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## HISTOLOGICAL CHANGES CORRELATED WITH EVOLUTIONARY CHANGES OF BODY SIZE

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### I. ALLOMETRY IN EMBRYOLOGY AND IN EVOLUTION

Nearly all evolutionary changes of species are accompanied by changes in body size. In very many cases a successive enlargement of body size takes place in phylogeny, a phenomenon known as Cope's Rule. This rule holds good especially for vertebrates, but for many groups of invertebrates as well (Cope, 1884, 1896; Déperét, 1907; Rensch, 1943, 1947). In other cases, chiefly among small insects, reductions of body size have taken place during evolution and are correlated with the reduction of certain normal structures, e.g., the wing veins. But in whatever direction the changes of body size occur, they are accompanied by alterations in the proportions of some organs and structures. This fact was partly known to G. Galilei (1618, p. 559). It was confirmed by B. Robinson (1748) with regard to the relative size of the heart, and by A. von Haller (1762) with regard to the relative size of the brain and eyes. These are organs that become relatively smaller with increasing body size. C. Bergmann (1847, 1852) gave a causal explanation of these changes of proportions by pointing out that organs which function as surfaces (such as epidermis, intestine, lungs) increase in growing organisms as the square, while the bulk of the body is cubed. Recently these problems were thoroughly analyzed by D'Arcy Thompson (1917), Klatt and Vorsteher (1923) and especially by J. Huxley (1932). Following Huxley we now speak of positive allometric growth when an organ grows more rapidly than the whole body, and of negative allometric growth when it grows more slowly.

During the postnatal development of a bird, the growth of brain and eyes, for instance, is negatively allometric, i.e., at birth they are relatively much larger than in adulthood, whereas the growth of bills and legs is positively allometric.

The proportion of an organ to the rest of the body may thus shift allometrically either during ontogeny or during phylogeny. If definite growth gradients are inherited, an increase of body size in a line of descent must be accompanied by large alterations in the proportions of parts of the body. Many orthogenetic changes of organs and many excessive characters can thus be interpreted (Huxley, 1932), provided there is a selective advantage in a steady alteration of body size. I believe I have shown the great probability of such a directed selection in lines of descent showing increasing body size (Rensch, 1947). It seems to be of great importance to point out that natural selection often acts primarily on body size and only secondarily on single organs. As a consequence, the proportions of the organs are changed. In cases of great size differences this may lead to a transformation of the structure of the whole body. It is therefore very important to study allometric growth in all groups of animals during ontogeny as well as phylogeny. Studies of growth gradients during ontogeny were made especially by J. Huxley and his school, first with the carapace and legs of Crustacea but later with many other characters of animals and plants. Though these embryological investigations have yielded copious quantitative data, they consist so far only of selected examples which show the applicability of the principle of allo-



metry to various morphological and physiological researches. Eventually, however, all characters utilized in embryological, evolutionary, and taxonomic research will need such an analysis.

When applying the rules of allometry to a phylogenetic problem, it must be carefully determined in each case if the evolutionary change of size is caused merely by a prolongation or abbreviation of ontogenetic development. According to my experience, shifts in proportions are not always produced in this manner. The relative length of intestine among homeothermic animals, for instance, is greater in larger than in related smaller species (of corresponding habits), although growth of the intestine is negatively allometric during the last postnatal phase (Rensch, in press). Furthermore, the hairs of mammals and the feathers of birds are relatively shorter (at the same season) in large species than in related smaller ones, although in these cases characters of marked positive allometry are involved. Also, hairs of larger rodents, like rats, consist of several rows of cells, whereas hairs of mice have only a single row. This also shows that the hairs of rats cannot be considered merely as allometrically enlarged hairs of mice. Thus, not all phylogenetic changes of size occur along allometric gradients.

It has been shown, moreover (Rensch, 1947, p. 140), that the curves which represent the growth gradients of large species in a system of coordinates are not simply the continuation of the curves of related small species (as would have to be the case if the growth ratios remained constant). Rather, they run parallel or even form different (in smaller species mostly steeper) angles with the abscissa. In such cases, therefore, only the allometric trend remains the same (e.g., negatively allometric). The available data indicate the general rule that large species are not merely allometric alterations of related smaller species. It appears therefore certain that natural selection controls not only body size as a whole but also

individual growth gradients. When analyzing evolutionary changes of body size, we must determine for each organ the portion of the change that is due to allometric growth, and the portion that is due to special selective factors.

Theoretically, there exist several possibilities. (1) The growth ratios may have remained constant during the evolutionary change of body size, but those variants which begin with a higher initial value (e.g., with a larger first *anlage* of the organ) have been preserved by natural selection (fig. 1A). (2) The allometric trend may be altered, that is to say, a positively allometric growth gradient may ascend more steeply (fig. 1C), or a negatively allometric growth gradient may drop more slowly (fig. 1B). (3) While the allometric conditions of the last postnatal period of growth may remain the same (e.g., negative allometry), this period may be preceded by a prolongation or an intensification of an earlier period of positive allometric growth (fig. 1D). It is well known that in many growing organs a repeated change of positive and negative allometry takes place during development. This third case with its different variations seems to be common, as many organs show periods of accelerated

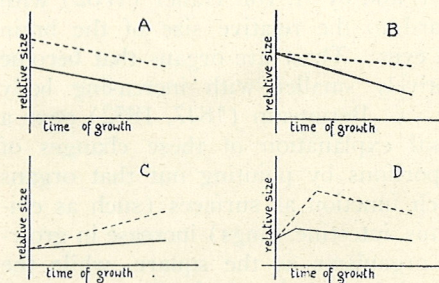


FIG. 1. Four different possibilities of embryological changes which result in the same relative enlargement of an organ. Solid line: curve of allometric growth (e.g., organ in per cent of body size) of the ancestor; dotted line: of the enlarged descendant. A. Increased initial size. B. Decrease of negatively allometric growth. C. Increase of positively allometric growth. D. Increase only of initial period of positively allometric growth.

embryonic growth. For instance, the eyes and the nervous apparatus connected with them show accelerated growth shortly before the young animal opens the eyes. The relative length and intensity of this period may have a greater effect on final size than the subsequent negatively allometric period. (4) Finally, the above mentioned three possibilities may be combined in various ways. A causal analysis of evolutionary variations in growth requires therefore detailed embryological researches.

Further questions arise in applying the principle of allometry to histological structures of related species of different body size. It is to be expected that tissue structure too will change markedly owing to the interaction of gradients of different rates of growth, and that this may lead to a decided change in the function of an organ. The present paper consists of a short presentation of three problems from this field, the study of which we have begun in the Zoological Institute of the University of Münster: (1) the (largely) allometrically caused formation of new histological structures in species with enlarged body size, (2) the reduction of histological structures to the indispensable components when body size is reduced to the lower evolutionary limit, and

(3) the alterations of structure, taking place in very small species in order to compensate for other disadvantages of structure. The following account is based primarily on the investigations of three of my students: W. Partmann, H. Goossen, and K. W. Harde. Some of these problems have been treated already in my recent book (Rensch, 1947).

## 2. CHANGE OF HISTOLOGICAL STRUCTURE CORRELATED WITH EVOLUTIONARY INCREASE OF BODY SIZE

In the case of so-called permanent tissues ("Dauergewebe"), the differences between closely related large and small species are due to differences in cell size and not to changes in cell number. In these cases the cells lose their capacity for division early with the result that there often exists a constancy of cell number (eutely), e.g., in a ganglion. In extremely large animals this results in the production of giant nerve cells with a peculiar lobulated, fenestrated or sponge-like outer zone (so-called paraphytes), as described by G. Levi (1925). On the contrary, in tissues in which the cells continue to divide, the difference in the size of cells between large and small species is usually insignificant. In these

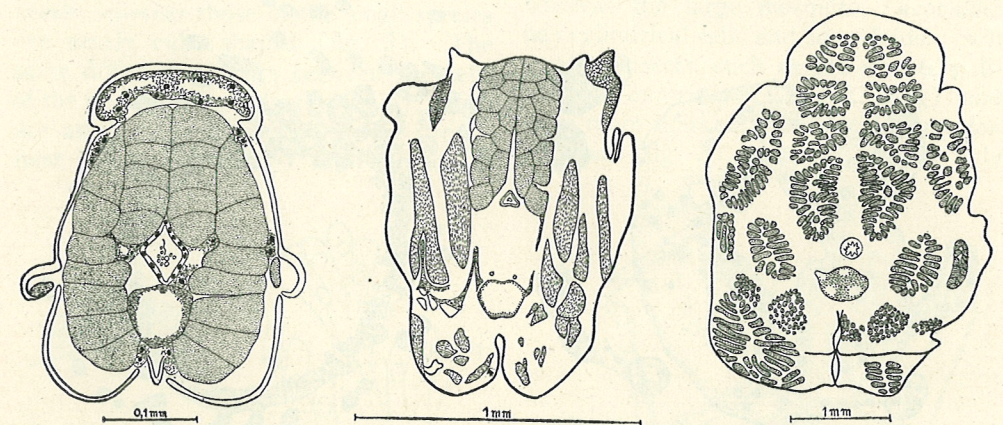


FIG. 2. Homologous transverse sections through the thorax of three Nematocera (Diptera) of different sizes showing the change of structure in the flight muscles (dotted). (Ventral cord of the nervous system coarsely dotted, light inside.) Left, *Contarinia* spec.; middle, *Culex pipiens*; right, *Ctenophora atrata* (after Partmann).



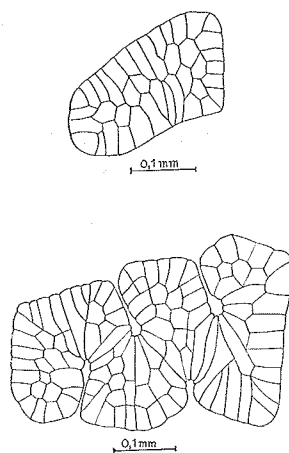


FIG. 3. Transverse sections of the second dorsal longitudinal muscle in two Cyclorapha (Diptera) of different sizes. Upper: *Musca domestica*; lower: *Eristalomyia tenax* with intramuscular folds (after Partmann).

instances the organs differ principally in the number of cells.

#### Flight Muscles

If certain tissues of small animals are composed of relatively few cells, an increase in the number of cells occasionally alters the possibilities of providing these tissues with nutriment and oxygen. This

is particularly the case with the flight muscles of insects. In this group of animals, in which a closed system of blood vessels is absent, too great an increase in the number of muscle fibers would produce compact bundles, the inner parts of which could not be nourished efficiently. In larger species therefore a new histological structure is developed; the flight muscles lose their compact structure and are divided into many bundles. This is illustrated in figure 2 by homologous transverse sections of three Nematocera (Diptera) of different size (based on the work of W. Partmann). The minute gall-midge *Contarinia* (1.5 mm. long) has compact musculature in comparison to the mosquito *Culex* and the large crane-fly *Ctenophora* (29.5 mm. long), both of which show a strong parcelling of the muscle fibers. In the figure the transverse sections of the three different sized species of Diptera are shown at equal size. Actually the individual muscle packages of *Ctenophora* are larger than those of *Contarinia*. Among other flies Partmann found similar conditions, but in the large species *Eristalomyia*, for instance, the individual muscle packages are loosened up in a very different manner by the development of a novel and hitherto not yet ob-

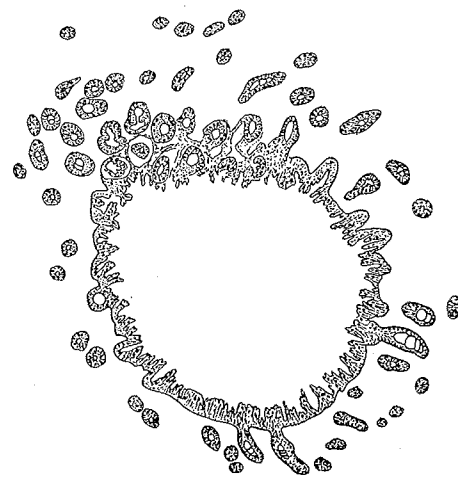
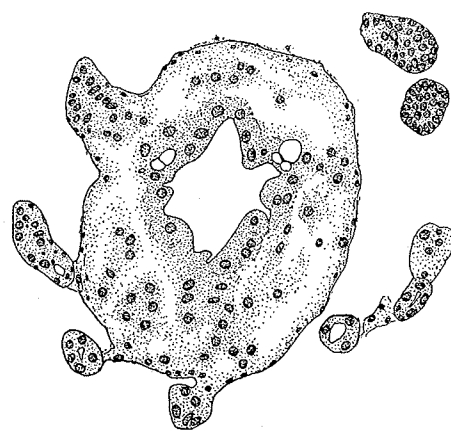


FIG. 4. Transverse sections through homologous parts of the mid-intestine in Dytiscidae of different sizes. Left: *Laccophilus obscurus*; right: *Dytiscus marginalis*.

served type of structure. The muscles are folded into a series of longitudinal pleats between which branches of the tracheal system enter (fig. 3).

#### Intestinal Cells

The intestine of the Diptera follows a rule which is valid for all animals; in large animals it is not only absolutely but also relatively longer than in small animals. Except for those Nematocera (Diptera) that have a straight intestine, this lengthening is combined with an increase in the number of loops (W. Partmann), the origin of which can be traced to special growth centers. Furthermore, the surface of the intestine is increased in large insects by the formation of more folds in the intestinal wall. Figure 4 shows this difference between a large and small species of Dytiscidae (water beetles). To facilitate comparison the transverse sections are drawn at equal size. In this manner the cell nuclei of the large *Dytiscus* are reduced to points, but it can easily be seen that the interior surface of the intestine is divided by many fine folds, whereas in the small *Laccophilus* the lumen shows only a few coarse folds.

This difference is, in part, caused by the fact that the intestinal cells are long cylindrical or club-shaped in the large beetle, whereas those of the small species are nearly cube shaped (fig. 5). The same difference occurs between the cells of the mid-intestinal glands (fig. 6), which are attached to the intestine like prominent humps or tubes. The number of

glands of the middle intestine is much higher in the large species than in the small one; figure 4 shows in the former case 64, in the latter case only 8 sectioned gland tubes. The marked elongation of the cell form of large species can also be

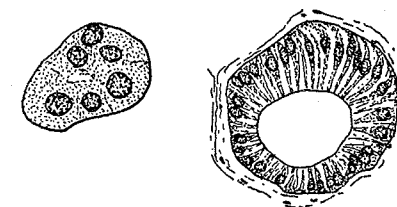


FIG. 6. Transverse sections through the glands of the mid-intestine in Dytiscidae of different sizes. Left: *Laccophilus obscurus*; right: *Dytiscus marginalis*.

seen if we compare two related beetles of the family of Scarabaeidae: the large *Geotrupes stercorosus* (10–16 mm. long) has cells of a similar slender form to those of the large water beetle in its middle intestine, the small *Melanopterius punctatosulcatus* (4–6.2 mm. long), on the other hand, has stouter intestinal cells. This rule of folds and of cell form is equally valid among the Diptera according to W. Partmann's investigations. The small dark-winged fungus gnat *Lycoria* shows cuboid cells in the middle intestine, whereas the large mosquito *Theobaldia* has cylindrical cells and some folds. Still smaller insects, such as the minute gall-midge *Contarinia* (1.5 mm. long) and even more markedly the aphid *Phoradon persicae* (fig. 7), have in general only

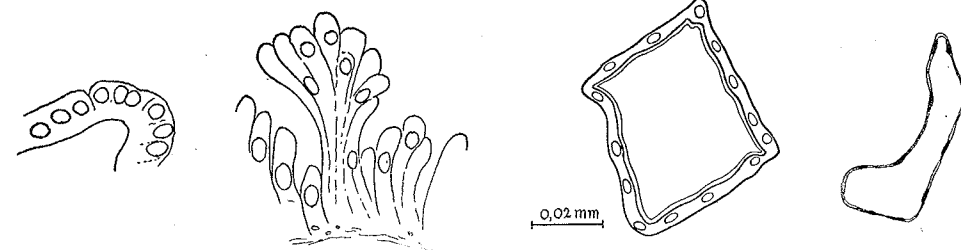


FIG. 5. Cells of the mid-intestine of two Dytiscidae of different sizes. Left: *Laccophilus obscurus*; right: *Dytiscus marginalis*.

FIG. 7. Transverse sections through the anterior mid-intestine of very small insects. Left: gall-midge *Contarinia* spec. (after Partmann); right: aphid *Phoradon persicae*.

pavement epithelium in the middle intestine.

Since the ontogenetic development of the intestinal epithelium begins with flat or cubic cells which tend later to attain cylindrical shape, the assumption is obvious that development is terminated precociously in very small species (Partmann). And conversely, since a special growth gradient is actively stretching the intestinal cells in a longitudinal direction, the evolutionary increase in size of an insect produces very slender cells, and the epithelium and the glands of the middle intestine become thus quite another type of structure. Evolution in such cases represents an "addition to the final stages," an "anaboly" in the sense of Sewertzoff (1931). [The longitudinal direction of growth is probably affected mechanically by the mutual pressure of the neighboring cells.]

#### The Nervous System in Insects

Of special importance are the changes of histological structure in the central nervous systems. Here again the same rule is apparently valid for the whole animal kingdom. In all groups (with simi-

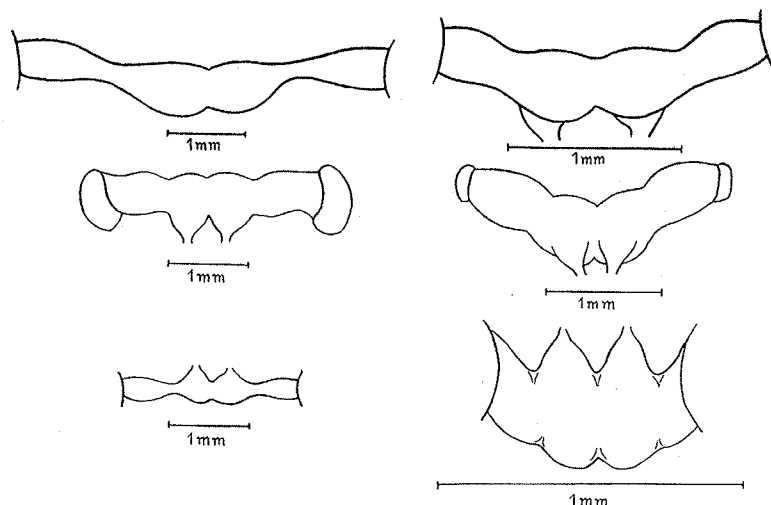


FIG. 8. Shape of brains in beetles of different sizes. Pairs of species of the same family. Large sized species on the left. Above, Dytiscidae: left, *Dytiscus marginalis*; right, *Ilybius fenestratus*. Middle, Scarabaeidae: left, *Melolontha vulgaris*; right, *Phyllopertha horticola*. Below, Carabidae: left, *Carabus nemoralis*; right, *Argutor diligens* (after Goossen).

lar modes of life) the large species have relatively smaller brains than related smaller species. This has long been known for vertebrates as Haller's Rule, but H. Goossen has recently pointed out that the same correlation is valid for insects. For example, the cockchafer *Melolontha vulgaris* (body length 23 mm.) has a brain weight of 5 per mille of the body weight. In the related but smaller beetle *Phyllopertha horticola* (body length 9.2 mm.) the brain weight is 28.8 per mille of the body weight. The larger brains also show different proportions. They are less compact and the optic lobes are relatively more slender and longer. Since in larger species the brain occupies less space in the head capsule, the optic lobes are extended in a nearly straight line, whereas in small species they are stouter and form an angle (fig. 8). The three optic masses (lamina ganglionaris, medulla externa, and medulla interna), which are in close proximity in small species, move apart in larger species. In the small aphid *Phoradon persicae* they are especially tightly pressed together.

The most pronounced histological

changes are shown by those parts of the brain which among insects are commonly regarded as an index for the degree of complication of the nervous processes and thus for the psychic qualities, namely the corpora pedunculata. As H. Goossen could show, these organs are not only relatively larger in large species, but the various growth gradients determining their shape must have also a different rate, for the corpora pedunculata of large species are much more differentiated and

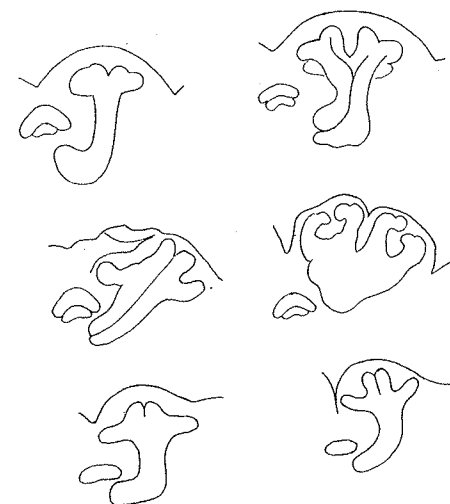


FIG. 9. Maximum sections through the corpora pedunculata and the central bodies of different sized insects of three families. Above, Scarabaeidae: left, *Phyllopertha horticola*; right, *Melolontha vulgaris*. Middle, Vespidae: left, *Ancristocerus parietinus*; right, *Vespa crabro* (after Goossen, transformed). Below, Blattidae: left, *Blatta orientalis*; right, *Periplaneta americana* (after Bretschneider and Hanström from Goossen).

have a richer surface than those of related smaller species (fig. 9). The much discussed shape differentiations depend therefore not only on the evolutionary level of an insect group, as is generally assumed, but to a considerable degree also on body size. Calculating the upper line of delimitation of the corpora pedunculata (on the largest horizontal sections) in per cent of half the width of the protocerebrum, the following values (after Goos-

sen) are found among comparable large and small species of Coleoptera and Hymenoptera:

TABLE 1

Species pairs	Body length	Relative size of corpora pedunculata
<i>Carabus nemoralis</i> <i>Agonum muelleri</i>	20.0 mm. 6.6 mm.	102.0 per cent 39.4 per cent
<i>Hydrous piceus</i> <i>Hydrophilus caraboides</i>	42.4 mm. 15.9 mm.	93.1 per cent 36.5 per cent
<i>Melolontha vulgaris</i> <i>Phyllopertha horticola</i>	22.0 mm. 9.4 mm.	195.8 per cent 96.6 per cent
<i>Vespa crabro</i> <i>Ancristocerus parietinus</i>	22.2 mm. 6.2 mm.	339.0 per cent 212.7 per cent

In addition to this enlargement of the surface, there is also an increase in the number of globuli cells. The corpora pedunculata are thus a part of the brain which does not have a constant cell number even during short steps of evolution. This is illustrated by the following figures:

TABLE 2

Species pairs	Body length	Number of nuclei of globuli cells
<i>Dytiscus marginalis</i> <i>Ilybius fenestratus</i>	27 mm. 12 mm.	615 188
<i>Melolontha vulgaris</i> <i>Phyllopertha horticola</i>	20.6 mm. 9.9 mm.	1176 624
<i>Vespa crabro</i> <i>Ancristocerus parietinus</i>	22.2 mm. 7.9 mm.	1009 500
<i>Bombus lapidarius</i> <i>Andrena vulgaris</i>	17.8 mm. 6.2 mm.	811 545

Finally, it may be mentioned that the size of the central body in the brain of insects is inverse to that of the corpora pedunculata, therefore relatively smaller in large species. Its diameter, calculated in per cent of half the width of the protocerebrum, is, for example, in *Carabus nemoralis* (body length 20.8) 46.3 per cent, in *Agonum muelleri* (body length

6.6 mm.) 56.5 per cent; in *Melolontha vulgaris* (body length 216 mm.) 39.8 per cent, in *Phyllopertha horticola* (body length 9.9 mm.) 45.0 per cent, in *Vespa crabro* (body length 22.2 mm.) 30.8 per cent, in *Ancristocerus parietinus* (body length 6.6 mm.) 36.4 per cent.

#### The Brain of Vertebrates

Very similar conditions are found in the brain of vertebrates. The pallium of the forebrain is not only absolutely, but also relatively, larger in large species than in related small species, whereas in the latter the other parts, the so-called "brain stem," are relatively larger. Certain histologically definable areas of the cerebral cortex, which are known to have different functions, show a different development. R. Brummelkamp (1940) states that during the individual development of a mammal, such as the sheep, the histologically different areas grow isometrically so that the parts of the cortex do not show any shifting of proportions at different developmental stages of brain size. K. W. Harde of our Zoological Institute came to a different conclusion. He found that in white mice the large, distinctly circumscribed, histologically defined units, as well as also the smaller regions, show very different growth rates. The holo-

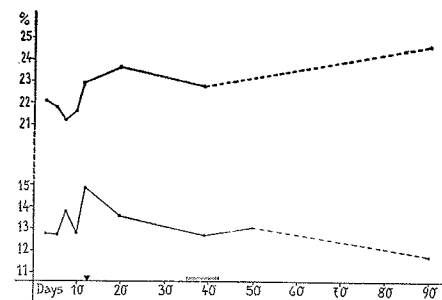


FIG. 10. Differences in growth rates of histologically defined regions in the brain of the white mouse. Relative surface values in per cent of the surface of the whole hemisphere. Upper: of the holocortex 2-stratificatus. Lower: of the holocortex 5-stratificatus. Wedge: day of opening the eyes. Grating: attainment of maturity (after K. W. Harde).

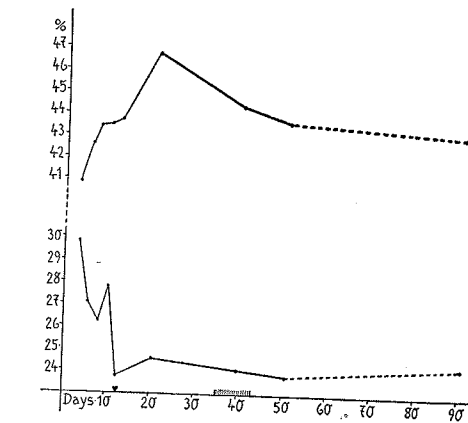


FIG. 11. Differences in growth rates of brain regions in the white mouse. Relative surface values in per cent of the whole semicortex. Upper: of the regio praepyramidalis. Lower: of the regio peramygdalaris (after K. W. Harde).

cortex 2-stratificatus (function of smelling), for example, shows negatively allometric growth in relation to the cortex of the whole hemisphere up to the tenth day of postnatal development, but then growth becomes positively allometric with an interruption between the twentieth and the fortieth day. The holocortex 5-stratificatus (motor functions), on the contrary, reaches its relative maximum size by the thirteenth day (average day for opening the eyes) and from then growth is negatively allometric in relation to the cortex of the whole hemisphere (fig. 10). The regio praepyramidalis and the regio peramygdalaris may be chosen as examples for differences in the allometry of different regions. Calculated in per cent of the whole semicortex, the former region shows a strong positive allometry up to the twentieth day, then a negative allometry. The regio peramygdalaris, on the contrary, has a distinctly negative (although dissimilar) allometry up to the thirteenth day (opening of the eyes) and then grows isometrically (fig. 11).

Similar growth rates of the brain regions occur also during evolution, as is evident from a comparison of the relative size of the same histological regions of adult specimens of the mouse, rat, and

rabbit. Most groups of areas of the holocortex 5-stratificatus show—according to the data of Gurewitsch et al. (1929)—a relative decrease in the rabbit compared with the rat, and in the rat compared with the mouse, corresponding to the prevailing negative allometry in mice pointed out by K. W. Harde. The areas 4 + 6 + 12 + 23 + 24 added together and calculated in per cent of the whole holocortex 5-stratificatus give the following results: mouse 23.5 per cent, rat 19.0 per cent, rabbit 16.4 per cent. The growth of areas 17 + 18, on the contrary, is positively allometric correlated with body size: mouse 7.1 per cent, rat 8.9 per cent, rabbit 14.5 per cent. A detailed comparison of the individual development of the forebrain of mouse and rat, using the methods of K. W. Harde, is now being undertaken by one of my students (Ch. Schulz). In this way it will be possible to estimate to what extent growth ratios have remained the same and how far evolutionary differentiations have taken place.

In any case, this much is already clear, that an isometrical growth of all histologically circumscribed regions of the forebrain occurs neither during individual development nor during evolution. On the contrary, owing to differences of the growth gradients, a marked alteration in the histological structure of the brain takes place if the body size is enlarged. The hypothesis of E. Dubois (1898, 1930), that the evolutionary increase of the forebrain occurs by jumps, each of which doubles the brain mass, is consequently very improbable.

A modified version of this hypothesis, proposed by Brummelkamp (1939), namely that smaller, so-called  $\sqrt{2}$ -jumps take place, seems likewise not to be in accord with the above-mentioned results. On the contrary, the alteration of the brain structure during the evolutionary increase occurs in a rather complicated manner and probably in different ways.

These findings on histological alterations of structure encourage speculation on the phylogenetic origin of new parts

of the brain, for example, new areas or new regions. A brain region which grows by positive allometry and therefore becomes relatively larger during the evolutionary increase of body size may become larger than its function requires. In that way, brain parts may arise which are available for new functions. Among such additional brain functions are to be mentioned particularly the more complicated associative integrations of the nervous impulses. The so-called associative centers of higher vertebrates may be such positively allometrical parts (although, of course, selection independent of the constant growth ratio may also be effective). Such an enlargement of an area may be accompanied by a new histological differentiation, as we have described above for the corpora pedunculata of insects. I consider it probable that especially the speech center, Broca's region, which has raised man in a decisive manner above the ape stage, may be one of these positively allometrical regions. An investigation of this problem is planned.

#### 3. REDUCTION TO THE INDISPENSABLE STRUCTURES IN VERY SMALL SPECIES

If an organism becomes smaller during evolution, this is connected with a reduction in the number of successive cell divisions in tissues the cells of which are permanently capable of division. The cells usually become only slightly smaller or not at all so, but their number becomes greatly reduced. As a consequence, many differentiations and sometimes even whole organs disappear if they are no longer able to function properly on account of their low cell number. This is particularly evident for the male copulatory organ of small land prosobranchs of the large family of Cyclophoridae. The diameter of the shell of most of the snails of this family exceeds one centimeter. A well developed penis is found in all these larger forms. In the small *Moulinia* species of southeastern Asia (shell length mostly 4–8 mm.) the penis is either rudimentary (*M. pellucidum*) or is lacking entirely (*M.*

*floresiana*) (Tielecke, 1939). In the still smaller species of *Diplommatina* (e.g., *D. schmidti*) it is likewise lacking. The small marine prosobranch *Caecum glabrum* (shell length 1 mm.) can survive without gills (Götze, 1938), as the diffusion distances are short and the relatively large surface of the foot is sufficient for breathing. Very small Turbellaria have no ramifications of the intestine (Rhabdocoela); very small Cestodes do not show ramifications of the uterus, etc.

In very small insects some segments of the tarsus have usually disappeared. Most larger Coleoptera, Diptera, Hymenoptera, Lepidoptera, etc. have five tarsal segments but the minute Thysanoptera have only one to two, the very small Zoraptera two, the Mallophaga one to two, the Siphunculata only one. Among the beetles the minute Ptiliidae (dwarf beetles, body length 0.25–1.4 mm.) have three tarsal segments, of which the first and the second are only indistinctly separated, and the same holds good for the equally small Sphaeriidae.

Such limitations determine, in many cases, the lower size limit of a group of animals. Most important in this respect is probably the limitation of egg number (Rensch, 1947). Since the size of eggs cannot be indefinitely reduced for ecological and cytological reasons, the smallest animals can often contain only one mature

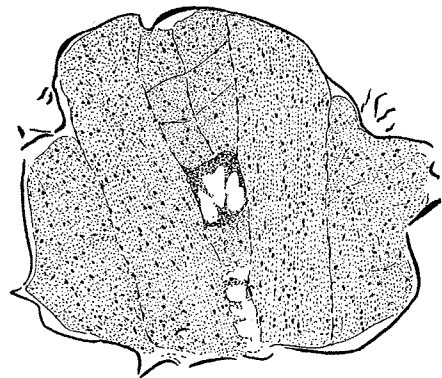


FIG. 12. Cross section through the thorax of the aphid *Phoradon persicae*. It is filled to capacity by flight muscles.

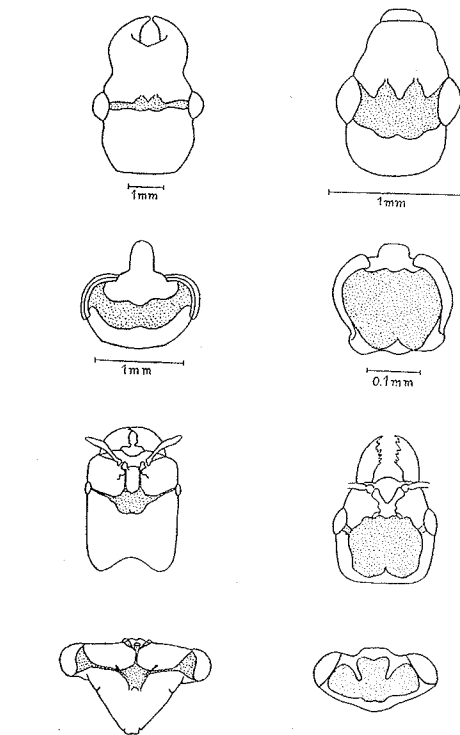


FIG. 13. Filling of the head case with brain in related species of different size. Top row, Carabidae: left, *Carabus nemoralis*; right, *Argutor diligens*. Second row, Nematocera: left, *Ctenophora atrata*; right, *Rhabdophaga heterobia* (after Goossen). Third row, Formicidae: left, *Pheidole instabilis*, soldier; right, worker (after Wheeler). Bottom row, Homoptera: left, *Cicada fraxinis* (after Berlese); right, *Phoradon persicae*.

egg in their uterus, e.g., the smallest Gastrotricha and Rotatoria, the minute marine prosobranch *Caecum glabrum*, and probably also the very small frog *Phyllobates limbatus* of Cuba. Only 1–2 eggs ripen simultaneously in very small land snails, e.g., species of *Vertigo*, *Punctum pygmaeum*, *Pyramidula rupestris*, etc. A further evolutionary decrease in size of such small animals is therefore not probable.

The lower limit of body size is controlled also by a maximum filling of the body with organs. As shown in figure 2, the thorax is completely filled with flight muscles in the smallest gall-midges (Ceci-

domyidae). The same occurs in small plant lice (Aphidae) (fig. 12), etc. The ventral cord of the nervous system and also the intestine occupy relatively much space in small species, whereas there is no space left for air sacs of the tracheal system. The head capsule of very small insects is almost completely occupied by the central nervous system, as shown in figure 13 for several groups of insects. Here too an even more extreme filling up of the head capsule, i.e., a continued evolutionary decrease of body size is improbable, inasmuch as even within the brain the individual masses are often strongly pressed together like the three optic masses mentioned above. A terminal stage of evolution among very small insects is also reached in respect to the shape of the intestinal cells. As figure 7 shows, the tendency of cell shortening has resulted in the smallest species in the development of a single layer of very flat cells. Thus, the lower limit of function is reached or probably already overstepped, for the middle intestine can now perhaps work only inefficiently, that is to say, may be suited only for a special type of food like that of the aphids.

In this manner the smallest known species of each group of animals are characterized by the most complete utilization of space in the body and by the reduction of the organs to the indispensable minimum.

#### 4. ALTERATIONS OF CONSTRUCTION AT THE LOWER LIMIT OF BODY SIZE

It is known that a more or less steady increase of body size has occurred (Cope's Rule) in the course of the evolution of many groups of animals and especially of vertebrates. Nevertheless, we may presume that a continued diminution of size offers selective advantages in the case of some already very small species because in this way still unoccupied niches of the habitat become accessible, or perhaps because the general advantages (more intensive metabolism, quicker succession of generations, etc.) are favorable. A further decrease of size has apparently taken

place sometimes in lines of descent in which the existing structures had already been reduced to a minimum. In such cases a change of construction is necessary. I have shown previously (1947, fig. 46) that the pelvis of very small mammals is modified by the temporary or constant opening of the symphysis of the pubis because in these very small species the young are relatively too large or too large-headed at birth to pass through a normally-shaped pelvis. On the same occasion I demonstrated (op. cit., figs. 47–48) that the cell layers of the retina are thickened in very small birds and mammals in order to make possible a sufficient resolution of the image in spite of the small size of the eye.

Similar changes of construction or function are found also in other cases. For instance, in very small insects, where the brain has only little room in the head capsule, the optic lobes are attached at an angle (figs. 8, 13). As the number of ommatidia of very small insects is low because the size of the cells cannot be indefinitely decreased, these species have a very limited capacity for seeing the configuration of the surroundings. The eyes therefore have become unimportant and changes of instinct may take place. The smallest workers of the ant *Atta sexdens*, which only have two to three ommatidia on each side, work nearly always in the dark interior of the nest, and they do not gather building material as do the larger workers (0.9–3.3 mm. long) (Goetsch, 1940).

The above described maximum filling of the thorax with flight muscles in small insects limits the decrease of the body size, but this limit too is overcome by a change of construction. Since the muscles, if further reduced, are no longer sufficient for flight, a mechanism for floating in the air was developed by long ciliated wings which enable the insect to make use of the viscosity of the air. Such fringes on the wings are found among the smallest species of very heterogeneous orders of insects; on the fore and hind wing of Thysanoptera (some species were cap-

tured by airplanes at great heights), in the small Hymenoptera *Alaptus* (Myrmecidae) and *Prestwichia* of only 0.2 mm. length (the latter floating also under water), in the smallest Zoraptera and Corrodentia, and at the hind wings of the dwarf beetles (Ptiliidae), point beetles (Clambidae), and Sphaeriidae of 0.3–1.5 mm. length, as well as on the wings of the smallest moths like *Lyonetia* (fig. 14), but in a less pronounced manner also among most of the other very small insects (e.g., among the Chrysomelidae in *Haltica*, among winged Pselaphidae,

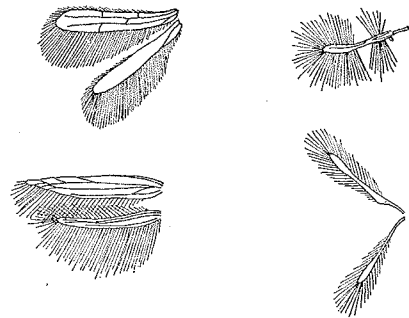


FIG. 14. Change of construction in very small insects: development of long ciliated wings. Above: left, *Aeolothrips fasciata* (Thysanoptera); right, *Oligella foveolata* (Coleoptera). Below: left, *Lyonetia* spec. (Lepidoptera); right, *Alaptus* spec. (Hymenoptera) (after Handlirsch and Sharp).

among the small Ichneumons, in the small Chalcididae, etc.).

The circulatory system of the smallest Archiannelids shows another interesting change of construction. The larger representatives of this group of worms (not distinctly separated from the Polychaeta), like *Protodrilus* (body length 1–20 mm., mostly more than 3–4 mm.), have a system of branched blood vessels like the Polychaeta. The genus *Nerilla* (1–2 mm. long) has developed a compact blood sinus, surrounding the stomach dorsally and laterally from which a vessel arises dorsally. This goes forward, bifurcates there, turns down to the ventral side, and reunites into a ventral vessel. The still

smaller *Dinophilus gyrotilatus* (0.7–1.3 mm. long) has only a blood sinus around the stomach and a ventral vessel in the region of the ovarium. Finally, in *Diurodrilus* (only 0.3 mm. long) the circulatory system has entirely disappeared. It is superfluous in such a small organism since diffusion alone can supply the needs of the tissues (Remane, 1932). In the microscopic Oligochaet *Aeolosoma* a parallel development took place, closely corresponding to the *Nerilla* type.

An interesting change of function occurs in the minute marine prosobranch *Caecum glabrum* (shell 1 mm. long). It does not move like other snails with the aid of contractions of the foot muscles, for these are strongly reduced as mentioned above, but solely by the stroke of ciliae (Götze, 1938).

Such changes of construction and of function must be considered as secondary consequences of the manifold histological alterations of structure connected with evolutionary increase or decrease of body size, partly owing to allometry, partly due to the directing effect of selection.

#### SUMMARY

1. The analysis of the alterations of proportion, connected with changes of body size, requires not only the examination of the growth gradients in development but also of the selective influences. A large species is not merely an allometrically changed version of its small ancestor.

2. Evolutionary changes of body size often produce accompanying obligatory histological alterations of structure. An increase of the body size thus produces in several cases new structures, a phenomenon demonstrated for the flight muscles, the middle intestine, and the brain of insects.

3. The differentiation and shape of the corpora pedunculata is not only an index of the evolutionary level of the insect species in question, but it also depends on the body size. The adjacent globuli cells are much more numerous in larger species.

4. In the vertebrate forebrain the histologically recognizable regions of the cortex have different growth ratios. The evolutionary increase in size (Cope's Rule) therefore causes a strong modification of brain structure.

5. In very small species of a group of animals some organs either disappear (e.g., the penis of very small land Prosobranchia, segments of the tarsus in certain insects), or are reduced to the minimum limits.

6. The lower limit of body size within a group of winged insects is in part controlled by the maximum filling of the thorax with flight muscles and of the head capsule with brain.

7. Changes of construction and of function that compensate for structural disadvantages of the minimum size may take place near the lower limit of body size. The development of long fringes on the wings of very small insects of several orders is an example of this phenomenon.

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