Japan. Gihôdo, Tokyo.
- 1960₁. The genus *Microdrosophila* Malloch from Japan (Diptera, Drosophilidae). Kontyû, 28: 211-222.
- 1960₂. Allomorphosis of the wing-veins vs. wing-membrane in insects. Natur. Sci. Rep. Ochanomizu Univ., 11: 35-50.
1963. Caenogenetic differentiation of mouth hooks in drosophilid larvae. Evolution (in press).
- Patterson, J. T. 1943. The Drosophilidae of the Southwest. Univ. Texas Publ., 4313: 7-214.
- Patterson, J. T. and W. S. Stone 1952. Evolution in the genus *Drosophila*. MacMillan, New York.
- Rensch, B. 1948. Histological changes correlated with evolutionary change of body size. Evolution, 2: 218-230.
1954. Neuere Probleme der Abstammungslehre. Ferdinand Enke, Stuttgart.
1960. Evolution above the species level. Columbia Univ. Press, New York.
- Rosenblad, L. E. 1941. Description of ejaculatory sac diverticula in certain Drosophilidae. Amer. Natur., 75: 285-288.
- Simpson, G. G. 1953. The major features of evolution. Columbia Univ. Press, New York.
1961. Principles of animal taxonomy. Columbia Univ. Press, New York.
- Sneath, P. H. A. 1961. Recent development in theoretical and quantitative taxonomy. Syst. Zool., 10: 118-139.
- Sturtevant, A. H. 1942. The classification of the genus *Drosophila*, with descriptions of nine new species. Univ. Texas Publ., 4213: 5-51.
- Throckmorton, L. H. 1962₁. The problem of phylogeny in the genus *Drosophila*. Ibid., 6205: 207-243.
- 1962₂. The use of biochemical characteristics for the study of problems of taxonomy and evolution in the genus *Drosophila*. Ibid., 6205: 415-487.
- Wheeler, M. R. 1949. The subgenus *Pholadoris* (*Drosophila*) with descriptions of two new species. Ibid., 4920: 143-156.
1952. The Drosophilidae of the Nearctic Region, exclusive of the genus *Drosophila*. Ibid., 5204: 162-218.
1960. Sternite modification in males of the Drosophilidae (Diptera). Anal. Entom. Soc. America, 53: 133-137.
- Wheeler, W. M. 1893. The primitive number of Malpighian vessels in insects. Psyche, 6: 478-564.