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Studies on the adaptive evolution of the larvae of *Trichoptera*

[Pp. 311—398, 33 text-figs.]

Studia nad ewolucją przystosowawczą larw chruścików *(Trichoptera)*

Изучение адаптационной эволюции личинок ручейников (*Trichoptera*)

Abstract: In the first part of this paper the author describes the stages of the adaptive evolution of the caddis larvae from the passage of the larvae of the caddisflies' ancestors from land to cold flowing waters, through the passage of the caddis larvae themselves from flowing to stagnant waters. to their return, via flowing waters, to the land environment. These considerations are based, in addition to structural characters, on the functional parameters found in experimentally induced responses as traces of old functions preserved in the present modes of behaviour. Cenogenetic adaptations have been recognized as modifications of the palingenetic adaptations in the evolution of caddisflies.

A relationship between the development of motor activity and that of the efficiency of the photoreceptors has been demonstrated in the second part of the paper. The developmental process of motor activity from asymmetrical uncompensatory movements to symmetrical compensatory ones, or to locomotion on a horizontal plane is described. The time parameters that have an effect on the origin and maintenance of a visual sensation have been determined, and their selective value in the process of natural selection has been established.

In the part given to the final conclusions the author presents his own interpretation of the adaptive process, and as its characteristics he mentions universality, multiformity, complementarity, feedback and symmetry in time. He reduces the adaptive processes in the historical development and the adaptations associated with the reception of information from environment to unity.

CONTENTS

PART ONE

1. Introduction

A specific mode of life has evolved in the adaptive process of insects as a result of the synchronization of the ontogenetic developmental cycle with the physical rhythms of the surroundings, which condition the normal course of the functions of particular developmental stages. A peculiar part falls to the larval stage, whose fundamental function is growth and accumulation of matter. In insects having complete metamorphosis (*Holometabola*) this function stops at the time of attainment of the pupal stage and in those with incomplete metamorphosis (*Hemimetabola*), when they reach the imaginal stage.

In modern opinions, the organism is an open system characterized by a non-stop interchange of substances with its surroundings (Bertalanffy, 1950, 1952). The inflow of substances from the environment exceeds their outflow in the period of growth, until the organism attains the stationary phase. The storage of energy is a basic physiological phenomenon, which makes the survival of the organism possible and forms reserves that mould its adaptive faculties. The exhaustion of these reserves, caused by unfavourable environmental changes which go beyond the tolerance of the system, leads to the loss of ecological position. Kožančikov (1937) pointed out that during the growth of an organism the consumption of energy increases evidently with deviations from the optimum conditions.

The vast diversity of adaptive capabilities of insects points at their possibilities to acquire and keep an ecological position. This is especially well seen in larvae, in which the inflow of substances from the environment prevails in the interchange and in this connection the constructive influence of the environment is greater than it is in the case of more conservative imagines, which are in the stationary phase. The adaptation of insects to life in water environment took place in early developmental stages, for there are no species among them whose imagines are aquatic and larvae terrestrial. The adaptive faculty of the larvae is therefore greater, which is also indicated by the great diversity of their adaptations.

Except for the members of the family *Xiphocentronidae* (STURM, 1960) and the genus *Enoicyla* RAMB. (*Limnephilidae*) (ULMER, 1903; HICKIN, 1958), which occur on moist mossy tree stumps or rocks, the caddis larvae live in various water environments, ranging from very turbulent ones, such as mountain torrents and waterfalls, to stagnant waters. Connected with this fact are their appropriate functional adaptations expressed by the mode of supplying their living requirements. The problem of the evolution of these adaptations is the object of the present study.

Its first part is theoretic in character and gives a synthesis of the facts drawn from literature with the results of the author's own studies and observations, included in the course of theoretic considerations. The second part presents a separate investigation, the purpose of which was to elucidate the relationship between the genesis of locomotive movements in the caddis larvae and their photoreception.

2. Origin and evolution of caddisflies

The most ancient fossil remains belonging to members of the order *Trichoptera* come from the Lower and Upper Lias of England (TILLYARD, 1933) and Germany (HANDLIRSCH, 1906—1908), the Rhaetic of Argentina (WIELAND, 1925) and the Lower Cretaceous of Mongolia (COCKERELL, 1924). They have been preserved in the form of imprints of wings, the venation of which very much resembles that of the most primitive modern families *Rhyacophilidae* and *Philopotamidae* (ROSS, 1956). The structure of the wings allowed the distinction of 24 species, grouped in 2 fossil families, *Necrotauliidae* and *Prosepididontidae* (FISCHER, 1960).

In the members of the fossil species, e. g. *Necrotaulius furcatus* (GIEBEL), there is no connection between the median vein M and cubital vein Cu_1 in the basal part of the wing, whereas in *Necrotaulius intermedius* HANDL. these veins are connected as in the recent species. In the Upper Triassic of Queensland (Australia) TILLYARD (1917) found remains of forewings with their longitudinal venation similar to that of the extinct caddisflies, but with a larger number of crossveins in the apical part. Basing himself on this discovery, he distinguished the family *Mesopsychidae*, containing two genera, *Mesopsyche* and *Triassopsyche*. Their similarity to the caddisflies consists in the reduction of the number of branches of the sectoral radial vein R_s and medial vein M to four in both the genera and in the branching of cubital vein Cu_1 in *Mesopsyche*. However, the number of crossveins in the middle-radial region, being atypical of the early caddisflies, raises the question whether the caddisflies proper could have evolved directly from these forms. It seems that the *Mesopsychidae and Necrotauliidae* rather arose from a common stem to evolve separately.

The forms discovered by TILLYARD (1933) in the Upper Permian of New South Wales (Australia), for which a new order has been erected and denominated *Paramecoptera* because of their similarity to the members of the order *Mecoptera*, also show a comparatively close relationship to the *Mesopsychidae*. *Belmontia mitchelli* TILL., with branching Cu_1, resembles the *Mesopsychidae* most of all the members of this order. This species probably belongs to the forms which, on the one hand, evolved from a common stem with the *Mecoptera* and, on the other hand, gave rise to an evolutionary branch common to *Mesopsychidae* and *Trichoptera*.

In the Mecopteran species Cu_1 does not branch. In this connection ROSS (1956) put forward the hypothesis that the anterior branch of this vein had coalesced with M_4 and separated from its maternal vein in the scorpionflies. This hypothesis is acceptable, because in substance it explains the generic relationships of the orders *Mecoptera* and *Trichoptera*.

In the caddisflies, however, the number of the crossveins is smaller and, in addition, there is a greater differentiation of the hindwings. To be sure, the wings are more homonomous in the members of primitive families, but in most caddisflies the anal portion of the wing is better developed. According to MARTYNOV'S (1925) modification of COMSTOCK and NEEDHAM'S theory, the evolution of the insect wings happened by the reduction of original veins (specialization by reduction) and formation of new ones (specialization by addition). The evolution of the caddisfly wings would thus consist in the reduction of crossveins and development of anal veins.

The members of the suborder *Annulipalpia* — except the family *Hydropsychidae* — and those of the primitive families of the suborder *Integripalpia*, i. e., *Rhyacophilidae*, *Glossosomatidae* and *Hydroptilidae*, have 3—4 anal veins, A_1—A_4, in the hindwings. Veins A_5 and A_6 have evolved partly or completely in the *Hydropsychidae* and the remaining families of the *Integripalpia*. The mechanism of evolution of these veins and their increase in number have been explained by MARTYNOV (1925). In the anal part of a wing, at its base, is the jugal fold, which links the forewing to the hindwing during flight. When the wings are folded, it becomes tucked up along a narrow chitin strip, termed by MARTYNOV the "plica anojugalis". He has also found that, as in the scorpionflies, on the jugal fold of the caddisfly there occur 2 veins, which he calls the "vena cardinalis" and "vena arcuata". The first of them runs from the base of the wing at the height of the third axillary sclerite and the other one branches from it. MARTYNOV found that in the members of the family *Polycentropodidae* a small depression had evolved behind A_4 at the margin of the wing, and a new vein, A_5, had branched off from A_4, without reaching as far as this depression. The new vein grows in the same way as the arcuate vein does from the cardinal. Hence MARTYNOV inferred that A_5 is homologous with the arcuate vein and that the anal veins grow successively out of the cardinal vein. In the insects observed at rest the anal portion of the wing is tucked up exactly along vein A_5 and its extension towards the depression at the wing margin. In the families *Phryganeidae* and *Limnephilidae* the hindwings have a relatively large surface area and, if they were folded up in the jugal part only, they would protrude from under the forewings. The fact that they fold up in the anal part is, in MARTYNOV'S opinion, another piece of evidence that this part has arisen in the same manner as the jugal part.

Some later fossil remains of caddisflies have been found in Baltic amber from the Lower Oligocene (ULMER, 1912) and in Miocene shales from western North America (ROSS, 1956). About 152 species have been described; most of them belong to the recent family *Polycentropodidae*, and yet they do not live at. present Not a member of the now most abundant family *Limnephilidae* has been found. Thus it may be supposed that anal vein A_5 did not evolve completely until the later geological periods.

The caddisflies have differentiated into two basic groups, which form two evolutionary branches classified as the suborders *Annulipalpia* and *Integripalpia* (MARTYNOV, 1924). These suborders include the following families:

Annulipalpia

1. *Philopotamidae* *
2. *Stenopsychidae*
3. *Xiphocentronidae*
4. *Psychomyidae* *
5. *Polycentropodidae* *
6. *Dipseudopsidae*
7. *Hydropsychidae* *

Integripalpia

1. *Rhyacophilidae* *
2. *Glossosomatidae* *
3. *Hydroptilidae* *
4. *Rhynchopsychidae*
5. *Lepidostomatidae* *
6. *Plectrotarsidae*
7. *Limnephilidae* *
8. *Thremmidae*
9. *Goeridae* *
10. *Phryganopsychidae*
11. *Phryganeidae* *
12. *Brachycentridae* *
13. *Limnocentropodidae*
14. *Pisuliidae*
15. *Calocidae*
16. *Pycnocentrellidae*
17. *Beraeidae* *
18. *Sericostomatidae* *
19. *Helicophidae*
20. *Philanisidae*
21. *Antipodoeciidae*
22. *Odontoceridae* *
23. *Molannidae* *
24. *Philorheithridae*
25. *Helicopsychidae*
26. *Calamoceratidae*
27. *Leptoceridae* *

* Members of the families marked with an asterisk occur in Poland.

In the *Annulipalpia* the supratentorium of imagines has atrophied and the terminal joint of the maxillary palp is segmented. Most of the larvae of this group spin fishing nets. In the *Integripalpia* the supratentorium is retained, the apical joint of the maxillary palp unsegmented, and crossvein m reduced, whereas the larvae, except for some species of the *Rhyacophilidae*, which are free living, build cases of secretion produced by their silk glands or of materials available in their surroundings.

Klapálek (1893) divided the caddisfly larvae on the basis of their structuer into two main groups, which he named the "campodeoida" and "eruciformia". The campodeoid larvae show a number of primitive characters, which resemble those of the apterous insects of the genus *Campodea* (*Apterygota*, *Thysanura*). Their head is prognathous and the legs are the same or nearly the same length. The abdomen is generally devoid of tracheal gills and its segments are sharply delimited. They are predatory animals and do not make portable cases but construct fishing nets or cases permanently attached to the substrate. They inhabit flowing waters only. On the other hand, the eruciform larvae make portable cases and occur in both flowing and stagnant waters. They are mostly herbivores, their head is hypoghanthous, and the abdomen generally bears tracheal gills. The legs are specialized; only the middle and hind pairs are walking legs, the anterior, prehensile ones being considerably shorter. On the first abdominal segment there occur one dorsal and two lateral humps, which in literature are commonly regarded as organs which serve to hold the case. In fact, their role consists in fulfilling tactile functions and regulating the internal pressure, which will be described more in detail in the next section. Klapálek (1893) also distinguished the group of suberuciformia, in which he placed the family *Phryganeidae*. The members of this family have the characters of the eruciformia, but in respect of the type of head they come close to prognathism; like campodeoids they have loose, distinctly separated abdominal segments. Hence, their abdomen is flabbier and more contractile. The suberuciform larvae are predatory too.

The division of the caddisflies into these two basic groups, campodeoida and eruciformia, is such that the first of them, being more primitive, includes all the families of the suborder *Annulipalpia* and the families *Rhyacophilidae*, *Glossosomatidae* and *Hydroptilidae*, belonging to the suborder *Integripalpia*.

Some authors (Nielsen, 1957; Fischer, 1960; Lepneva, 1964, and others), however, identify the compodeoida with the suborder *Annulipalpia* and the eruciformia with the *Integripalpia*, and thus they place all the caddisflies with more primitive characters in one suborder only, though Nielsen (1957) pointed out on the basis of the structure of the copulatory organs of imagines that the evolution of the suborder *Integripalpia* was started by the line *Rhyacophilinae* — *Glossosomatinae* — *Hydroptilidae*. On the other hand, Ross (1967) holds the opinion that either suborder has evolved separately and, in consequence, contains both more primitive forms and those more specialized. This opinion, according to which the families *Philopotamidae* (*Annulipalpia*) and *Rhyacophilidae* (*Integripalpia*) have the most primitive characters in both suborders, seems to be convincing, the more so, since it may be inferred from the homology in the musculature of the anal prolegs, demonstrated by Pryor (1951), that the caddis larvae that make portable cases (eruciformia) come from the branch which initiated the evolution of the *Rhyacophilidae*. Studying the anal prolegs in different species, PRYOR (1951) also manifested a homology in their musculature in the members of the *Trichoptera* and *Megaloptera*. This fact throws light on the generic relationships of the caddisflies and neuropteroid insects.

Basing himself on an analysis of the external constructions built by the caddis larvae and the morphology of their legs and processes used to hold the case, ROSS (1964) presented the sequences of evolutionary stages of these insects. Starting from the free-living forms, i. e., the forms that make no constructions, which include the family *Rhyacophilidae* only, he distinguished 5 groups, of which each constitutes the next evolutionary stage in relation to the previous one.

Although the free-living forms do not build any protective constructions, they live in different gaps under and between stones in mountain torrents, thus availing themselves of natural shelter. In morphology they resemble, on the one hand, the most primitive family of the suborder *Annulipalpia*, the *Philopotamidae*, which make fishing nets in the form of simple tunnels of the secretion of their silk glands, open at both ends and anchored firmly to the substrate, and, on the other hand, the members of the family *Glossosomatidae*, which build domes of fine sand grains cemented with their gland secretion on submerged stones, also open at both ends. According to ROSS (1964), they gave rise both to the forms making fishing nets, from very simple ones (*Philopotamidae*) to those more complicated (*Polycentropodidae* and *Hydropsychidae*), and to the forms constructing domes attached to the substrate. Owing to the specialization of the larvae, such domes were next transformed into cases with free walls, i. e., such that none of the walls was formed by the substrate. The opposite arrangement of openings was, however, preserved. The larvae living in the cases of this type subsequently gave origin to the forms which make portable tube cases unattached to the substrate and with one — frontal — opening only.

ROSS's hypothesis seems reasonable, if we have regard to the fact that all the caddis larvae stripped of their cases or fishing nets behave like free-living larvae (rhyacophilids), that is, they take shelter in various retreats in which their bodies are surrounded on all sides or sink into a soft substrate before they start making new protective constructions. I observed such a behaviour of the larvae both during field experiments and under laboratory conditions. Another argument that supports ROSS's hypothesis is the fact that the caddis larvae which make portable cases anchor them to the substrate, while passing into the pupal stage. This would indicate that in their evolutionary history they lived in cases attached firmly to the substrate, from which they became detached owing to the deterioration of oxygen and food conditions. The change released their searching reflexes and, in consequence, led to an increase in their autonomy. The construction of portable cases and their transportation was also connected with the appropriate differentiation of the legs and their adaptation for walking.

However, Ross (1964) does not explain the mechanism of detachment of the larvae from the substrate, though in one of the earlier papers (Ross, 1957) he shows that the primaeval caddisflies occurred in environments characterized by low temperatures typical of mountainous regions and described them as "cool-adapted"; in the Cretaceous and at the beginning of the Cenozoic took place their specialization by fitting to warmer environments and such forms were designated as "warm-adapted. The cool-adapted caddis larvae inhabited cold, well oxygenated and fast flowing mountain torrents, the adaptation to warmer and more slowly flowing waters being possible owing to the development of physiological properties that facilitated the supplying of the organism with oxygen. Stimulated by lack of the sufficient amount of oxygen, the larvae increased the water flow through their cases by waving their abdomens rhythmically. This resulted in the development of the abdominal muscular system, and an increase in the respiratory surface of the abdomen by the appearance of tracheal gills. In this way Ross explains the adaptive process and specialization of the caddisflies in connection with their passage from cool mountainous regions to warm water reservoirs of the subtropical and tropical zones. Mountainous environments did not, therefore, favour the origin of new specialized forms but contributed to the preservation of the primitive nature of the existing ones.

The adaptive process connected with the passage of the caddisflies from flowing to stagnant waters seems to have run in the same way. A change in living conditions caused the appearance of new forms of behaviour, a direct result of the changed manners of satisfying their living requirements, followed by a morphological differentiation and, no doubt, the development of perceptive abilities or, in other words, the physiological improvement of the reception of information from the surroundings.

3. Morphological analysis of caddis larvae and their constructions

The literature on the morphology of larvae of different caddis species includes as many as hundreds of publications. Their list is given in the catalogue of caddisflies by Fischer (1960—1972) and, in so far as the species occurring in Poland are concerned, in a paper by Tomaszewski (1965). The fullest information concerning this domain will be found in the papers by Lestage (1921), Nielsen (1942, 1948) and Hickin (1946) for the European species, Lepneva (1964, 1966) for the East-European and North-Asiatic species, Ulmer (1955, 1957) for the South-East Asiatic species, and Ross (1944, 1959) and Flint (1960, 1964a, b, 1968a, b) for the North and Central American ones. Special papers given exclusively to the constructions made by the larvae are those by Wesenberg-Lund (1911), Botoşăneanu (1963), Tobias (1963) and Ross (1964).

Caddis larvae hatch in the oligopodal stage and moult 5 times as they grow. The abdomen, at first smaller than the thorax, outsizes it considerably in the next developmental stages.

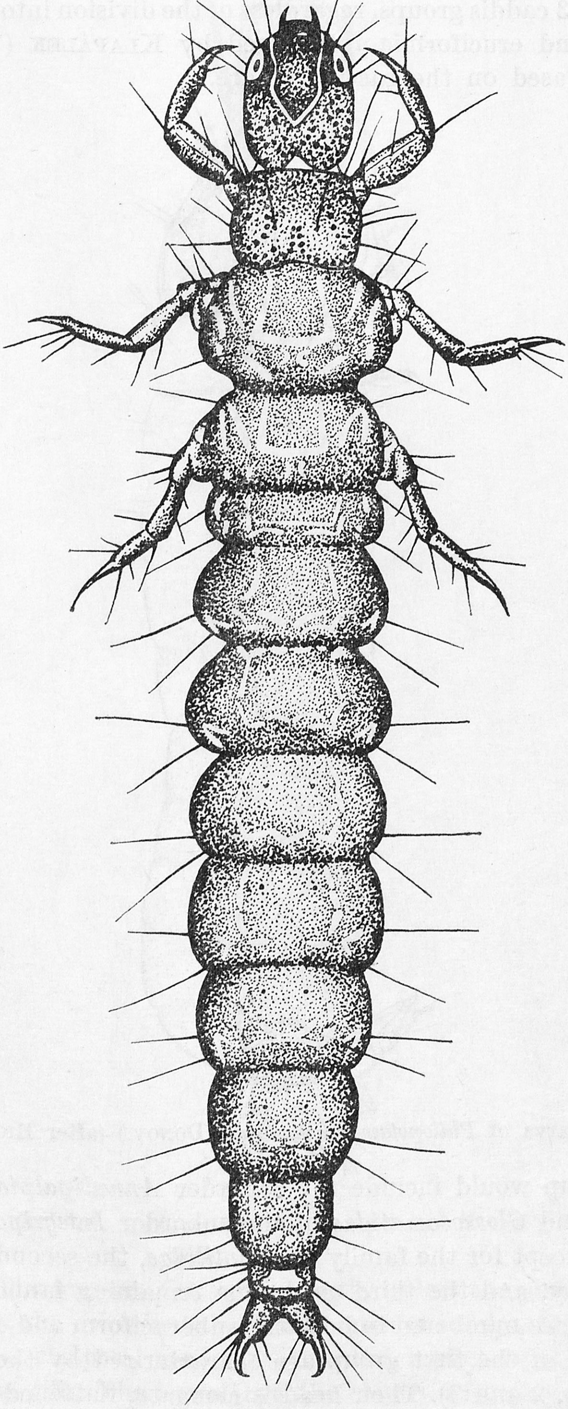

Fig. 1. Larva of *Rhyacophila fenestra* Ross (after Ross, 1944)

The morphological structure of the larvae and their constructions allows the distinction of 3 caddis groups, regardless of the division into the campodeoida, suberuciformia and eruciformia introduced by Klapálek (1893) and Ross's (1964) division based on the case structure.

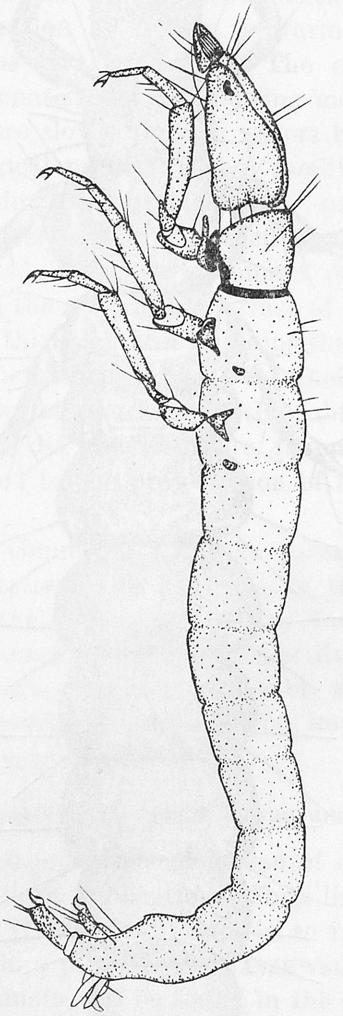

Fig. 2. Larva of *Philopotamus montanus* (Donov.) (after Hickin, 1946)

The first group would include the suborder *Annulipalpia* and the families *Rhyacophilidae* and *Glossosomatidae* of the suborder *Integripalpia*, or the campodeoid group except for the family *Hydroptilidae*, the second group the family *Hydroptilidae* only, and the third group the remaining families of the *Integripalpia* or the species numbered in both the suberuciform and eruciform division.

The members of the first group are characterized by their most primitive structure (Figs. 1, 2 and 3). Their head is elongate, flattened and prognathous. The thoracic and abdominal segments have the shape of sharply delimited convex annuli. The pronotum is the most differentiated and most heavily

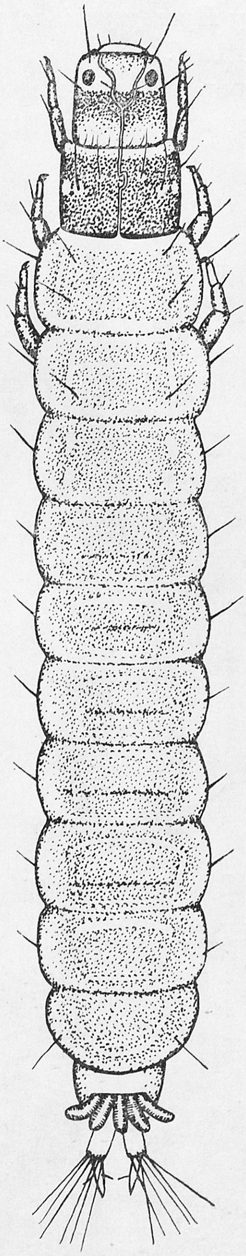

Fig. 3. Larva of *Lype reducta* (HAG.) (after HICKIN, 1950)

sclerotized part. The legs are the same length, unless the anterior pair is somewhat shorter than the other ones. The abdomen is flabby, soft and ends in the anal prolegs called claspers, used for backward movements. The last segment bears also the anal gills. The larvae breathe chiefly with the skin surface of the abdomen and a dense network of tracheal capillaries is visible through the skin. Tracheal gills occur only in some free-living members of the *Rhyacophilidae* and in the larvae of the family *Hydropsychidae*, whose abdominal segments are relatively more heavily sclerotized.

Most members of this group make protective constructions in the form of fishing nets of various shape and cases and tunnels of fine sand grains. The species of the family *Philopotamidae* make tubular nets (Fig. 4), which in the *Polycentropodidae* are already more complicated. The larva of *Neureclipsis bimaculata* (L.) builds its net in the form of a horn (Fig. 5) with a crumpled cone, in which it takes shelter. Originally, however, this net is a simple tunnel, which in the next instars the larva makes into something like a plankton net (Wesenberg-Lund, 1943). *Plectrocnemia conspersa* (Curt.) hides in a limp tunnel joined to a baglike net hung on submerged plants (Fig. 6). Sinking plankton

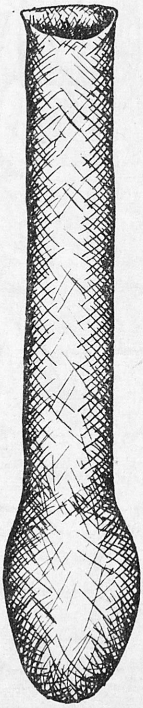

Fig. 4. Fishing net of larva of *Wormaldia occipitalis* (Pict.) (after Nielsen, 1942)

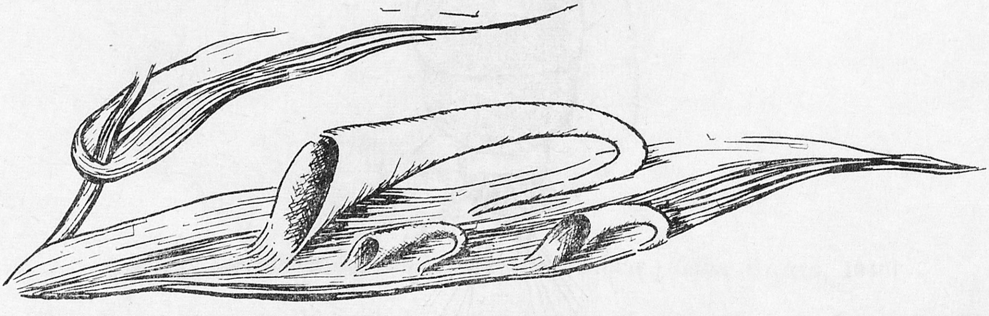

Fig. 5. Fishing nets of larvae of *Neureclipsis bimaculata* (L.) (after Lepneva, 1964, fragment)

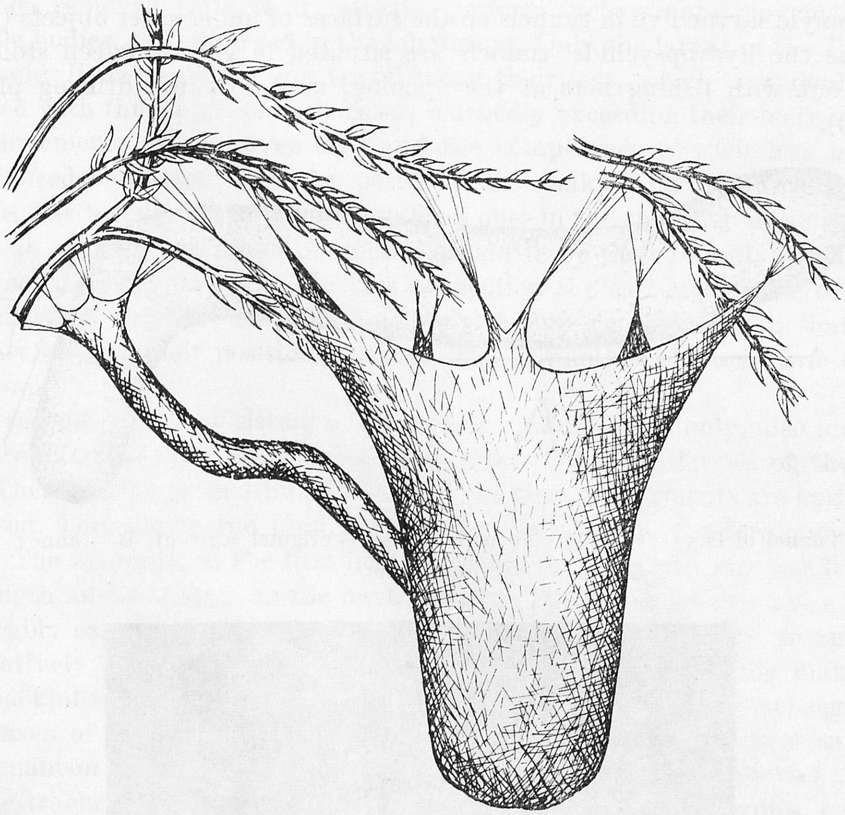

Fig. 6. Fishing net of larva of *Plectrocnemia conspersa* (Curt.) (after Nielsen, 1942)

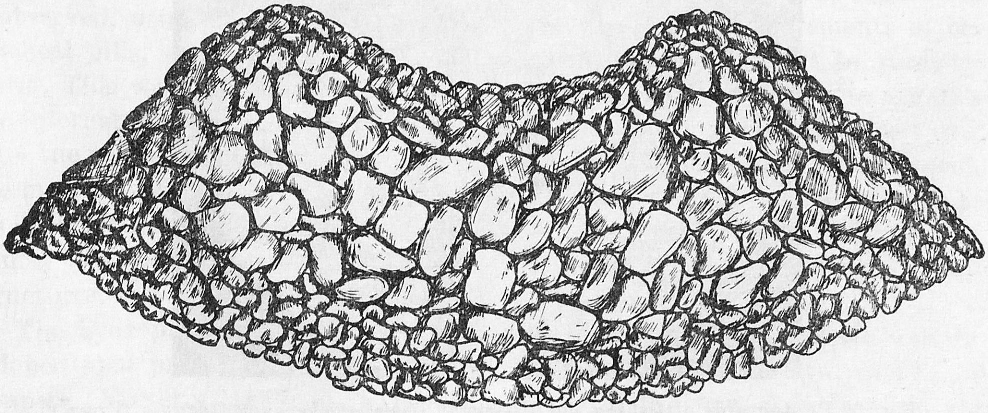

Fig. 7. Case of larva of *Synagapetus* sp. with circulatory openings on the dorsal side

is trapped in the net and the larva feeds on it. Glossosomatids make dome-shaped cases of fine sand grains on underwater stones in mountain torrents. Some species of the genus *Synagapetus* McLach. furnish their cases with additional openings in the dorsal wall, ensuring better water circulation (Fig. 7). The psychomyid larvae live in tunnels on the surfaces of underwater objects (Fig. 8), whereas the hydropsychids' tunnels are situated in gaps between stones and fitted out with fishing nets at the opening, used to catch drifting plankton (Fig. 9).

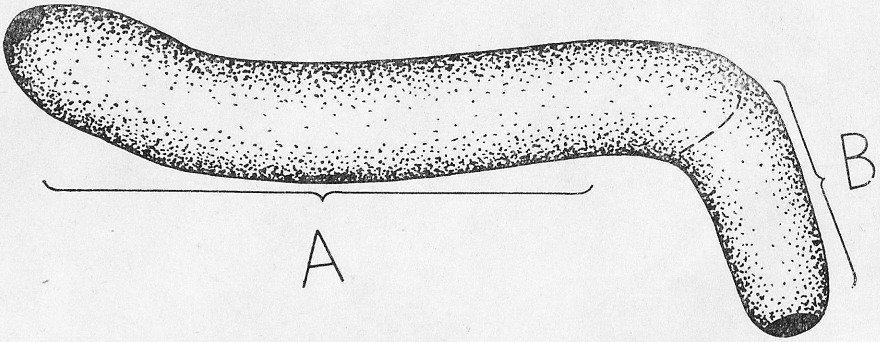

Fig. 8. Tunnel of larva of *Tinodes waeneri* (L.): A — original segment, B — annex oriented upstream

Fig. 9. Photograph of fishing net of larval *Hydropsyche angustipennis* (CURT.)

A common character of the group analysed is that all the protective constructions are permanently anchored to the substrate and the larvae are not, as a rule, adapted for fit locomotive movements, they can only turn over inside their cases or fishing nets, which they do chiefly with the help of their relatively well developed anal prolegs. Even the free-living larvae are unable to walk and, when removed from their retreats, perform incoordinate movements of the whole bodies, as I observed in the laboratory. Only the larvae of the *Psychomyidae* and *Hydropsychidae* can travel using their legs, which is undoubtedly connected with the length of their cases, markedly exceeding their body length. Their movements are however slow and the competence of their legs is very much limited compared with the portable-case- making larvae. Nevertheless, these families belong to the most specialized ones in the suborder *Annulipalpia*. The larvae of the group under discussion do not leave their retreats throughout the period of development and in this connection the capactiy of the constructions in which they live exceeds their body volume considerably so that they can easily change their position in them. This is another characteristic of the first group.

The second group, consisting of the family *Hydroptilidae* only, also includes campodeoid larvae, but they differ very much from the larvae of the first group. Their head is prognathus too, but all the thoracic segments are uniformly sclerotized. The middle and hind legs are the same length, the fore ones being shorter. The abdomen in the first instar is narrower than and more or less the same length as the thorax. In the next instars it grows and attains a size which considerably exceeds its size in the larvae of the first group (Figs. 10 and 11). The relatively large respiratory surface of the abdomen probably makes up for the lack of tracheal gills. Tracheal lamellae occur on the abdominal segments of the larva of *Ithytrichia lamellaris* Eat. (Fig. 11) in a manner that suggests the mechanism of formation of the tracheal gills in eruciform larvae. To be sure, the tracheal gills occur also in some members of the first group, namely, in rhyacophilids and hydropsychids; however, they are not inert structures but are seated on muscled stems, which the larvae can move. In the laboratory I observed, using a colposcope, the rhythmical centripetal movements of the tracheal gills, especially when the larvae had been transferred to stagnant water. This would indicate, on the one hand, that they also serve to regulate the internal pressure and, on the other hand, that they are structures left over after the reduction of the abdominal prolegs during the embryonic development; the more so, since they are also preserved at the bases of the mid- and hindlegs. As in the eruciform larvae the tracheal gills do not appear before the 2nd instar, it may be inferred that in the members of the third group they are cenogenetic structures.

The hydroptilid larvae of the first instar are free living and have well-developed anal prolegs, which in the fifth instar become reduced to short anal claspers (Nielsen, 1948). This is connected with the fact that they do not build their cases before the last instar, when they make them exclusively of the secretion of their silk glands or line with algae or sand grains (Figs. 12 and 13). The cases are attached to leaves of submerged plants by means of a silk thread and they cling closely to the flanks of the larva body.

The third group comprises the largest number of caddis families. The family *Limnephilidae* is one of the most numerous and most widely distributed in the

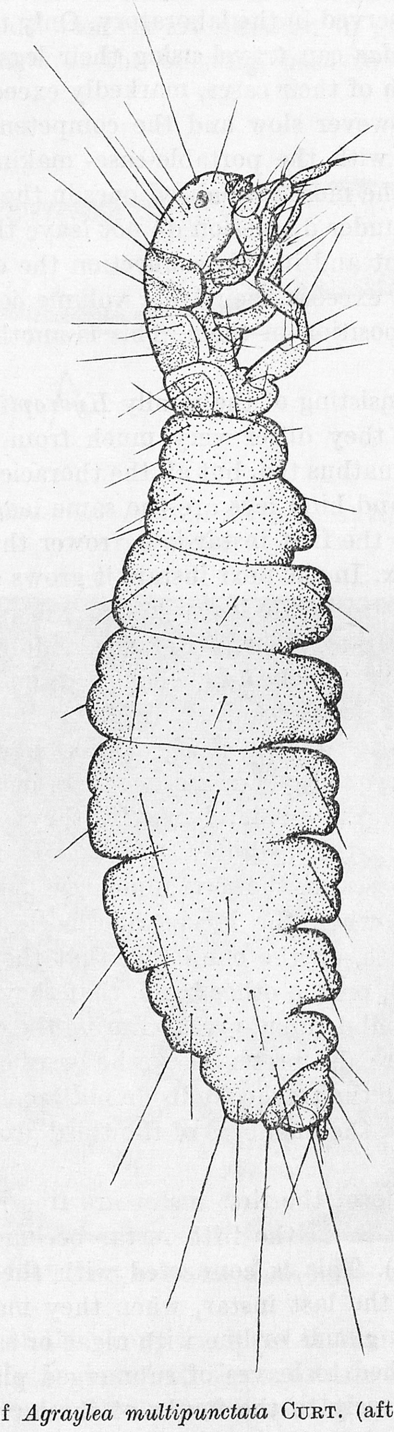

Fig. 10. Larva of *Agraylea multipunctata* CURT. (after NIELSEN, 1948)

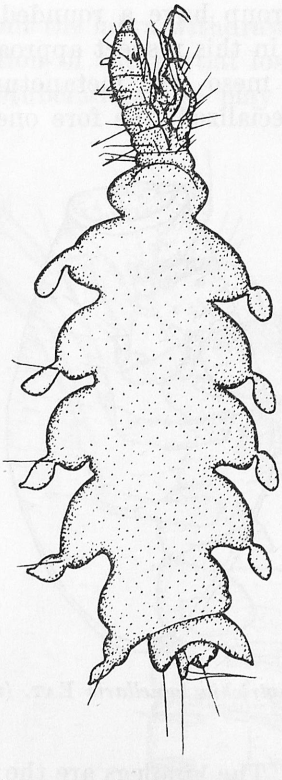

Fig. 11. Larva of *Ithytrichia lamellaris* Eat. (after Nielsen, 1948)

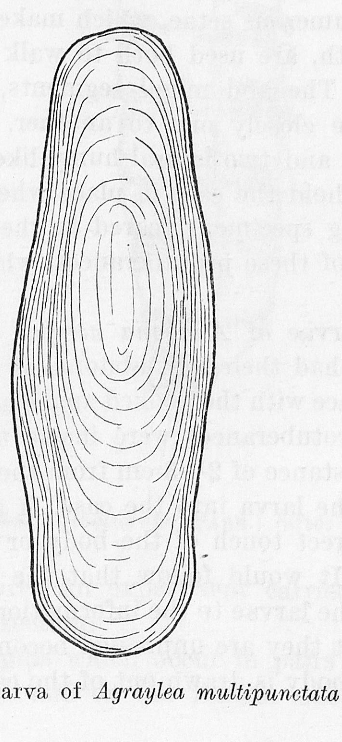

Fig. 12. Case of larva of *Agraylea multipunctata* Curt.

world. The larvae of this group have a rounded hypognathous head except for the *Phryganeidae*, which in this respect approach prognathism. The pronotum is sclerotized most, the meso- and metanotum being stiffened with hard plates only. The legs are specialized; the fore ones are the shortest and used to seize food and build cases. The hindlegs are the longest and used for walking or, in some leptocerid species, specialized for swimming. In this last case they are furnished with numerous setae, which make swimming easier. The midlegs, of intermediate length, are used both to walk and to catch hold of different underwater objects. The abdominal segments, except the first one, are flat annuli, which adhere closely one to another. Instead, on the first segment there are one dorsal and two lateral hump-like protuberances (Fig. 14). They admittedly serve to hold the case in place when the larva crawls. Colposcopic observations of living specimens reared in the laboratory drew my attention to another function of these protuberances, which are soft and pressed by the case walls only.

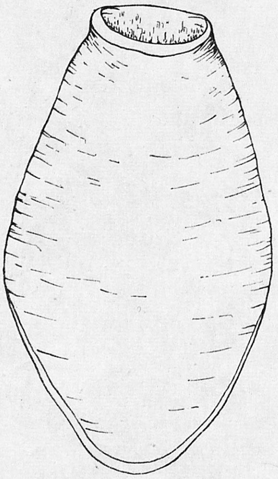

Fig. 13. Case of larva of *Ithytrichia lamellaris* Eat. (after Richters-Tobias, 1963)

The travelling larvae of *Anabolia nervosa* (Curt.) and *Limnephilus flavicornis* (Fabr.) often had their first abdominal segment drawn out of the case, which was kept in place with the hooked anal claspers at the end of the abdomen. If the abdominal protuberances were inside the case, a slightest movement of a glass rod at a distance of 2—3 cm from the protruding thorax caused a rapid with-drawal of the larva into the case. If the protuberances were completely uncovered, a direct touch of the body or case was necessary to provoke a reflex of retreat. It would follow that the pressed protuberances enhance the sensitiveness of the larvae to the information coming from the surroundings, whereas the fact that they are unpressed becomes a signal for the larva of the degree to which the body is drawn out of the case, because after each exposure of the first abdominal segment the larva withdraws it into the case. Then there follows a sort of compensation of the partial loss of sensitiveness, its course being rhythmical. These protuberances also play an important role in the re-

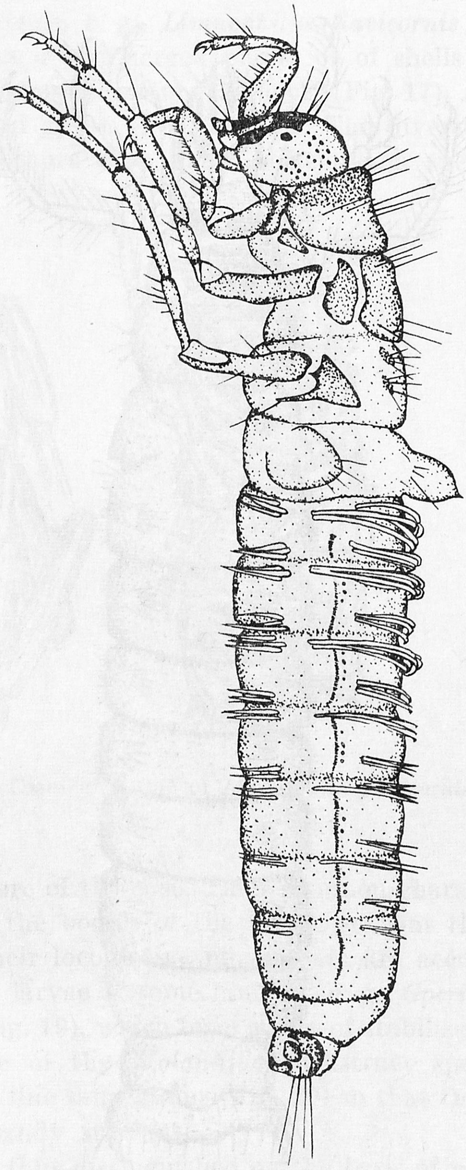

Fig. 14. Larva of *Limnephilus flavicornis* (FABR.) (after HICKIN, 1946)

gulation of the internal pressure. An experiment carried out in this respect will be described in the next section.

Unlike the bushy tracheal gills which occur in pairs on the flanks of the body in the rhyacophilid larvae and on the ventral side in the hydropsychid ones, those of the larvae of the third group grow in the form of threads, single or arranged in bundles, on each side of the abdomen. In many species, e. g., n those of the families *Molannidae*, *Brachycentridae*, *Goeridae* and *Sericostomatidae*, they are reduced (Fig. 15) and sometimes, as in *Brachycentrus subnubilus* (CURT.), occur only on several segments of the abdomen. This is probably associated with the occurrence of these species in relatively well-oxyge-

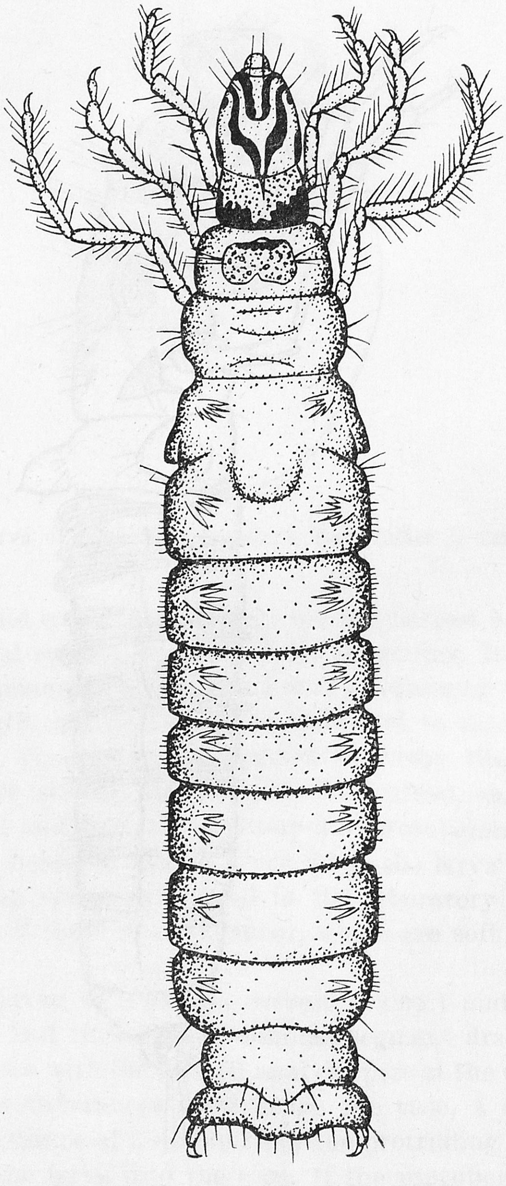

Fig. 15. Larva of *Molanna angustata* CURT.

nated water, i. e., in rivers and exposed parts of the littoral zone of lakes. The terminal abdominal segment bears short anal claspers, which end in a hooked claw each. The larva uses them to withdraw into the case. All the larvae of this group build various portable tubular cases of materials that make up the substrate of their occurrence, e. g., *Limnephilus flavicornis* (FABR.) of plant detritus and fresh stalks of submerged plants or of shells (Fig. 16), *Phryganea grandis* L. of spirally arranged plant fragments (Fig. 17), *Potamophylax rotundipennis* (BRAU.) of sand grains (Fig. 18), etc. The diversity of protective constructions is vast, because each genus, often even species, is characterized by a different structure of the case. Their common character is that they cling relatively closely to the bodies of the larvae so that the larvae cannot turn over in them. All their locomotive movements are accompanied by dragging the cases about. The larvae of some families, e. g., *Goeridae*, make cases fitted with lateral wings (Fig. 19), which form a sort of stabilizers in the lotic environment, whereas those of the *Molannidae* construct specific protective roofs with lateral wings of fine sand grains (Fig. 20) so that the case merges into the background of the sandy substrate.

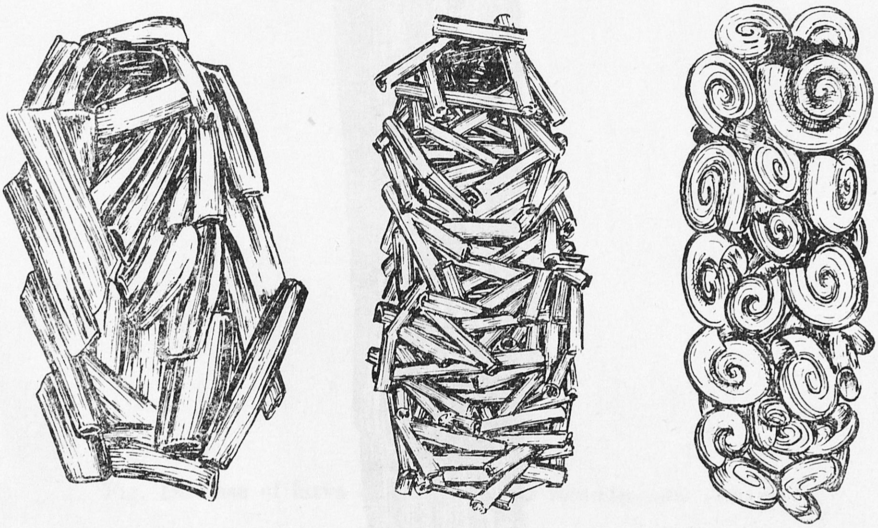

Fig. 16. Cases of larvae of *Limnephilus flavicornis* (FABR.)

The three groups thus distinguished on the basis of nothing but the general morphological structure of the larvae and their constructions are reasonable and seem to form an evolutionary sequence of the caddisflies.

Each biological classification, as a rule, boils down to the search of adequate morphological equivalents. Often, however, this does not render the essence of division and not uncommonly also shallows it. Not all the aspects of life have their morphological equivalents and, therefore, they can be characterized only by means of specific parameters, which are no less important than the structural characters, for the evolution of reflexes and behaviour is ruled by the same principles as the evolution of structure. However, a homologous

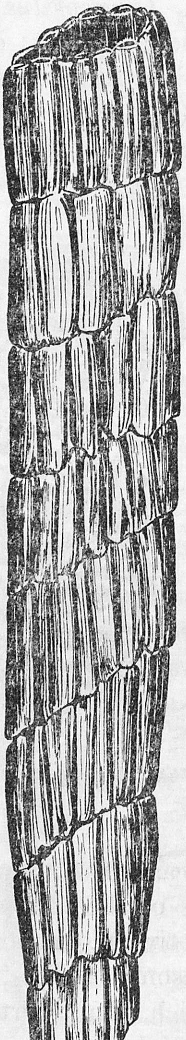

Fig. 17. Case of larva of *Phryganea grandis* L.

behaviour or parameter of an isolated phenomenon, e. g., general spatial orientation or a definite reception, can be manifested only by experimenting. For this reason the division into the above-mentioned groups will also be substantiated in the next sections.

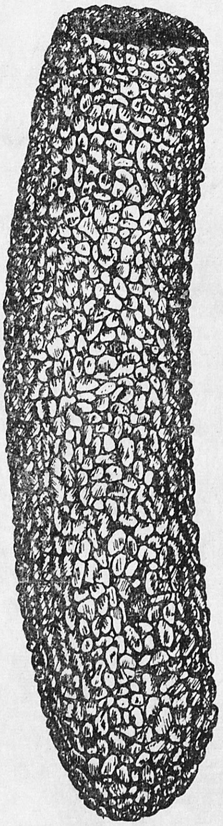

Fig. 18. Case of larva of *Potamophylax rotundipennis* (Brau.)

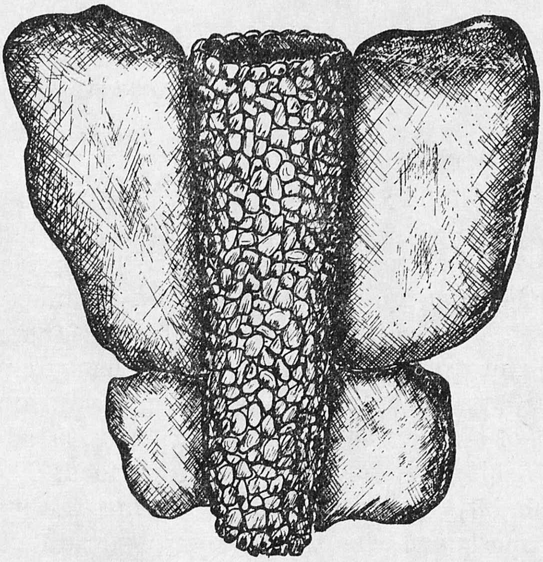

Fig. 19. Case of larva of *Goera pilosa* (Fabr.)

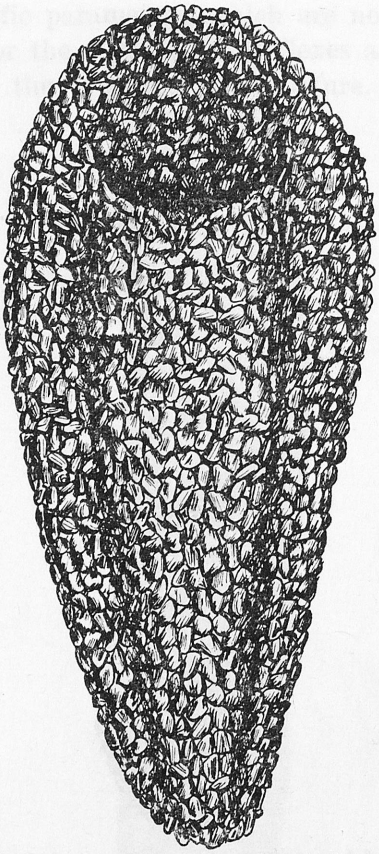

Fig. 20. Case of larva of *Molanna angustata* Curt.

4. The mode of supplying vital needs and the behaviour of the larvae in the light of the author's own studies and observations

The behaviour of larvae is closely associated with the manner in which they supply their living requirements, i. e., the oxygen and food requirements. This manner also suggests the division of the caddisflies into 3 groups closely corresponding with the groups distinguished in the previous section.

The larvae of the first group live only in environments characterized by strong water current. They occur in mountain torrents, rivers and welter zones of large lakes. Their protective or fishing constructions are permanently anchored to the substrate, with their openings facing up the stream, which incessantly washes the bodies of the larvae, supplying them with adequate amounts of oxygen and their fishing nets or cases also with food. The free-living larvae (*Rhyacophilidae*) inhabit gaps between pebbles in fast-flowing streams. The lack of tracheal gills in most members of this group is natural seeing that they live in well-oxygenated everchanging water. On being transferred to stagnant water, the larvae living in one-directional water currents, e. g., those of the

Rhyacophilidae, *Glossosomatidae*, *Philopotamidae*, *Hydropsychidae* and some species of the *Polycentropodidae*, leave their retreats, simultaneously performing rhythmic movements of the abdomen, the wave-like motion of which causes a continuous exchange of water in its immediate vicinity.

I reared the larvae of the families mentioned in small tanks, using the method based on a closed system of circulating water, which flowed down from a higher level (TOMASZEWSKI, 1955). The method was improved by introducing full automaticity and the use of a cooler. A large aquarium with water-plants and aerators was placed, as the main tank, at the top level of the rack. At lower levels there were small breeding tanks, to which water flowed down through a system of rubber pipes ending in glass pipettes with outlet diameters of 0·5—1 mm. Fixed vertically on one of the walls of the tank, the pipettes were bent at an angle of 90° close to its bottom. A horizontal narrow stream of water, the direction of which could be freely changed, was attained in this way. The excess of water flowed from the tanks through rubber pipes and the cooler, which was a system of curved glass pipes placed in a thermos filled with ice, to the terminal tank, from which it was pumped using a rotary pump driven from an electric engine to the main tank fitted with a float switch. The float rose and lowered, as the water level fluctuated in the tank, and the engine was switched off and on.

The larvae of *Rhyacophila septentrionis* MCLACH. (*Rhyacophilidae*), *Synagapetus* sp. (*Glossosomatidae*) and *Philopotamus motanus* (DONOV.) (*Philopotamidae*) from mountain torrents in the Śląski Beskid Mts. and those of *Hydropsyche angustipennis* (CURT.) (*Hydropsychidae*) and *Neureclipsis bimaculata* (L.) (*Polycentropodidae*) from the River Widawka in the Bełchatów District, deprived of their retreats and placed in breeding tanks, behaved all in the same manner in the first phase of "habituation". Like the free-living larvae of *Rh. septentrionis* MCLACH., they, first of all, began to seek natural retreats in the close neighbourhood. If they did not find gaps between the stones, they buried themselves in the gravel on the bottom of the tank. They wandered about by means if swimming movements of the abdomen and anal prolegs, using their legs only to catch hold of the substrate.

In this situation the behaviour of the glossosomatid, philopotamid, hydropsychid and polycentropodid larvae is homologous with that of the free-living larvae of the *Rhyacophilidae*. A photograph (Fig. 9) illustrates the manner in which the larva of *Hydropsyche angustipennis* (CURT.) buries itself in the bottom layer of the aquarium. It, however, shows a later phase, because the larva has already strengthened its retreat by gluing the grit grains surrounding its body with the secretion of its silk glands and has spun a fishing net at its entrance. I managed to take this photograph owing to the fact that the larva had employed a glass wall of the tank as one of the walls of the tunnel.

Later, only the larvae that stayed in the zone of water streams which flow out of the pipettes constructed fishing-nets and domeshaped cases (*Synagapetus* sp.). On the contrary, the larvae which thrown into the aquarium at random took shelter out of the range of water streams did not build any structures but left their retreats looking for new ones and despite the incessant undulation of the abdomen died in a few days.

The water current supplying the larvae with sufficient amounts of oxygen and food is therefore a stimulus for them to improve their protective constructions and to spin fishing nets, whereas its lack releases search reflexes, largely restricted in this group of caddisworms by their poor adaptation for locomotion.

As soon as the water stream had been stopped or its direction changed, the free-living larvae of the *Rhyacophilidae* and other families mentioned above came out of their retreats, nets and cases, and when the stream had been restored in the same direction as before, they repeated the first phase of behaviour and then started to build new structures. Only the rhyacophilid larvae did not go beyond the first phase.

The behaviour of the larvae of the third group, which make portable cases, was very much the same. They did not need movements of water in their environment and were reared in stagnant water. Stripped of their cases, they buried themselves entirely in the bottom layer of the aquarium in the first phase and next glued together the sand grains or detritus fragments surrounding their bodies directly, using the secretion of their silk glands. A similar behaviour was also observed by SZLEP (1958) in the larvae of *Molanna angustata* CURT. Having satisfied their tactile demands, the larvae emerged from the thus constructed tunnels, generally without drawing their bodies out of them beyond the first abdominal segment, which bears the abdominal protuberances, and started to build tubular cases. If they had not enough building material, they constructed their cases in one of the corners of the tank so that its walls should partly form the walls of the case also. In this instance the case was stably anchored to the substrate, as with the members of the first group, and the larvae performed incessant undulating movements of their abdomens. It follows that also the movements of the travelling larvae are associated with satisfying their oxygen requirements. Oxygen dissolves very slowly in stagnant water and after its exhaustion in the space between the case walls and the abdomen of the larva, the locomotive movements of the larva undoubtedly cause an exchange of the water surrounding its body.

In another experiment the larvae of *Limnephilus flavicornis* (FABR.) and *Phryganea grandis* L., which are members of the third group, were placed singly in crystallizers, where building material suitable for cases was not only too scanty for covering the whole body of a larva, but also consisted of grit grains and vegetable fragments too big to be fitted tightly together. As a result, there were large gaps in the cases and the larvae filled them up with their gland secretion. Under the same circumstances the larvae of *Hydropsyche angustipennis* (CURT.) built their tunnels in a similar manner. This throws some light on the genesis of net building. In rapid mountain torrents fine sand grains and light detritus are washed downstream, which makes it difficult for the larvae to bury themselves in the bottom. The occurrence of relatively large pebbles made the larvae fill up the gaps between them with silk gland secretion, to which their food in the form of fine plankton stuck. The larvae ate up the secretion with the food trapped in it and, next, refilled the openings between the stones. The development of their ability to produce thread was thus promoted and in course of time the forms evolved by natural selection that filled the gaps between stones in a possibly economical manner, arranging and joining threads loosely opposite to the water current. Probably the very water current made it impossible for the larvae to spread the net tight and thus bag-shaped structures resembling fishing nets were formed. In the adaptive process here presented the environment played a specific role and picked out the forms which had developed the ability of orientation in relation to the direction and force of the current and which built the most expedient constructions.

This hypothesis contradicts Ross's (1964) opinion on the direct origin of the case-making caddisflies from free-living rhyacophilids, because the behaviour of the larvae belonging to the third group under the laboratory conditions resembling the hypothetical conditions of their ancestors bears traces of their old functions. This would indicate that the larvae that spin fishing nets have arisen from the forms which made primitive retreats attached firmly to the substrate. They next gave origin also to the caddisflies whose larvae make dome-shaped cases placed on submerged stones, whereas the family *Rhyacophilidae* would be a specialized side-branch which has evolved from the stem common to the net-spinning caddisworms. Ross (1964) did not quite explain the mechanism of evolution of the net-spinning faculty, leaving the problem open. Thus, the hypothesis given above is the only explanation of this phenomenon offered so far, but it entails a change in the opinion on the caddisfly phylogeny.

As can be seen from the considerations presented in the second section of this paper, the generic affinities between the caddisflies and scorpionflies seem to rouse no doubts. The wing structure in the scorpionflies points at their primitive character. These insects occur mostly in shadowed and damp gardens, forests, etc. Their larvae live in damp earth, mould and moss. Basing himself on his abundant study materials, Gilarov (1948, 1949 and 1957) put forward and motivated the theory about the specificity of soil environment as the link connecting the water and land environments. Soil is a system of 3 elements — a solid, an airy and an aqueous — and in the evolution of arthropods it was an intermediate stage on their way from the aquatic mode of living to the terrestrial one. Although Gilarov proved this process only in one direction, that is, from water through soil on to the land, the adaptive process of the larval ancestors of caddisflies seems to have happened in the opposite direction on the same way. This is indicated by the fact that, when deprived of their constructions, the larvae first seek a natural retreat and bury themselves in the substrate. This is a homologous behaviour associated with their historically conditioned need to be guided by their tactile information and bearing characteristics of a palingenetic adaptation. Hence the inference that the present responses of the larvae reveal traces of their ancient functions.

ŠMALGAUZEN (1966) presented his theory on the relative nature of adaptations, namely, that they are possible only in relation to the living conditions in which the given organism evolved historically or which occurred repeatedly as local or temporary phenomena in its history. Adaptive reactions are justified and even limited by the evolution of the organism. Each adaptive process has therefore its history and the passage from one environment to another is not irrelative to the properties moulded by the previous habitat.

ŠMALGAUZEN'S (1966) opinion allows the conclusion that the passage of the larval ancestors of caddisflies from life in soil to the aquatic ways of living revealed the adaptive reserves which had protected their existence during the evolution and, later, were used to create new forms of organization.

If the larvae of these ancestors lived in conditions similar to those in which the recent scorpionflies occur, their steam- or water-saturated habitat made them develop suitable tolerances, and these formed their adaptive reserves allowing the accomodation to respiration in water, which is really conditioned historically, as it had existed before, in the evolution of arthropods.

The adaptation for respiration with oxygen dissolved in water was favoured by the well-oxygenated cold water of mountain streams, which, as can also be seen from the previous sections, make the original habitat of the caddis larvae. The adaptation of the larvae of the ancestors of caddisflies to the soil habitat, like that of the caddis larvae to the flowing waters, has left its functional traces with the portable-case-making larvae. The construction by these larvae of cases attached to the substrate when there is not enough building material, the undulation of the abdomen and filling up the gaps between pebbles with silk-gland secretion are, very much like burying oneself in the substrate, homologous with the behaviour of the larvae of the first group, which build fishing nets and cases attached to the substrate, and associated with the adaptation of the larval ancestors of caddisflies to the soil environment. In consequence, the supplying of oxygen requirements by travelling larvae through exchanging the water in the case when they move about is also derived from the ways in which these requirements were supplied by the larvae inhabiting lotic waters.

The larvae of the family *Psychomyidae*, which belong to the first group of caddisflies, occur in shallow rivulets and on the stony bottom in the welter zone of large lakes. On submerged stones and other suitably large objects they construct tunnels of fine sand grains (Fig. 8). They feed on minute organisms supplied by water flowing through the tunnel (TOMASZEWSKI, 1955). I found that in rivers the tunnels are short (from 3 to 5 cm), generally straight, and have one of the terminal openings turned against the water current. In the lakes the tunnels are, however, more contorted in shape and their length is up to 8 cm, although both varieties are built by larvae of one and the same species, *Tinodes waeneri* (L.). In this environment one of the openings of the tunnel is often directed upwards. It has been shown by an experimental study (TOMASZEWSKI, 1955) that the length of these tunnels and their tortuous shape are connected with the changeable directions of the water currents. In the welter zone of lakes the water movements proceed in many directions, which change with wind. They, besides, break in different directions against underground objects (stones, plants) and the shore. The continuous flow of water through the tunnels, supplying the larvae with oxygen and food, is the basic condition of their life. This is why after each change in the direction of water movements the larvae build additional segments of the tunnels so that their opening is directed against the water current; as a result, the tunnels are long and tortuous. In a calm period the larvae change the position of their tunnels within 4 minutes so that one of the openings is directed upwards and cause a flow of water by undulating their abdomens in order to draw the sinking minute organisms into the tunnels. However, in quite quiet water the larvae die in a fortnight. This adaptation thus allows the larvae to survive a period of temporary unfavourable conditions. The calm never lasts as long as a fortnight on a lake, especially in its exposed parts; its spells are rather short. Psychomyids have, therefore, great adaptive reserves. Their undulation of the abdomen to incite a water flow is also homologous with the behaviour of the larvae of the third group, when deprived of their cases they are forced to build retreats attached to the substrate. The psychomyid larvae are thus forms of the first caddis group characterized by incomplete functional adaptation to stagnant water, whereas larval *Plectrocnemia conspersa* (CURT.), which, like the other species of the family *Polycentropodidae*, as a rule lives in cold mountain streams and rivers, but is also met with in the littoral zone of large lakes (WESENBERG-LUND, 1943), has attained the state of full adaptation to the living conditions existing in these aquatic habitats. If in the mountain brooks the fishing nets of the larvae of this species are directed against the stream, in the lottoral zone of lakes they occur in the form of bags hanging from submerged plants (Fig. 6) and serving as traps for the sinking plankton.

The larvae of the species *Plectrocnemia conspersa* (CURT.) of the family *Polycentropodidae* therefore represent the forms adapted for life in both these habitats. Together with the members of the family *Psychomyidae*, which show an incomplete adaptation to stagnant water, they are undoubtedly forms characteristic of the phase of passage from the flowing water to the welter zone of lakes, where shallow water is well aerated owing to the action of the wind.

The larvae of the family *Hydroptilidae*, which is the only member of the second group of caddisflies, live in slow-flowing and overgrown streams and rivers and in the littoral zone of lakes, in small bays sheltered from the wind. If in the larvae of the first group the water movements in relation to their bodies are indispensable, in the case of hydroptilid larvae the movements of their bodies in relation to the water are sufficient. These larvae are free-living for four instars (NIELSEN, 1948) and in the fifth instar build cases (Figs. 12 and 13) anchored with silk threads to the submerged plants. The young larvae, as I have found in the laboratory, also bury themselves in a light substrate of detritus or among fallen leaves of plants. Their tracheal system is poorly developed. A few tracheae can be seen under the skin of the abdomen, which, as the larva grows and develops, expands to a relatively vast size (Figs. 10

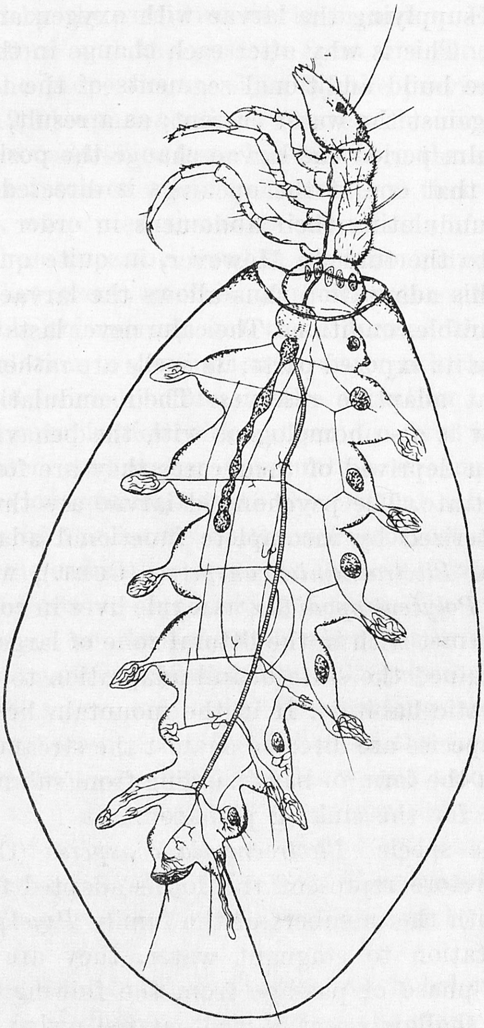

Fig. 21. Structure of larva of *Ithytrichia lamellaris* EAT., showing the tracheal system (after LAUTERBORN, 1902)

and 11). The lack of lasting retreats and cases in the first instars, sure enough, made such growth of the abdomen possible in contradistinction to the larvae of the third group, in which the tubular cases enclose their bodies tightly as early as the first instar and keep the size of the abdomen within definite limits. Instead, tracheal gills have developed from the skin folds similarly to the tracheal lamellae in *Ithytrichia lamellaris* EAT. (Fig. 21). The cases made by the hydroptilid larvae are transparent or coated with threadlike algae, diatoms, or fine sand grains. The larvae do not come out of their cases and produce a water flow in them by undulating movements of the abdomen; in quite quiet waters the openings of the cases are considerably enlarged. While rearing the larvae of *Oxyethira* sp., Wesenberg-Lund (1943) placed them in crystallizers with water plants. After some time the larvae stretched long silk threads between the plants and balanced on them like equilibrists. They besides lowered themselves down the threads to the bottom of the tank. Behaviour of this type, consisting in moving along silk threads stretched between plants occurs also in the larvae of *Hydroptila* and *Agraylea*.

The members of the second group of caddisflies have therefore freed themselves from the imperative of environment to a certain degree. The environmental conditions of stagnant waters caused the development of vital activity of the larvae and their passage from the passive ways of living, characteristic of the caddisworms of the first group, to more active ones, by which they gained more autonomy.

Their becoming independent of water movements was connected with the detachment of the larvae from the substrate and the development of their locomotive faculty. It consists in the differentiation of the legs and their specialization for walking movements. The larvae of the third caddis group have achieved a full adaptation in this respect.

The larvae of the first group have relatively stiff legs and their coxae are pushed aside. In this connection the capacity of their protective and fishing structures considerably exceds the volume of their body. The larvae can easily turn over and change their position. They are insensitive to the gravitional force, for they can be found in all possible positions. In the members of the second group the coxae are directed downward and the femora somewhat forward so that the larvae can move their legs in the vertical plane. This is also connected with the structure of their cases, flattened laterally and with free spaces in the dorsal and ventral parts, enabling the dorso-ventral movements of the abdomen and protrusion of the legs to the front. The larvae of the third group can utterly protrude their legs forward. Each pair of their legs is longer than the preceding one so that, when the larva is hidden in the case, its tarsi project beyond the edge of the frontal opening. When travelling, the larva draws itself out of the case with the help of the third pair of legs hooked on the substrate. The detachment of larvae from the substrate and their crawling from place to place have undoubtedly conditioned the smaller size of the cases, which cling relatively closely to their bodies. Withdrawal of larvae into the narrow cases has led to the development of their ability to straighten and fold the legs to the front. The locomotive faculty of the cadis larvae arose owing to the complementary action of a complex of factors and is characterized by its phasal development, from the ability to move the coxae downwards from the horizontal position to their complete folding forward along the thorax. If the legs were the same length, the larvae would not be able to draw themselves out of their cases and crawl, because their forelegs do not serve for locomotion, in which the main role is played by the hindlegs. Moreover, the larvae show positive geotaxis and they are informed about the right position of their body by the weight of the case. This phenomenon has arisen as a result of the evolution of secondary orientation and has been fixed along with the evolution of the locomotive ability. It is, no doubt, a cenogenetic adaptation, the more so since the present behaviour of the portable-case-making larvae also shows traces of the lack of geotaxis, which certainly are vestiges of some functions of their ancestors.

The laboratory larvae stripped of their cases bury themselves in the substrate before they start building new cases. In the first phase of behaviour they can be seen in various positions. They do not leave their retreats in the substrate before they have glued together sand grains or vegetable particles all round their bodies, and then they gradually pull out the cemented mass, as the building of new well-fitting cases proceeds out of the substrate. Their crawling to another place is the next stage, in which the ventral side of the larvae's bodies is turned in accordance with the action of the gravitational force. These observations constituted the basis of the experiments described below.

Single larvae of *Limnephilus flavirocnis* (FABR.), *Limnephilus rhombicus* (L.), *Anabolia soror* McLACH., *Nemotaulius* (*Macrotaulius*) *punctatolineatus* (RETZ.), *Potamophylax rotundipennis* (BRAU.), *Brachycentrus montanus* KLAP., *Molanna angustata* CURT. and *Goera pilosa* (FABR.) were placed in glass vessels filled with water. Their responses to a touch with a glass rod, bent at a right angle at the end, were observed. The larvae hidden in the cases did not respond to a touch from the dorsal side at all, or withdrew still further inside, whereas the travelling larvae, when their thorax or case was touched, withdrew rapidly, retracting the body and folding the legs to the front. The same larvae stripped of their cases showed a different mode of behaviour. Touched from the dorsal side, they turned towards the rod and remained in this position longer than the time of touching. If the touch lasted for 1 second, the response took more than 2 seconds. If the larvae were touched 3 times at one-second intervals, they remained in the upturned position for over 5 seconds. In another experiment the glass rods were placed so that, resting on the tank edges, they suspended just above the larvae. After the first touch of the larvae with another glass rod they turned over. After 2—4 touches at one-second intervals they caught hold of the suspending rod, remaining in this position for a time longer than the duration of the stimulation, and next returned to their normal position. When the excitation was repeated rhythmically ten times, the larvae kept their upturned position for 20 seconds. The longer the stimulation, the longer was the response, which, measured from the moment when the stimulation was interrupted, always exceeded it in duration, and the larvae even travelled along the suspending rod, hanging on it with their backs partly touching the bottom of the tank.

The continuance of the reaction for a time longer than the time of stimulation indicates the inertness of this phenomenon and, conseuently, its share in the adaptive process. Each reactive system, changing its state in response to information from the surroundings, is characterized by inertia. This state, induced by the accomodation of the biological system to new environmental conditions, which accomodation is characteristic of each adaptive process (ROTHSCHUH, 1959), can be fixed by natural selection. ŠMALGAUZEN (1962) defines such a phenomenon as modyfying adaptive changes that mark out the direction of the evolutionary process of the given organism, and BRAESTRUP (1968) calls this a modificatory steering, owing to which at the passage to a new niche there occurs the formalization of the modified state by natural selection. This formalization or, according to WADDINGTON (1942) canalization, is the condition of the survival and evolution of next generations.

The above-described reaction is homologous with the lack of geotaxis in the behaviour of the larvae of the first and second groups of caddisflies and is also related to the positive thigmotaxis, revealed in the behaviour of the larvae stripped of their cases in the experiment carried out. This supports the theory that the building of portable cases is a cenogenetic adaptation which has arisen from the palingenetic adaptation associated with the satisfying of tactile requirements. On the other hand, positive thigmotaxis in the larvae deprived of their protective structures becomes transformed into defensive reactions when their tactile requirements have been satisfied, for the same stimulus makes the larvae hide rapidly in their cases. Thus thigmotaxis becomes inverted from positive to negative in the same way as the positive thermotaxis of thermophilous animals changes into a reaction of escape, if the ambient temperature exceeds a definite value.

The satisfaction of tactile reguirements is a phenomenon consisting in production of hypertension by means of external agents. In caddis larvae defensive reactions are probably released at a definite internal pressure.

In the previous section I described the hump-like processes on the first abdominal segment. Pressed by the case walls, they enahance the sensitivity of the larva to information from its surroundings. Observations carried out on the larvae stripped of their cases under a binocular microscope showed that the apical portions of these protuberances are rhythmically retracted into the inside of the body. These movements consist of several shallow and one deeper retractions of their cones. Tenfold measurements taken with a stop-watch on the larvae of *Limnephilus flavicornis* (FABR.) and *Limnephilus rhombicus* (L.) showed that the shortest time of retraction of the protuberances and keeping them drawn in was 17 seconds and the longest time 20 seconds. The most frequently repeated values were 17 and 20 seconds, whereas the re-bulging took 2·5 seconds at the shortest and 3·5 seconds at the longest. This phenomenon indicates the densification of the internal environment in the larva body.

In order to examine the relationship between the function of these protuberances and the circulatory system, an experiment was carried out, which was expected to elucidate the functional correlation of these organs with the heart rhythm.

Larvae of *Limnephilus flavicornis* (Fabr.) were placed singly in small glass crystallizers with water at a temperature of +24°C, and their heart pulsation, visible through the skin of the abdomen, was observed using a binocular microscope. Ten larvae of this species were examined and a uniform heart rhythm of 45 contractions per minute was found in them. The crystallizers with 5 larvae were next placed in dishes with ice. As will be seen from Table I, there was a fall in the number of heart contractions per minute in the larvae studied, as the water was cooled in the crystallizers.

Table I

Cardiac rhythm of larvae of *Limnephilus flavicornis* (Fabr.) at gradually lowered ambient temperature

Larva	Frequency of heart contractions of 5 larvae						
	+24°C	+18°C	+14°C	+10°C	+7°C	+4°C	+2°C
1	45	34	25	12	8	8	8
2	45	32	27	14	8	8	8
3	45	36	26	17	8	8	8
4	45	34	20	13	8	8	8
5	45	30	22	14	8	8	8

The table shows that also at temperatures from +7 to +2°C the heart rate is uniform and, as evidenced by this experiment, it is not affected by the irritation of the larvae with a glass rod or seizing them with forceps.

In the larvae examined the temperature of +7°C is the activity threshold, because from +7°C downwards their movements become slower and slower and the sensitivity of their bodies to touch decreases. At +2°C the larvae are inert and show no responses.

At the same time the contractions of the protuberances on the first abdominal segment were observed. At temperatures from +2 to 7+°C they were more or less regular, whereas from +7°C downwards, despite the steady rhythm of heart-beat, their intensity decreased along with the decline of their mobility, until the pulsation of the protuberances ceased completely at +2°C. When the crystallizers had been removed from the ice and the water in them became gradually warmer, the larvae resumed their normal activities and regained sensitivity to touch at as low a temperature as +7°C, when the abdominal protuberances began to pulsate normally.

The crystallizers with the remaining 5 larvae were also placed in dishes with ice. As the water was cooled, the heart pulsation behaved as in the previous series, and at a temperature of +7°C and during its further lowering to +2°C the heart rate was established at 8 contractions per minute. When the temperature was lowered on to +1·5°C, the heart-beat became arhythmical and its rate descreased below 8 contractions per minute.

When the water was rewarmed, the heart rate of 8 contractions per minute was restored at +7°C, but the larvae remained motionless. The warming up to +24°C accelerated the heart rate to 15 contractions per minute, which, however, was not accompanied by the restoration of the mobility of the larvae and the pulsation of their abdominal protuberances, and all these larvae died after the lapse of some time.

The experiment was repeated on five other larvae. After the water was cooled to +1·5°C, the crystallizers were removed from the ice. Next the water was allowed to warm up to +7°C and then the abdominal protuberances were artificially pressed with soft forceps at two-second interwals. Technical difficulties did not permit the simultaneous exertion of pressure on all the three protuberances, but only on the lateral ones or on the dorsal hump. Nevertheless, all the larvae came back to life and resumed normal activities. They were next reared on and in their development passed through the pupal stage.

A similar experiment was made on 5 larvae out of the water environment. The larvae removed from water did not show any fall in the heart rate as long as the abdominal protuberances pulsated. They stopped pulsating after 8—15 minutes, and from that moment onwards the heart rate decreased and the beat became arhythmical. The larvae in this state were placed back in water and the artificial pressure of the protuberances with forceps was applied in three of them. The larvae treated in this manner revived, whereas in the other two all the evident signs of life disappeared.

The foregoing experiments indicate that the contractions of the protuberances of the first abdominal segment are connected with the regulation of internal pressure, but their movements, being unautonomous, are controlled by information from the surroundings.

They probably play the same role as the rhythmical inward movements of the tracheal gills in the rhyacophilid and hydropsychid larvae, whose relatively thick body tegument does not allow appropriate contractions of the abdomen along its axis. Such contractions are possible in the larvae devoid of tracheal gills, owing to the loose joints of the segments of the abdomen and its flexibility.

The tracheal gills of the portable-case-making larvae are homologous to the tracheal lamellae of *Ithytrichia lamellaris* Eat., which grow out on the dorsal and ventral side of the abdominal segments. In these lamellae Lauterborn and Rimsky-Korsakov (1902) found large accumulations of tracheal capillaries (Fig. 21), similar to those in the tracheal gills of the travelling larvae.

Close-fitting cases of the members of the third group, adapted in respect of weight and size for transport, made it impossible for the respiratory surface of the abdomen to increase by augmenting its area, as it does in the larvae of the second group; the more so, because the tracheal gills appear in the travelling larvae in their postembryonic development, when their bodies are already enclosed in the cases. It is therefore natural that they are formed from the outfoldings of the abdominal skin.

Such tracheal gills must have evolved parallel to the formation of locomotive power and the acquisition of ability to construct portable cases. In the light of the foregoing they are of caenogenetic origin.

However, not all the species classified in the third group of caddisflies occur exclusively in stagnant waters. Many of them are also encountered in the zone of welter of the waves and in fast-flowing mountain-brooks. They include numerous species of the family *Limnephilidae*, such as the members of the tribes *Stenophylacini*, *Chaetopterygini* and *Chilostigmini* and the subfamilies *Ecclisopteryginae* and *Apataniinae*. The families *Goeridae*, *Brachycentridae*, *Beraeidae*, *Sericostomatidae*, *Lepidostomatidae*, *Odontoceridae* and some others are also represented in this group.

In the larvae that live in stagnant waters the tracheal gills occur on abdominal segments II—VIII. On the other hand, in many members of the species which inhabit the welter of waves in lakes or mountain-brooks the number of tracheal gills is partly or completely reduced. For example, the larvae of *Allogamus auricollis* (Pict.) have single tracheal gills on abdominal segments II—VII, those of *Crunoecia irrorata* (Curt.) on segments II—VI and of *Chaetopterygopsis maclachlani* Stein on segments II—V. In *Potamophylax nigricornis* (Pict.) the tracheal gills are not so well developed as they are in the related species *Potamophylax stellatus* (Curt.) (Nielsen, 1942). Nielsen thinks that this is associated with the fact that the larvae of *Potamophylax nigricornis* (Pict.) come out on to the land, as he found them on pads of dead soaked leaves by the edges of brooks. Larvae of *Crunoecia irrorata* (Curt.) and *Beraea pullata* (Curt.) were also found under similar conditions. The larvae of this last species have no tracheal gills at all, not unlike the larvae of *Enoicyla pusilla* (Burm.). I observed them in large numbers on big stones emerging from brooks and hardly washed over by water in the Śląski Beskid Mts. The larvae of *Enoicyla pusilla* (Burm.) are, however, land forms, which can be met with among fallen moist leaves, on mossy stones and rotten tree trunks (Wesenberg-Lund, 1943) and in watery meadows amidst a forest (Hickin, 1958).

The larvae of *Brachycentrus montanus* Klap., which live in mountain brooks and rivers, have tracheal gills, very short but forming bundles of 4—5 threads each, on segments II—VII, in which they resemble the larvae of *Oligoplectrum maculatum* (Fourc.), met chiefly with in lowland rivers. In *Micrasema longulum* McLach. the tracheal gills are lacking, but this species dwells in fast-flowing cold mountain-brooks. *Sericostoma personatum* (Spence), living in flowing water, has tracheal gills on abdominal segments II and III (Lestage, 1921).

The larvae of *Notidobia ciliaris* (L.) have tracheal gills on segments I—VIII (Silfvenius, 1905), but they live in the littoral zone of lakes. In the brook larvae of the same species the tracheal gills are reduced and very often present only on segments II and III.

The foregoing examples support the statement that these caddisflies have developed a secondary adaptation to flowing-water conditions, accompanied by the reduction of the tracheal gills. This is also indicated by the occurrence of the larvae of *Enoicyla pusilla* (Burm.) on land; this species belongs to the very well specialized family *Limnephilidae*, which is also shown by the structure of wings in the imago (see Section 2). The reduction of tracheal gills is therefore an adaptation to flowing water in forms evolutionarily adapted to stagnant water. In consequence, the adaptation of the larvae of *Enoicyla pusilla* (BURM.) to life outside the water environment is also a secondary adaptation to life on land.

Although the larvae of the third group are adapted for locomotive movements, the species that occur exclusively in flowing water arrange their cases so that their frontal openings are directed against the stream. I observed this phenomenon in mountain-brooks and it is often mentioned in literature. The reduction of tracheal gills is natural in this situation. JAKUBISIAKOWA (1933) observed some regularity in the arrangement of the larvae of *Goera pilosa* (FABR.) and the attachment of their cases to the stones in the littoral zone of Kierskie Lake. She found that most of the larvae occurred on the stone surfaces that faced the lake and in the gaps between the stones. She also observed the larvae settled on molluscs, e. g., on fresh-water mussels (*Unio* sp.), their cases being directed with their frontal openings towards the siphons. The travelling larvae that live in the littoral zone of lakes and in mountain-brooks are able to attach their cases to underwater objects with the secretion of their silk glands. Then they show lack of geotaxis, as they may be found in different positions. They are chatacterized by positive geotaxis only when moving. In addition, the larvae with tracheal gills, as I have observed in the members of *Brachycentrus montanus* KLAP., *Crunoecia irrorata* (CURT.), *Chaetopterygopsis maclachlani* STEIN and *Potamophylax stellatus* (CURT.) can regulate the flow of water through their cases in rapid currents by closing the frontal openings with their heads, which are relatively bigger than the heads of the larvae inhabiting stagnant waters. This is the phenomenon of phragmosis, which makes it possible for them to regulare the flow of water.

When these larvae were exposed to the action of a water stream in the laboratory experiments, they always became motionless and closed the openings of the cases with their heads. The water stream is thus the stimulus that incites the larvae to stop moving and attach themselves to the substrate.

As I have observed in natural conditions, the travelling larvae that live in mountain-brooks avoid rapid currents. They rather stay in places where the current breaks up and is slower or even imperceptible to the human eye. Unlike the larvae of the first group, when transferred from flowing water to a vessel with stagnant water, they do not leave their cases in search of new retreats, which is only natural, because in their evolution they passed through a stage of adaptation to stagnant waters. Their secondary adaptation to flowing waters also results from a historically evolved faculty, as the forms from which they derive lived in cold lotic waters. Similarly, the secondary adaptation of the larvae of *Enoicyla* RAMB. to life on land probably became possible owing to the ability acquired by them of regulation of their internal pressure, because, as can be seen from the experiments above, the heart rhythm of the larvae examined out of the water environment does not change, unless there is a drop in the frequency of pulsation of the protuberances on the first abdominal segment.

The foregoing considerations show that in the adaptive evolution of the caddis larvae each relatively terminal state is determined by the original conditions, for their return from stagnant waters to flowing waters and on to land proceeds along the same way as the passage of the larvae of the caddisflies' ancestors to aquatic life and the cenogenetic adaptation of the caddisflies to stagnant waters did.

The adaptive changes that have arisen in this way result from the modificatory steering of the adaptive process by the environment. They have been fixed by natural selection and hence in the experimentally induced reactions of caddis larvae one can distinguish traces of old functions, which were essential for their existence at some stages of their evolution.

5. Conclusions

The conclusions made in the course of the considerations presented in the particular sections of the first part of this paper are as follows:

1. The origin of caddisflies from a line common to them and to scorpionflies (*Mecoptera*) seems to be beyond any doubt.

2. The most primitive caddis larvae belong to the families *Rhyacophilidae*, *Philopotamidae* and *Glossosomatidae*.

3. The case-making larvae do not descend directly from the family *Rhyacophilidae*, but from an ancestor of this family, which also gave origin to the net-spinning forms. This fact contradicts Ross's opinions (1964); nevertheless, the same conclusion can be drawn from Pryor's study (1951) on the homology in the musculature of the anal prolegs.

4. The original habitat of caddis larvae are mountain-brooks of cold water rich in oxygen.

5. The division of the caddis larvae into three biological groups seems to be well grounded, since they are factual and reflect the phases and mechanism of the adaptive process of these insects.

6. The members of the first group are characterized by the most primitive structure and by their complete dependence on the movements of water in their habitat. Lack of the well-developed ability to perform locomotive movements of their legs is due to their passive ways of satisfying the living demands.

7. The fact that the larvae experimentally deprived of their fishing nets and protective shields bury themselves in the substrate is a response connected with their satisfaction of tactile requirements. This response is a fixed vestige of the adaptation of caddisflies' ancestors to life in soil and, therefore, it is a response arising from a palingenetic adaptation.

8. In the larvae of the first group the capability of building fishing nets and cases attached to the substrate, moulded under the influence of the steering action of environment, is a cenogenetic modification of a paligenetic adaptation

fixed by natural selection. Lack of geotaxis in these larvae confirms this thesis.

9. The second group of caddisflies is characterized by the relative activeness of motion and, consequently, a certain degree of independence on the environmental imperative. This is indicated by their increased respiratory surface and ethological adaptation to life in stagnant waters.

10. The members of the third group of caddisflies are marked by the greatest autonomy and relatively full vital activity. Their mode of satisfying living requirements is active, and their positive geotaxis appeared when the larvae became detached from the substrate and developed the faculty of locomotion.

11. The experimentally induced disappearance of geotaxis is related to the palingenetic adaptation and behaviour of the larvae of the first and second groups.

12. The construction of portable cases is connected with the development of locomotive ability. Thus, very much like positive geotaxis, it is a cenogenetic adaptation which took origin from a palingenetic adaptation associated with positive thigmotaxis.

13. Positive thigmotaxis turns into defence reactions as soon as the tactile requirements, resulting from the palingenetic adaptation, have been satisfied.

14. Physiological functions of the abdominal protuberances on segment I have been ascertained. Their pulsation is controlled by information from the surroundings and, as shown by experiments, their action is connected with the regulation of internal pressure, which exercises an influence on the sensitivity of the larvae to information from their environment. The protuberances have arisen as a result of the division and specialization of biological functions and are a structural cenogenetic adaptation.

15. The tracheal gills of the travelling larvae are homologous with the tracheal lamellae of the larvae of *Ithytrichia lamellaris* Eat. In this connection their origin is also cenogenetic.

16. The adaptation of the travelling larvae to the environment of flowing water is a secondary adaptation to the initial conditions.

17. The existence of larval *Enoicyla* Ramb. out of the water environment is an example of the re-adaptation of the caddis larvae to life on land and is associated with the mode of life of caddisflies' ancestors, but the making of portable cases, satisfaction of tactile requirements and securing of the suitable degree of humidity in the space between the case and the body undoubtedly caused the omission of the typical phase of soil inhabitation.

18. The traces of old functions, manifested by the experimentally induced reactions, constitute actual, though latent, features characteristic of evolution.

PART TWO

STUDIES ON PHOTORECEPTION IN CADDIS LARVAE

1. Introduction

An essential aspect of life of animals is their spatial orientation, in which the photoreceptors play an important role as links of information. The informative capacity of photoreceptors determines their sensitivity, which varies with their adaptation to light in time (Fidos, 1967, 1968). In his work on the effect of light on the tactic responses of the larvae of the species *Molanna angustata* Curt. Grębecki (1955) empirically demonstrated a great sensitivity of their photoreceptors, because the intensity of light used in the experiments corresponded with the "threshold stimulus of human eye"[1]. He also dealt in his study with the phenomenon of adaptability to light in time and found that a continuous light stimulus brings about evident adaptation, which leads to the complete vanishing of phototactic responses. No adaptation, however, occurs in the case of interrupted stimulation, which evokes normal responses. This may be presented as follows:

interrupted stimulation $\dashrightarrow$ tactic responses, no adaptation
continuous stimulation $\longrightarrow$ no responses, adaptation

Grębecki (1955) explains the occurrence of responses by the shock nature of stimulation, although, as he writes, "continuous light is a common ecological factor". His experiments were, in the first place, concerned with the primaeval orientation of larval *Molanna angustata* Curt. The evolutionary nature of this orientation is unquestionable, since it is a functional property of the structure that has arisen by way of phylogenetic evolution. Primaeval orientation is a historically conditioned adaptation of the organism and therefore the photostereotactic responses resulting from it should not take place owing to the continuity of the stimulus that causes the process of adaptation, unless by the stimulus we mean the artificial opposite of the natural stimulus. Moreover, adaptation decreases the sensitivity of the photoreceptors and, consequently, the light stimuli which produce stereotactic reactions in a natural environment would have to be markedly differentiated in respect of their energy.

The photoreceptors of each organism are adapted for the reception of light of a definite strength and quality, specific to them. The strength of an external stimulus need not equal the strength of the physiological impulse, because, if the organism is not equipped with a mechanism for automatic regulation, the environment itself constitutes a regulating barrier. If the light stimuli went beyond the functional possibilities of the photoreceptors, the shock nature of the stimulation would be indubitable, but this fact would generate rather lethal conditions. The conception of the shock action of discontinuous stimulation should thus be excluded as well, since it comes very close to the theory about the shock nature of spatial orientation in animals.

Although light seems to be a continuous factor in nature, it is a very changeable stimulus for animal organisms. Each environment, according to the elements that it contains, is very variable and differentiated with respect to the spectral composition of light. Each movement has its reflection in the light.

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[1] By the threshold stimulus of human eye Grębecki probably meant the differential threshold of perception, a subjective parameter under the conditions of experiments, their numerical values not being given.

The caddis larvae are bottom dwellers living in mountain-brooks and the littoral zones of other water reservoirs. They generally occur in shallow waters, where, in addition to the specific refraction and reflection of particular light waves, each unevenness of the water surface (e. g., ripples) brings about changes in the lighting. The light rays are reflected and refracted in various directions according to their angle of incidence. Stimulative luminosity in water can never be identified with the lighting at the water surface, as is commonly done, because it becomes markedly impoverished by the percentage of rays that have been reflected.

In this environment there occurs, in addition, the phenomenon of extinction, the degree of which is various for particular lengths of light waves (James and Birge, 1938) and depends on the transparence and depth of water (Sauberer and Ruttner, 1941; Harnisch, 1951). The undulating water surface acts as a set of convergent and divergent lenses, which are in constant motion, and the animals living in such conditions, e. g., caddis larvae, receive flickering light. Besides, the very movement of animals in relation to individual elements of the environment causes that they receive various quantities of light at the time of motion. The organ of sight is in addition an inertial system (Luizov, 1961; Fidos, 1967), which consists in the fact that the visual impression still lingers, when the stimulus has been cut off, and the one that follows also becomes fixed after some time. Hence, the perception rate should conform to the properties of the motor activity of the animal, and the sensitivity of its photoreceptors (thresholds of sensitivity) should also be related with this.

The purpose of the experiments presented below was to check the soundness of these assumptions nots only as to their cognitive nature, but chiefly with regard to their evolutionary aspect.

2. Material and methods

Larvae of the fifth instar belonging to the groups of caddisflies distinguished in the first part of this work were used for study. Particular groups were represented by the following species:

Group I — *Rhyacophila septentrionis* McLach.
Hydropsyche angustipennis (Curt.)
Group II — *Agraylea multipunctata* Curt.
Group III — *Limnephilus flavicornis* (Fabr.)
Potamophylax nigricornis (Pict.)

The larvae used in the experiments with light stimuli were adapted to darkness or a definite strength of light and placed in water, 2 cm deep, in rectangular (20 × 14 cm) or round (dia. 8 cm) glass vessels.

The round vessels were used to check whether or not the phenomenon of the so-called peripheric reaction (Grębecki, Kinastowski and Kuźnicki, 1954), which occurs in the caddis larvae as a manifestation of their spatial orientation, changes the picture of experiments as compared with that obtained with the rectangular vessels in the given lighting conditions.

The peripheric reaction results from the geometrical regularities of movements of the portable-case-making larvae and consists in a constant angle of rebounding from the obstacle encountered (90° in relation to a perpendicular one). In this connection a larva placed in a round vessel moves exactly along its circumference, along its "shortest chords".

The phenomenon of extinction of light rays, being very slight in two-centimetre-deep water, may be left out of this study.

The larvae examined received some amounts of white spot light produced by filament lamps (type RFT — 100 watt, 12 volt and type ZWLE — 20 watt, 6 volt). The strength of light was regulated with diaphragms in the lighting equipment or by changing the distance of the source of light from the subjects examined. Measurements of luminosity were made using a Ju 16 type lux-meter produced in the U.S.S.R. Only the values of stimulative luminosity as expressed by the results of light measurements under the vessel were taken into account.

In physiological optics the sensitivity of photoreceptors is characterized by threshold values, the measuring methods of which have been drawn from works by FIDOS (1966, 1968) and modified for the present study, as demanded by the technical aspect of the experiments. The differential sensitivity threshold (ΔB) has thus been included as the smallest value of the differences in illumination between two neighbouring fields to which the larvae responded under definite adaptive conditions:

$$\Delta B = B_o - B_t$$

where B_o is the illumination of the test area (stimulative luminosity) and B_t the illumination of its background, to which the larvae were adapted (adaptive luminosity).

The contrast sensitivity threshold (ε), which is expressed by the ratio of differential sensitivity threshold (ΔB) to illumination of background (adaptive luminosity)

$$\varepsilon = \frac{\Delta B}{B_t} = \frac{B_o - B_t}{B_t}$$

was also calculated in order that the perception of light contrasts and their values should be examined.

The times taken by reception of visual information, adaptation, and subsidence of the light stimulus action are given in the tables. The differential (ΔB) and contrast (ε) sensitivity thresholds are individual parameters, and for this reason all the experiments were carried out on series of 10 specimens in order to make the calculation of statistical data possible. Preliminary studies on a larger number of specimens (30) gave the same or very similar mean results and, therefore, a series of 10 larvae may be acknowledged to be representative. All the experiments were made in a dark room.

In the experiments which were designed to show whether uniform continuous light has an effect on the motor activity of the larvae, the glass vessels had their side walls and bottom covered with white paper and they were lighted from above through a pane of frosted glass. The strength of light was determined before each experiment. It was measured under the vessel through an opening cut out in the paper and next covered again.

The effect of contrast illumination on the locomotor activity of the travelling larvae was examined using vessels with black paper stuck all over its sides and lighted from below through a plate of frosted glass. On the other hand, a glass insert with squares of black paper stuck on it so that they formed a dark and light chequered pattern was slipped under the bottom of the vessels. The sides of the squares were more or less adjusted to the body length of the larvae examined and they were, respectively, 10, 20 and 30 mm long. The strength of light of the light fields was regulated with the help of a rheostat by the transformer of the lighting lamp and by laying a sheet of white paper under the chequer.

Each larva was observed for 30 minutes, which period was constant in all experiments. The time of movement of the larvae was measured with a stopwatch to an accuracy of 1 second.

3. The course and discussion of experiments

3.1. Thresholds of differential sensitivity under the conditions of adaptation to darkness and time of adaptation to light

The objective of the first set of experiments was to investigate the behaviour of larvae in uniform continuous lighting. The larvae were placed singly in the vessels prepared, after they had got adapted to darkness during the night directly preceding each run of the experiment. The stimulative luminosity was increased in each successive experiment and both the time from the moment when the light was switched on to the appearance of the optomotorial reaction (t_i) and the duration of reaction (t_a) were measured. Practically, each of the larvae examined was stimulated with illumination of 0·125, 0·25, 0·50, 0·75, 1, 3, 10, 50, 100 and 200 lux after it had been adapted to darkness during the night. The time of stimulation with illumination of particular values was 30 minutes. The duration of the motor activity induced in the larvae is given separately for each species in Tables II—VII, whereas the mean time of inertia compared with the mean time of motor activity is presented in percentages in Table VIII.

Tables II—VII show that in each series of 10 specimens representing a given species only 5—7 larvae moved under the influence of 0·125-lux illumination, but all of them exhibited motor activity with the illumination of 0·25 lux, and besides the mean duration of their activity was longer (Table VIII). As a result, we can determine the differential sensitivity threshold (ΔB) for the larvae of all the species examined at an adaptive luminosity $B_t = 0$, as ranging between 0·125 and 0·25 lux.

Table II

Time of acquirement of visual information (t_i) and time of motor activity (t_a) in larvae of *Rhyacophila septentrionis* Mc Lach. in 30-minute periods of illumination with continuous uniform light of various strength (in seconds)

Larva No.	0·125 lx		0·25 lx		0·50 lx		0·75 lx		1 lx		3 lx		10 lx		50 lx		100 lx		200 lx	
	t_i	t_a	t_i	t_a	t_i	t_a	t_i	t_a	t_i	t_a	t_i	t_a	t_i	t_a	t_i	t_a	t_i	t_a	t_i	t_a
1	3	6	3	10	3	48	2	98	1	120	1	612	0	1506	0	1800	0	1800	0	1800
2	—	—	3	8	3	52	2	114	1	134	1	813	0	1800	0	1800	0	1800	0	1800
3	3	4	3	10	2	23	2	86	1	280	1	746	0	1234	0	1800	0	1800	0	1800
4	3	3	3	15	3	96	2	72	1	312	1	750	0	1590	0	1800	0	1800	0	1800
5	—	—	3	12	3	87	2	120	1	144	1	812	0	1612	0	1800	0	1800	0	1800
6	3	7	3	9	3	49	2	44	1	198	1	903	0	1800	0	1800	0	1800	0	1800
7	—	—	3	9	2	34	2	58	1	256	1	406	0	1402	0	1800	0	1800	0	1800
8	3	6	3	18	3	56	2	86	1	143	1	991	0	1615	0	1800	0	1800	0	1800
9	—	—	3	24	3	67	2	131	1	211	1	524	0	1800	0	1800	0	1800	0	1800
10	3	2	3	14	3	82	2	182	1	160	1	856	0	1412	0	1800	0	1800	0	1800
$\bar{x}$	1·8	3	3	13	2·6	59	2	99	1	196	1	741	0	1577	0	1800	0	1800	0	1800

Table III

Time of acquirement of visual information (t_i) and time of motor activity (t_a) in larvae of *Hydropsyche angustipennis* (Curt.) in 30-minute periods of illumination with continuous uniform light of various strength (in seconds)

Larva No.	0·125 lx		0·25 lx		0·50 lx		0·75 lx		1 lx		3 lx		10 lx		50 lx		100 lx		200 lx	
	t_i	t_a	t_i	t_a	t_i	t_a	t_i	t_a	t_i	t_a	t_i	t_a	t_i	t_a	t_i	t_a	t_i	t_a	t_i	t_a
1	—	—	3	8	3	42	2	114	1	222	1	374	1	678	0	1420	0	1800	0	1800
2	3	7	3	15	2	56	2	99	2	247	1	402	1	712	0	1324	0	1800	0	1800
3	3	11	3	19	2	101	2	151	1	306	1	312	1	684	0	1115	0	1800	0	1800
4	3	9	3	12	3	36	2	119	1	312	1	356	1	713	0	1224	0	1800	0	1800
5	—	—	3	9	3	45	2	106	1	259	1	324	1	706	0	1348	0	1800	0	1800
6	—	—	3	7	2	39	2	82	2	272	1	371	1	678	0	1215	0	1800	0	1800
7	3	5	3	11	2	68	2	94	2	299	1	404	1	703	0	1607	0	1800	0	1800
8	3	7	3	19	2	87	2	140	1	309	1	467	1	694	0	1462	0	1800	0	1800
9	—	—	3	11	3	69	2	98	1	314	1	368	1	679	0	1454	0	1800	0	1800
10	3	4	3	16	3	74	2	96	1	286	1	392	1	702	0	1399	0	1800	0	1800
$\bar{x}$	1·8	4	3	13	2·5	62	2	110	1·3	283	1	377	1	695	0	1357	0	1800	0	1800

Table IV

Time of acquirement of visual information (t_i) and time of motor activity (t_a) in larvae of *Agraylea multipunctata* Curt. in 30-minute periods of illumination with continuous uniform light of various strength (in seconds)

Larva No.	0·125 lx		0·25 lx		0·50 lx		0·75 lx		1 lx		3 lx		10 lx		50 lx		100 lx		200 lx	
	t_i	t_a	t_i	t_a	t_i	t_a	t_i	t_a	t_i	t_a	t_i	t_a	t_i	t_a	t_i	t_a	t_i	t_a	t_i	t_a
1	3	4	3	4	3	19	2	21	1	71	1	135	0	306	0	452	0	491	0	620
2	3	6	3	15	3	24	2	38	2	53	1	144	0	343	0	298	0	402	0	514
3	—	—	3	8	2	13	2	41	2	99	1	128	0	401	0	507	0	606	0	701
4	—	—	3	6	3	16	2	56	1	74	1	182	0	348	0	494	0	701	0	742
5	—	—	3	9	2	19	2	19	1	77	1	140	0	299	0	486	0	523	0	689
6	—	—	3	11	2	12	2	24	2	86	1	126	0	280	0	492	0	532	0	544
7	3	6	3	14	3	18	2	35	1	79	1	114	0	279	0	390	0	496	0	579
8	—	—	3	10	3	21	2	39	2	76	1	132	0	302	0	456	0	512	0	524
9	3	8	3	9	3	14	2	29	1	81	1	141	0	366	0	412	0	467	0	513
10	3	7	3	14	2	17	2	31	1	104	1	120	0	312	0	436	0	519	0	567
$\bar{x}$	1·4	3	3	10	2·6	17	2	33	1·4	80	1	136	0	324	0	442	0	523	0	599

Table V

Time of acquirement of visual information (t_i) and time of locomotor activity (t_a) in larvae of *Limnephilus flavicornis* (FABR.) in 30-minute periods of illumination with continuous uniform light of various strength in a rectangular vessel (in seconds)

Larva No.	0·125 lx		0·25 lx		0·50 lx		0·75 lx		1 lx		3 lx		10 lx		50 lx		100 lx		200 lx	
	t_i	t_a	t_i	t_a	t_i	t_a	t_i	t_a	t_i	t_a	t_i	t_a	t_i	t_a	t_i	t_a	t_i	t_a	t_i	t_a
1	—	—	2	8	2	10	1	9	1	60	1	148	0	159	0	241	0	382	0	420
2	2	9	1	9	1	15	1	45	1	74	1	78	0	176	0	202	0	196	0	251
3	—	—	1	6	1	13	1	58	1	138	1	129	0	180	0	189	0	218	0	246
4	2	8	2	8	2	11	1	30	1	70	1	135	0	246	0	237	0	340	0	360
5	—	—	2	11	1	14	1	32	1	59	1	92	0	192	0	241	0	256	0	259
6	3	4	2	7	1	8	1	15	1	130	1	167	0	129	0	144	0	382	0	360
7	—	—	1	9	1	9	1	29	1	119	1	130	0	181	0	186	0	301	0	338
8	—	—	2	9	1	14	1	43	1	134	1	130	0	156	0	231	0	263	0	341
9	2	7	1	9	1	10	1	15	1	92	1	119	0	217	0	199	0	264	0	323
10	2	6	1	10	1	12	1	29	1	79	1	139	0	121	0	189	0	310	0	372
$\bar{x}$	1·1	3	1·5	9	1·2	12	1	29	1	95	1	127	0	186	0	220	0	291	0	327

Table **VI**

Time of acquirement of visual information (t_i) and time of locomotor activity (t_a) in larvae of *Limnephilus flavicornis* (Fabr.) in 30-minute periods of illumination with continuous uniform light of various strength in a round vessel (in seconds)

Larva No.	0·125 lx		0·25 lx		0·50 lx		0·75 lx		1 lx		3 lx		10 lx		50 lx		100 lx		200 lx	
	t_i	t_a	t_i	t_a	t_i	t_a	t_i	t_a	t_i	t_a	t_i	t_a	t_i	t_a	t_i	t_a	t_i	t_a	t_i	t_a
1	2	8	2	12	1	13	1	29	1	58	1	127	0	181	0	179	0	242	0	309
2	—	—	2	7	1	14	1	30	1	69	1	88	0	139	0	168	0	271	0	383
3	3	4	1	11	1	15	1	7	1	107	1	130	0	168	0	200	0	243	0	421
4	—	—	1	9	2	9	1	34	1	121	1	136	0	173	0	186	0	324	0	303
5	2	9	1	8	1	12	1	16	1	156	1	131	0	198	0	230	0	247	0	278
6	2	7	2	10	2	13	1	39	1	121	1	103	0	181	0	242	0	278	0	349
7	—	—	2	6	2	10	1	27	1	108	1	113	0	152	0	141	0	326	0	363
8	—	—	1	11	1	12	1	18	1	83	1	80	0	127	0	191	0	321	0	434
9	2	6	2	9	1	9	1	54	1	121	1	153	0	153	0	186	0	288	0	421
10	3	5	2	9	1	11	1	19	1	116	1	168	0	172	0	241	0	316	0	408
$\bar{x}$	1·4	4	1·6	9	1·3	12	1	27	1	106	1	123	0	164	0	208	0	286	0	307

Table VII

Time of acquirement of visual information (t_i) and time of locomotor activity (t_a) in larvae of *Potamophylax nigricornis* (Pict.) in 30-minute periods of illumination with continuous uniform light of various strength (in seconds)

Larva No.	0·125 lx		0·25 lx		0·50 lx		0·75 lx		1 lx		3 lx		10 lx		50 lx		100 lx		200 lx	
	t_i	t_a	t_i	t_a	t_i	t_a	t_i	t_a	t_i	t_a	t_i	t_a	t_i	t_a	t_i	t_a	t_i	t_a	t_i	t_a
1	2	8	2	8	2	11	1	49	1	123	1	156	0	139	0	13	—	—	—	—
2	3	4	2	7	2	14	1	33	1	94	1	201	0	141	0	24	—	—	—	—
3	—	—	2	12	1	13	1	68	1	141	1	248	0	162	0	38	—	—	—	—
4	2	6	1	10	2	8	1	29	1	112	1	256	0	193	0	34	—	—	—	—
5	2	5	2	6	1	17	1	45	1	153	1	233	0	202	0	45	—	—	—	—
6	2	7	2	5	1	21	1	39	1	124	1	189	0	170	0	56	—	—	—	—
7	—	—	1	9	1	10	1	62	1	131	1	193	0	154	0	33	—	—	—	—
8	—	—	1	10	2	19	1	51	1	86	1	148	0	101	0	19	—	—	—	—
9	3	6	1	6	2	15	1	47	1	111	1	154	0	123	0	24	—	—	—	—
10	3	4	2	9	1	18	1	49	1	132	1	182	0	110	0	16	—	—	—	—
$\bar{x}$	1·8	4	1·6	8	1·5	15	1	47	1	121	1	196	0	149	0	30	—	—	—	—

These experiments were carried out in rectangular vessels, but in the case of the travelling larvae of *Limnephilus flavicornis* (FABR.) round vessels were also used. It was thus possible to find that the shape of the vessel has no stimulative effect on the locomotor activity of the larvae. Although there was a stimulus in the round form of the vessel, the peripheric reaction was not released owing to the uniform constant illumination; this reaction, however, occurs with contrast illumination (see Subsection 3·3).

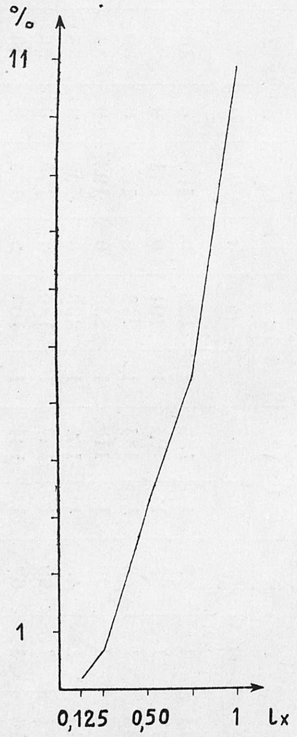

Fig. 22. Adaptation time curve in percentages of larvae of *Rhyacophila septenirionis* MC LACH. relative to the differences between adaptive background $B_t = 0$ and stimulative luminositties from 0·125 to 1 lux

The mean results obtained in the experiments carried out in rectangular and round vessels (Tables V and VI, respectively) are very much alike and for some values of illumination (e. g., 0·25 and 0·50 lux) the same. For this reason they may be reduced to means from the results of experiments with 20 larvae of *Limnephilus flavicornis* (FABR.) (Table VIII).

In the case of uniform continuous illumination the time of motor activity is also the time of adaptation to stimulative luminosity and depends on the strength of illumination (Table VIII). The intenser the illumination is, the stronger, as a rule, the excitation and the comparatively longer the adaptation. The relatively greatest increment in the time of adaptation, being a function of increasing differences between the stimulative luminosity and the initial adaptive background $B_t = 0$, was observed in the larvae of *Rhyacophila septetrionis* McLach. (Table VIII, Figs. 22 and 23) and *Hydropsyche angustipennis* (Curt.) (Table VIII, Figs. 24 and 25). In the larvae of *Rh. septentrionis* McLach this state is particularly distinct with illuminations above 3 lux, since up to this value they keep motionless for most of the time of stimulation. On the other hand, the larvae of *H. angustipennis* (Curt.) remain motionless most of the time at illuminations up to 10 lux, but the increase in the time of adaptation is somewhat larger for the values of illumination up to 1 lux (Fig. 24) and smaller for those above 3 lux (Fig. 25) than it is in *Rh. septentrionis* McLach. The mean time of adaptation of larval *Rh. septentrionis* McLach. at illuminations up to 10 lux lies within limits of the 30-minute stimulative luminosity. Since some larvae of this species showed full activenness at this illumination, just as for 50, 100 and 200 lux (Table II), it may be assumed that the time of adaptation begins to exceed the fixed time of stimulation from as low an illumination as 10 lux upwards. Practically, the time of adaptation is never longer than that of stimulation, for if the stimulation has been cut off but the reaction lingers on, it then includes the time of inertia. If, however, the reaction has a continuous course within the fixed time of stimulation and if this time were to be uninterruptedly prolonged to infinity, we might expect that the adaptation

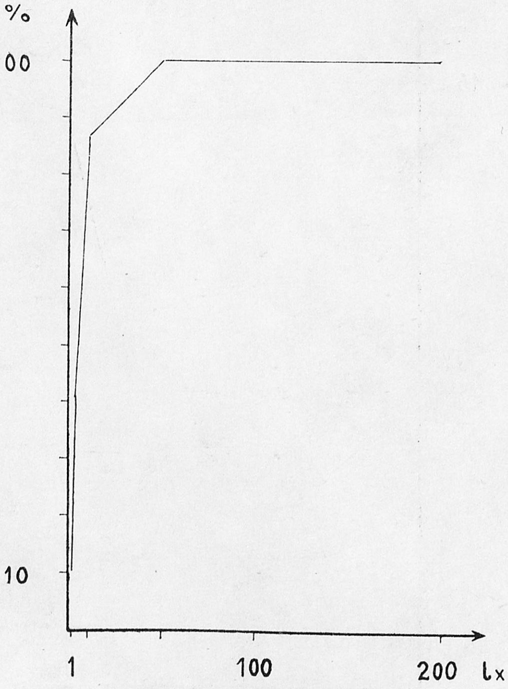

Fig. 23. Adaptation time curve in percentages of larvae of *Rhyacophila septentrionis* Mc. Lach relative to the differences between the adaptive background $B_t = 0$ and stimulative luminosities from 1 to 200 lux

will be completed after the period initially designed for stimulation. However unknown, the adaptation time will then be longer than the fixed time of stimulation.

If under laboratory conditions the time of adaptation to light exceeds the beforehand established time of definite stimulation, this may mean that the larvae are adapted for the reception of given information and the time of stimulation may be prolonged in order to ecxamine the duration of adaptation,

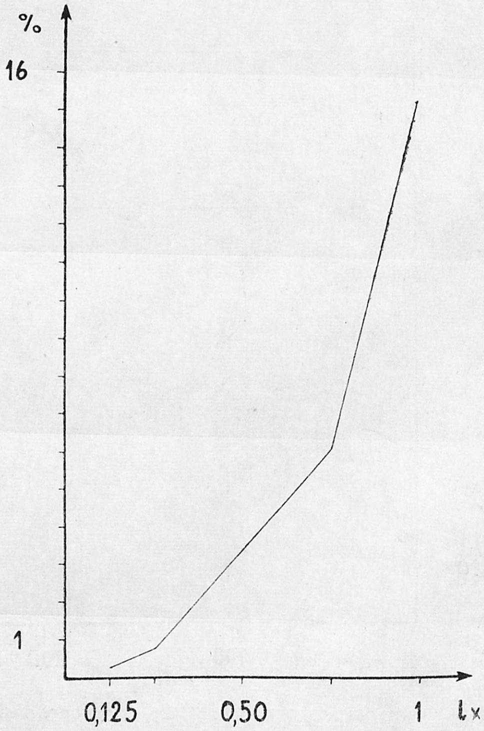

Fig. 24. Adaptation time curve in percentages of larvae of *Hydropsyche angustipennis* (CURT.) relative to the differences between the adaptive background $B_t = 0$ and stimulative luminosities from 0·125 to 1 lux

or that under natural conditions the appearance of an analogous stimulus lasting longer than the here used fixed time of stimulation will cause a forced adaptation at a suitable time and, according to the accomodative ability and tolerance, this adaptation may be fixed by natural selection in the sequence of successive generations. The occurrence of such a stimulus may be due to some changes that have taken place in the environment or it may be associated with the passage of the larvae to another mode of acquisition of food, e. g., their leaving dark retreats and acquiring food with the help of fishing nets, which entails their stay in a relatively strong illumination for a suitably long time.

Tables II—VII show that the time of motor activity or adaptation (t_a) varied from specimen to specimen with particular intensities of illumination

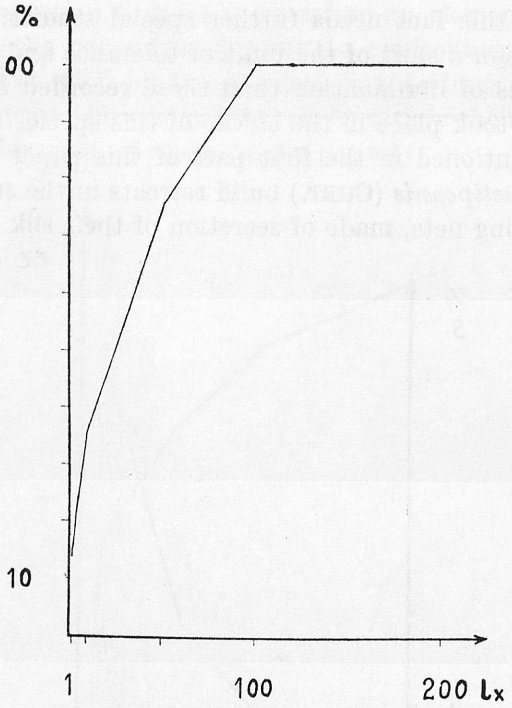

Fig. 25. Adaptation time curve in percentages of larvae of *Hydropsyche angustipennis* (Curt.) relative to the differences between the adaptive background $B_t = 0$ and stimulative luminosities from 1 to 200 lux

within groups. For example, in *Rh. septentrionis* McLach. examined at an illumination of 3 lux (Table II) larva No. 8 had the longest time of adaptation (991 seconds) and larva No. 7 the shortest (406 seconds). If we assume that the time of stimulation with this illumination is 500 seconds, the time of adaptation of larva No. 8 will exceed the fixed time of stimulation. This means that at the illumination of 3 lux, given here by way of example, the photoreceptors of larva No. 7 are more efficient than those of larva No. 8 and that they better tolerate the loads of light in time. This example as well as the wide range of the figures which in the table columns represent the time of adaptation proves also that the selection zone of this parameter is very wide, and the specimens with the parameters representing the extreme values, which may appear more suitable for the changes in the environment, have chances for better evolution.

In the larvae of *Hydropsyche angustipennis* (Curt.) the time of adaptation lies within the range of the 30-minute stimulation with illuminations up to 50 lux and in the case of the illumination of 100 lux it exceeds the fixed time of stimulation (Tables III and VIII). This is due to the application of fixed values of illumination. However, as the specimens examined showed the complete lack of full motor activity at an illumination of 50 lux, it may be supposed that the threshold values of illumination at which the adaptation time exceeds the fixed time of stimulation will be between 50 and 100 lux. Nevertheless, the explanation of this fact needs further special studies. In consequence of the adaptive evolution a shift of the limit of tolerance and accomodative abilities to higher values of illumination than those recorded for *Rhyacophila septentrionis* McLach. took place in the larvae of this species (Table VIII).

As has been mentioned in the first part of this paper (Fig. 9), the larvae of *Hydropsyche angustipennis* (Curt.) build retreats in the substrate in the form of tunnels with fishing nets, made of secretion of their silk glands, stretched at the tunnel entrance. The nets, as has been observed in the laboratory, are often examined by the larvae, which for this purpose go out of their dark retreats and stay for some time in better illuminated places, whereas the larvae of *Rhyacophila septentrionis* McLach. do not generally leave their shelters. However, these last larvae live in mountain-brooks, both in strongly shadowed places and in open sunlit ones, and in this connection the light that gets into their retreats varies, though not very much, in intensity. This may also explain the range of adaptation time in larval *Rh. septentrionis* McLach. (Table II).

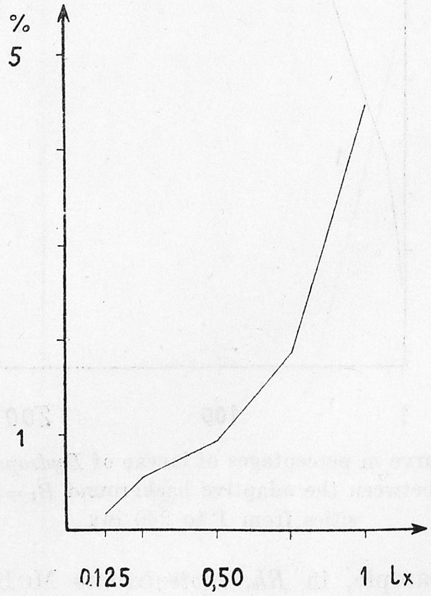

Fig. 26. Adaptation time curve in percentages of larvae of *Agraylea multipunctata* Curt. relative to the differences between the adaptive background $B_t = 0$ and stimulative luminosities from 0·125 to 1 lux

The range of adaptation time in the members of the species examined suggests that a similar range occurs within specific population. A reduced time of adaptation implies a relatively greater efficiency of the photoreceptors, which is of great importance to the larvae in the struggle for the attainment and maintenance of their ecological position, for it improves their reception and transformation of informative energy from the environment and, in consequence, their spatial orientation.

The time of adaptation to light is therefore an element which enters into the composition of the general adaptation to environment and is subject in its zones to natural slection by the physical surroundings and connected with the larvae's stay in light , necessary for them to satisfy their vital requirements, and with the development of their motor activity.

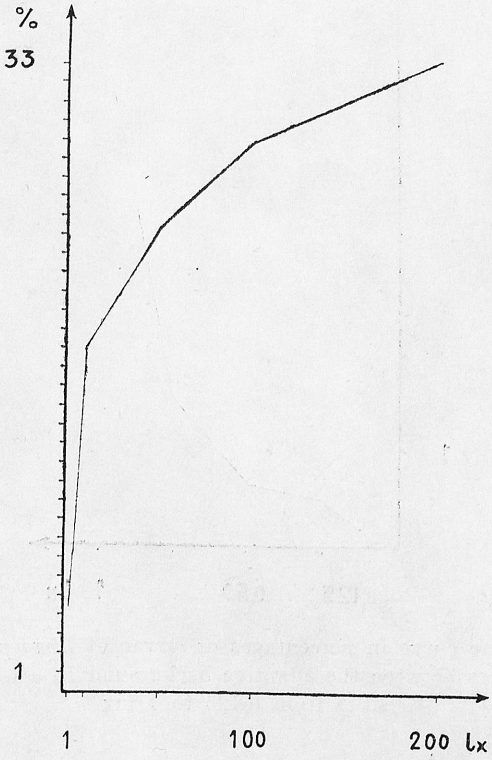

Fig. 27. Adaptation time curve in percentages of larvae of *Agraylea multipunctata* Curt. relative to the differences between the adaptive background $B_t = 0$ and stimulative luminosities from 1 to 200 lux

The larvae of *Agraylea multipunctata* Curt., belonging to the second group of caddisflies, show a further reduction in the time of adaptation (Table IV, Figs. 26 and 27) at particular illuminations used in the experiments. The increase in the time of adaptation as a function of growing differences between the stimulative luminosity and the initial adaptive background $B_t = 0$ is considerably smaller than in the previous species. At none of the illuminations used, not excluding 200 lux, does the adaptation time exceeds the fixed time of stimulation and so the larvae remain motionless for most of the latter time, i. e., 66·72—99·83 per cent of it, according to the intensity of illumination (Table VIII). This indicates that the larvae of *A. multipunctata* Curt. are adapted to withstand relatively greater light loads in their environment. They, besides, occur chiefly on submerged weeds in the littoral zone, in places which are not shadowed by the shore vegetation. Moreover, as in most members of the family *Hydroptylidae*, their cases, made of secretion of their silk glands (Fig. 12) are highly translucent.

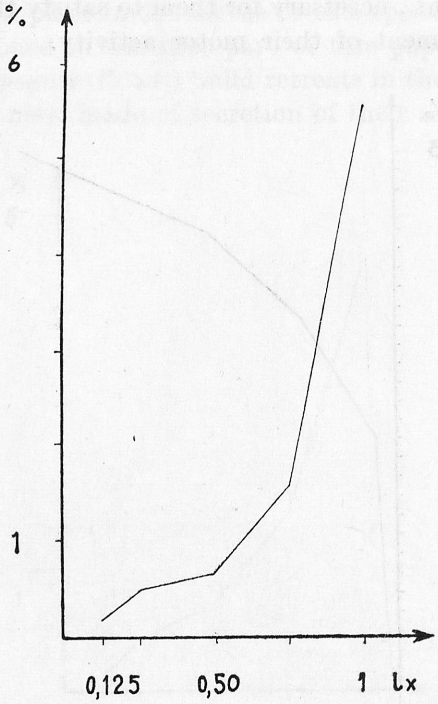

Fig. 28. Adaptation time curve in percentages of larvae of *Limnephilus flavicornis* (FABR.) relative to the differences between the adaptive background $B_t = 0$ and stimulative luminosities from 0·125 to 1 lux

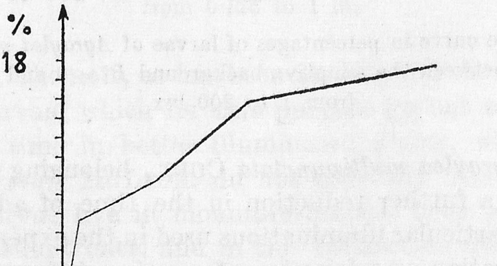

Fig. 29. Adaptation time curve in percentages of larvae of *Limnephilus flavicornis* (FABR.) relative to the differences between the adaptive background $B_t = 0$ and stimulative luminosities from 1 to 200 lux

The larvae of *Limnephilus flavicornis* (Fabr.), which here represent the third group of caddisflies (Tables V and VI, Figs, 28 and 29), have the adaptation time still more reduced as compared with *Agraylea multipunctata* Curt., especially at illuminations above 3 lux. Below this value the differences are small, which indicates a similar level of efficiency of the photoreceptors at low- value illuminations. The larvae remain inert for most of the time of stimulation (82·39—99·81 per cent) (Table VIII) and at illuminations above 3 lux the time of inertia (t_0) begins to increase more clearly in comparison with that in the larvae of the species belonging to the second group of caddisflies.

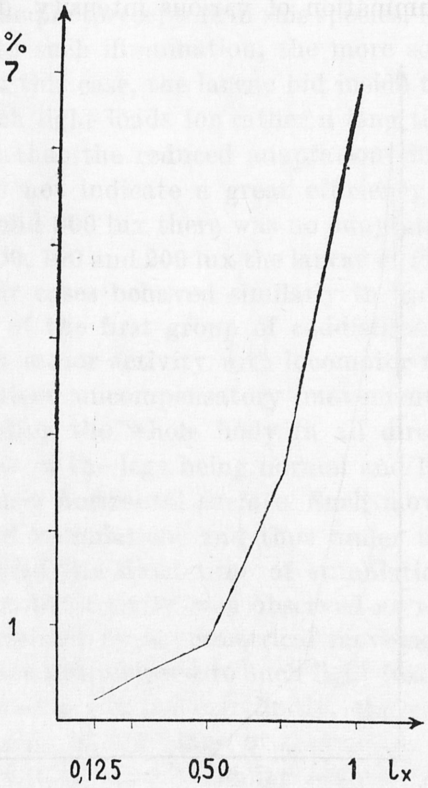

Fig. 30. Adaptation time curve in percentages of larvae of *Potamophylax nigricornis* (Pict.) relative to the differences between the adaptive background $B_t = 0$ and stimulative luminosities from 0·125 to 1 lux

As in the previous species, an increase in the time of adaptation in the larvae of *L. flavicornis* (Fabr.) at illuminations below 1 lux is brought about by small differences in lighting up, whereas above 1 lux, while the differences between the stimulative luminosity and the initial adaptive background $B_t = 0$ become greater and greater, the adaptation time deviates most from proportionality (Fig. 29). This example shows that the relative increments in the adaptation time can be induced only by successively increasing differences in illumination. It follows that in intense illumination larvae respond exclusively to big contrasts (see Subsection 3·3).

The larvae of *Limnephilus flavicornis* (Fabr.) are portable-case-making travelling forms. Their locomotor activity is possible only when the whole thorax is stuck out of the case. The photoreceptors must therefore be adapted for reception of light information which is markedly differentiated and varying with time, because illumination of various intensity, derived from light rays reflected from nearby objects, acts on them when the larvae are in motion.

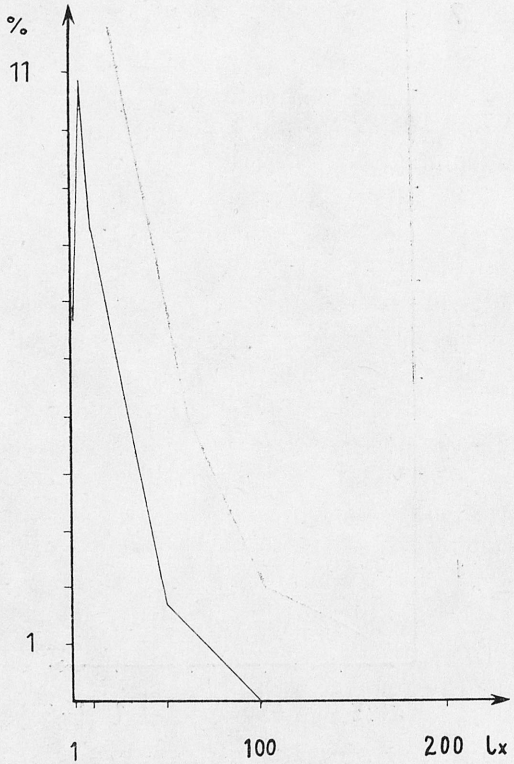

Fig. 31. Adaptation time curve in percentages of larvae of *Potamophylax nigricornis* (Pict.) relative to the differences between the adaptive background $B_t = 0$ and stimulative luminosities from 1 to 200 lux

The larvae of *Potamophylax nigrocornis* (Pict.), which also belong to the third group of caddisflies, resemble those of *Limnephilus falvicornis* (Fabr.) in respect of adaptation time (t_a), but this is the case at illuminations up to 10 lux (Table VII, Figs. 30 and 31). Below 10 lux the differences are small, the time of adaptation being either longer, at illuminations of 0·50, 0·75, 1 and 3 lux, or shorter, at 0·25 and 10 lux (Table VIII). On the other hand, a rapid drop in adaptation time is observed above 10 lux (Fig. 31). If at illuminations up to 3 lux the mean time of adaptation still showed an upward tendency, reaching 10·89 per cent of the fixed time of stimulation at 3 lux, at an illumination of 10 lux it fell as low as 8·28 per cent and at 50 lux to 1·87 per cent. In the case of illuminations of 100 and 200 lux there were no evident locomotor responses, and the larvae withdrew deep into their cases. This was therefore a sui generis escape reflex, consisting in an attempt to break off the connection with the external information in a specific manner. This behaviour suggests that the reduced time of adaptation at the illuminations of 10 and 50 lux does not indicate a greater efficiency of the photoreceptors in this species, but the lack of tolerance and accommodability to such illumination, the more so since after the period of adaptation, forced in this case, the larvae hid inside their cases. Apparently, they cannot endure such light loads for rather a long time. Another argument supporting the opinion that the reduced adaptation time at the illuminations of 10 and 50 lux does not indicate a great efficiency of the photoreceptors is the fact that at 100 and 200 lux there was no adaptation at all.

At illuminations of 50, 100 and 200 lux the larvae of *Potamophylax nigrocornis* (Pict.) stripped of their cases behaved similarly to the larvae of *Rhyacophila septentrionis* McLach. of the first group of caddisflies. At an illumination of 50 lux they began their motor activity with locomotor movements, which next turned into asymmetrical uncompensatory movements. These consisted in straightening and bending the whole body in all direction in an incoherent manner, the movements of the legs being normal and like those performed by the larvae travelling on a horizontal surface. Such movements were sustained throughout the time of stimulation, and thus under these circumstances the adaptation time exceeded the fixed time of stimulation. At illuminations of 100 and 200 lux full motor activity was observed as well, and from the very beginning it was represented by asymmetrical movements. This indicates the fact that these larvae are not adapted to such light loads. The foregoing observations allow the following conclusions: firstly, the case weight informs the larvae about the direction of the plane of travelling; secondly, the larvae of the species under discussion show a similar behaviour to that of the larvae of more primitive *Rhyacophila septentrionis* McLach. in definite conditions. These are undoubtedly traces of a function of their ancestors. They manifest themselves in definite conditions and protect the existence of the larvae, because if some sand is placed near them in the vessel, they bury themselves in it immediately. Light is the source of their motor activity and the portable protective structures caused its change into symmetrical compensatory movements, which were possible owing to the ability acquired by the larvae to perform the same movements of the left and right sides of the body and to tarvel on the horizontal surface (see also Subsection 3·3).

Like *Rhyacophila septentrionis* McLach., the larvae of *Potamophylax nigricornis* (Pict.) occur in mountain-brooks, but on the top and side surfaces of underwater stones, often on stones only washed by water. They represent the phase of passage from water on to land, because they are also met with near the banks of brooks, among damp dead leaves. Their taking shelter from light is therefore the function that prevents them from losing moisture.

Table IX

Time of acquirement of visual information (t_i) and time of locomotor activity (t_a) in larval instar II of *Limnephilus flavicornis* (Fabr.) in 30-minute periods of illumination with continuous uniform light of various strength (in seconds)

Larva No.	0·125 lx		0·25 lx		0·50 lx		0·75 lx		1 lx		3 lx		10 lx		50 lx		100 lx		200 lx	
	t_i	t_a	t_i	t_a	t_i	t_a	t_i	t_a	t_i	t_a	t_i	t_a	t_i	t_a	t_i	t_a	t_i	t_a	t_i	t_a
1	3	5	3	11	3	34	2	96	1	204	1	442	1	1121	0	1402	0	1800	0	1800
2	3	7	3	14	3	48	2	88	1	186	1	654	1	1258	0	1800	0	1800	0	1800
3	—	—	3	10	3	25	2	59	1	223	1	512	1	1020	0	1731	0	1800	0	1800
4	3	7	3	9	3	33	2	72	1	313	1	704	1	1342	0	1800	0	1800	0	1800
5	3	4	3	7	3	29	2	94	1	309	1	811	1	1412	0	1800	0	1800	0	1800
6	3	9	3	20	2	64	1	102	1	168	1	593	1	1216	0	1634	0	1800	0	1800
7	—	—	3	17	3	51	2	88	1	214	1	622	1	1308	0	1708	0	1800	0	1800
8	—	—	3	10	2	72	2	112	1	308	1	686	1	1367	0	1800	0	1800	0	1800
9	—	—	3	8	3	27	2	79	1	256	1	714	1	1408	0	1680	0	1800	0	1800
10	3	6	3	15	3	41	2	68	1	172	1	587	1	1514	0	1800	0	1800	0	1800
$\bar{x}$	1·8	4	3	12	2·8	42	1·9	86	1	235	1	632	1	1297	0	1715	0	1800	0	1800

The time of adaptation to light, as a parameter having selective values, is an important indication of the process of sight evolution and it determines the efficiency of the photoreceptors. The development of this efficiency, consisting in the reduction of the adaptation time, is phylogenetic, but the efficiency is also moulded in the individual development, as will be seen from Table IX, which presents the values of the time od adaptation for the second instar larvae of *Limnephilus flavicornis* (FABR.).

It is more convenient to use the second larval instar than the first instar for these experiments, because the former shows more distinct phototactic reactions. The reactions visible and provable in the first instar are, above all, thigmotactic ones. This indicates that the formalization of the sense organs in relation to the information channels of the environment proceeds by degrees in the postembryonic development.

Table IX shows that the time of adaptation to light in the second larval instar of *Limnephilus flavicornis* (FABR.) resembles that of *Rhyacophila septentrionis* McLACH. (Table II) and *Hydropsyche angustipennis* (CURT.) (Table III), and so that of the members of the first, most primitive, group of caddisflies. At illuminations up to 0·75 lux the time of adaptation is similar to that of both the species mentioned, but from 1 to 10 lux it somes close to the time found for *Rh. septentrionis* McLACH. and at an above 50 lux to the values obtained for *H. angustipennis* (CURT.), only that it begins to exceed the fixed time of stimulation at as low illuminations as 50 lux, and thus lower than in the case of this last species. The efficiency of the photoreceptors in larval instar II is still low compared with the last instar (Tables V and VI). The range of adaptation times in particular illuminations gives evidence of great tolerance and accommodability, which will develop in the next stages, and of varying selective values of this parameter in the postembryonic development.

A comparison of the values presented in Table IX with those in Tables V and VI indicates the direction of studies on the development of photoreceptor efficiency in the individual development of larvae and, in consequence, on the selective values of particular developmental stages. This problem will however be dealt with in another paper.

3.2. Time of acquirement of visual information and time of seeing inertia

The time from the outset of stimulation to the appearance of a response is the time of acquirement of visual or light information (t_i) and it depends on the strength of illumination. The values of this parameter are presented in Tables II—VII and IX, which also show the time of adaptation.

At the lowest illuminations used the time of acquirement of visual information is 2 or 3 seconds at 0·125 lux and 3 seconds at 0·25 lux in the larvae of *Rhyacophila septentrionis* McLACH. (Table II), *Hydropsyche angustipennis* (CURT.) (Table III), *Agraylea multipunctata* CURT. (Table IV) and the second larval instar of *Limnephilus flavicornis* (FABR.) (Table IX). It is also 2 or 3 seconds at 0·125 lux but below 2 seconds at 0·25 lux, and thus undergoing a reduction, in the members of the third group of caddisflies, *Limnephilus flavicornis* (Fabr.) (Tables V and VI) and *Potamophylax nigricornis* (Pict.) (Table VII), which have the most efficient photoreceptors.

At the other illuminations used the time of acquirement of visual information becomes still more reduced. The process of its reduction to 1 second begins at different illuminations in particular species, reaching 1 second at 3 lux in the larvae of *Rh. septentrionis* McLach., *A. multipunctata* Curt., *L. flavicornis* (Fabr.) and P. *nigricornis* (Pict.), only that in the last two species it begins at lower illuminations (0·25 lux). From 10 lux upwards the response is immediate, but the threshold illumination at which the response occurs immediately is certainly different in particular specimens and no doubt it lies between 3 and 10 lux. On the other hand, in the larvae of *H. angustipennis* (Curt.) and in larval instar II of *L. flavicornis* (Fabr.) the reduction in the time of acquirement of visual information to 1 second was noted at illuminations of 1, 3 and 10 lux, and the direct responses were observed at 50, 100 and 200 lux.

The time of acquirement of visual information (t_i) is therefore another parameter which undergoes a decrease in the evolution of the process of seeing, although this happens in a far less dynamic manner than in the case of adaptation time. It also becomes reduced in individual development as evidenced by its values in the larvae of *L. flavicornis* (Fabr.) in the second and fifth instars (Tables IX, V and VI).

The numerical values of the time of acquirement of visual information obtained experimentally under definite and fixed conditions of adaptive and stimulative luminosities are of relative values and characterize the efficiency of photoreceptors to a limited degree only. Neither do they fully characterize the rate of perception, for in the natural environment kinetic contrasts act on the photoreceptors owing to the motion of the larvae in relation to their surroundings and that of the surroundings in relation to the larvae, and under such changing conditions of illumination the time of acquirement of visual information merges with the time of inertia, because after the stimulus has been cut off the responses do not cease at once but continue for some time.

In this investigation the time of inertia is represented by the time of subsidence of the motor reaction after the interruption of the light stimulation. Larvae adapted to dark during the night were successively exposed to 10-second stimulative luminosity of continuous uniform light. The time of inertia was examined in reference to the same values of illumination as were used for the time of adaptation and that of acquirement of visual information. After the white light has been turned off, the movements of the larvae were observed by red light.

The time of inertia examined under definite conditions is naturally a conventional parameter, because the extinction of the light means the outset of another stimulus, darkness or, as in the present case owing to the necessity of observation, monochromatic light. Dim red light, used for observation, may however be regarded as "darkness", for the larvae did not respond to it by motor activity after they had been adapted to dark. Besides, in the natural environment of the larvae most of the red rays — about 90 per cent per 1 m of water depth — undergo extinction (SAUBERER and RUTTNER, 1941).

Within a frame of reference differing from that used before (when the larvae used for experiments are adapted to light of definite intensity) the time which has been assumed to be the time of inertia will be the sum of the time of aquirement of visual information and that of adaptation to dark. A comparison of the data presented in Tables X—XV with those from Tables II—IX shows that it is somewhat shorter than the time of adaptation to light. This is especially well seen at intenser illuminations. Hence it follows that the process of adaptation to dark proceeds faster than that of adaptation to light. This is, in addition, tantamount to the statement that the inertia time after a definite stimulation resulting from the assumed frame of reference is shorter than the time of adaptation to intenser illuminations. On the other hand, at weaker illuminations, i. e., at a stimulative luminosity of 0·125, 0·25 and 0·50 lux, if the sum of the time of acquirement of light information and the time of adaptation to light was 10 seconds or less (cf. Tables II—IX), that is, as much as or less than the time of stimulation used for examining inertia, and the motor reaction occurred after the extinction of the stimulus, then its duration was not the time of inertia because the adaptation had taken place during the stimulation. It was therefore the time of acquirement of information and that of adaptation to dark, as the phenomenon of inertia occurs only when the adaptation becomes interrupted by the next stimulus; this happens during the action of kinetic contrasts on the photoreceptors, and so at variable values of illumination.

Table X

Time of decline of stimulus action (inertia) in larvae of *Rhyacophila septentrionis* MC LACH. after 10-second stimulative luminosity using continuous uniform light of various strength (in seconds)

Larva No.	0·125 lx	0·25 lx	0·50 lx	0·75 lx	1 lx	3 lx	10 lx	50 lx	100 lx	200 lx
1	—	5	8	10	12	23	28	45	55	65
2	—	4	6	12	16	22	35	40	39	58
3	—	3	6	9	12	21	26	29	41	49
4	—	6	6	7	18	26	30	40	49	59
5	—	9	10	15	13	17	23	38	45	58
6	1	3	7	9	15	19	22	28	34	46
7	—	2	6	11	9	18	24	48	52	61
8	—	9	9	8	16	17	21	31	39	56
9	—	11	13	7	13	30	37	48	52	61
10	—	4	7	9	14	21	28	37	41	60
$\bar{x}$	—	6	8	10	14	21	27	38	45	57

Table XI

Time of decline of stimulus action (inertia) in larvae of *Hydropsyche angustipennis* (CURT.) after 10-second stimulative luminosity using continuous uniform light of various strength (in seconds)

Larva No.	0·125 lx	0·25 lx	0·50 lx	0·75 lx	1 lx	3 lx	10 lx	50 lx	100 lx	200 lx
1	—	2	9	11	13	21	24	31	38	41
2	2	4	8	8	12	19	22	37	43	57
3	3	3	6	9	16	22	26	32	39	43
4	3	4	7	8	14	24	29	36	41	49
5	—	6	7	9	12	21	30	33	39	46
6	—	6	8	10	14	19	24	29	40	52
7	2	5	8	12	14	23	31	36	38	44
8	1	3	6	9	11	20	27	36	43	58
9	—	7	10	10	11	22	29	34	48	52
10	3	4	7	8	15	19	24	33	41	56
$\bar{x}$	1	4	8	9	13	21	27	34	41	50

Table XII

Time of decline of stimulus action (inertia) in larvae of *Agraylea multipunctata* CURT. after 10-second stimulative luminosity using continuous uniform light of various strength (in seconds)

Larva No.	0·125 lx	0·25 lx	0·50 lx	0·75 lx	1 lx	3 lx	10 lx	50 lx	100 lx	200 lx
1	1	3	7	8	10	17	21	29	32	49
2	4	4	4	6	12	12	19	28	41	52
3	—	3	6	7	9	18	23	26	38	51
4	—	6	5	5	7	14	19	24	36	48
5	—	3	4	6	8	16	20	25	33	43
6	—	4	5	7	8	16	22	27	36	39
7	3	4	8	9	12	19	23	29	30	42
8	—	3	7	8	15	21	22	31	37	50
9	1	2	3	5	7	15	19	28	34	49
10	—	5	4	4	9	17	26	30	43	51
$\bar{x}$	1	4	5	6	10	16	21	28	36	47

As will be seen from Tables X—XV, the time of inertia depends on the strength of illumination and differs between the members of different groups of caddisflies. In the specimens examined it is characterized by its range, which shows a tendency to grow as the differences between the stimulative luminosity and the initial adaptive background $B_1 = 0$ increase. It may therefore be inferred that as the illumination intensifies, the selection zone of this parameter widens. This supports the conclusion, which may be drawn on the basis of the studies on the time of adaptation, that the process of adaptation of caddisflies to light consists in the adaptation of photoreceptors to intenser and intenser

Table XIII

Time of decline of stimulus action (inertia) in larvae of *Limnephilus flavicornis* (Fabr.) after 10-second stimulative luminosity using continuous uniform light of various strength (in seconds)

Larva No.	0·125 lx	0·25 lx	0·50 lx	0·75 lx	1 lx	3 lx	10 lx	50 lx	100 lx	200 lx
1	—	3	6	5	8	8	12	19	29	40
2	2	5	6	6	7	10	16	19	31	38
3	—	4	5	6	7	7	12	21	29	36
4	4	4	4	5	6	7	18	24	29	41
5	—	6	4	6	5	11	15	19	32	39
6	—	5	6	7	7	8	15	18	38	44
7	—	4	6	4	6	7	16	24	31	40
8	—	3	3	5	8	9	18	27	40	49
9	—	4	5	5	8	10	19	26	33	41
10	3	4	4	5	8	7	22	29	36	41
$\bar{x}$	1	4	5	5	7	8	16	23	33	41

Table XIV

Time of decline of stimulus action (inertia) in larvae of *Potamophylax nigricornis* (Pict.) after 10-second stimulative luminosity using continuous uniform light of various strength (in seconds)

Larva No.	0·125 lx	0·25 lx	0·50 lx	0·75 lx	1 lx	3 lx	10 lx	50 lx	100 lx	200 lx
1	2	4	6	6	8	10	14	25	—	—
2	1	6	7	6	6	8	16	19	—	—
3	—	4	5	7	9	12	17	24	—	—
4	—	5	4	5	8	11	13	18	—	—
5	1	3	3	4	6	10	19	23	—	—
6	1	4	5	7	9	11	18	26	—	—
7	—	3	4	6	8	10	21	29	—	—
8	—	3	5	5	6	9	19	29	—	—
9	4	5	4	5	7	8	16	26	—	—
10	2	4	5	6	6	7	14	21	—	—
$\bar{x}$	1	4	5	6	7	10	17	24	—	—

illumination in phylogeny. Besides, Tables X—XIV clearly illustrate the relative reduction of the inertia time at particular illuminations in the members of the caddisfly groups under examination. The highest mean time of inertia is observed in the larvae of *Rhyacophila septentrionis* McLach. (Table X) and *Hydropsyche angustipennis* (Curt.) (Table XI). A relative decrease in the time of inertia occurs in *Agraylea multipunctata* (Curt.) (Table XII), *Limnephilus flavicornis* (Fabr.) (Table XIII) and *Potamophylax nigricornis* (Pict.) (Table XIV). In larval instar II of *L. flavicornis* (Fabr.) (Table XV) this parameter comes close to the values obtained for *H. angustipennis* (Curt.) (Ta-

Table XV

Time of decline of stimulus action (inertia) in larval instar II of *Limnephilus flavicornis* (Fabr.) after 10-second stimulative luminosity using continuous uniform light of various strength (in seconds)

Larva No.	0·125 lx	0·25 lx	0·50 lx	0·75 lx	1 lx	3 lx	10 lx	50 lx	100 lx	200 lx
1	—	4	8	11	14	19	29	36	41	43
2	2	2	7	9	12	22	31	39	42	47
3	—	4	6	8	15	18	28	32	39	49
4	3	3	7	9	17	24	32	39	44	50
5	1	6	8	10	18	23	30	36	47	52
6	4	4	6	9	12	20	26	38	48	56
7	—	5	8	12	14	19	24	29	36	42
8	—	3	5	9	16	23	30	34	39	47
9	—	7	10	13	16	21	29	34	40	51
10	2	7	11	11	18	24	33	37	42	53
$\bar{x}$	1	4	8	10	15	21	29	35	42	49

ble XI) belonging to the first group of caddisflies. Thus the time of inertia like the time of acquirement of visual information and that of adaptation, undergoes a reduction in the phylogenetic and individual development.

3.3. Effect of contrast illumination on motor activity of larvae

Larvae used for the experiments with contrast illumination were also adapted to dark during the night. As at continuous uniform illumination, a period of 30 minutes was designed for observation of each larva.

In contrast illumination, obtained by the use of vessels with their side walls covered with black paper and lighted from below through a chequer of black squares, the motor activity of the larvae examined started at a differential increase of 0·125 lux in the illumination of the light fields in relation to the dark ones. However, not all the larvae moved. Six larvae of the species *Rhyacophila septentrionis* McLach., 6 of *Hydropsyche angustipennis* (Curt.), 5 of *Argaylea multipunctata* Curt., 5 of *Limnephilus flavicornis* (Fabr.) and 7 of *Potamophylax nigricornis* (Pict.), out of the 10 larvae of each species examined, moved, but an increase in illumination by 0·25 lux incited all the larvae to motion. This confirms the results of one of the preceding experiments that the threshold of differential sensitivity (ΔB) of photoreceptors in the dark adapted larvae lies between 0·125 and 0·25 lux.

Moreover, these lighting conditions made all the larvae move in the vessels throughout the time of observation, that is, for full 30 minutes. Hence it follows that contrast illumination has an effect on the motor activity of larvae.

The motor activity of the larvae of *Rh. septentrionis* McLach., *H. angustipennis* (Curt.) and *A. multipunctata* Curt. manifested itself by disorderly, incoordinate clinokinetic movements of the whole body. The intensity of these movements augmented with differential increase in the illumination of the light fields in relation to the dark ones. At the 3-lux illumination of the light fiels only the larvae of *A. multipunctata* CURT. went beyond the borders of the dark squares. The larvae of *Rh. septentrionis* McLACH. and *H. angustipennis* (CURT.) avoided the light fields at this illumination, but their movements continued throughout the time of exposure to light. The movements of the larvae of *A. multipunctata* CURT. became more orderly, if a few water plants had been placed in the vessel. The larvae wandered on them, gripping the leaves with the legs of the third pair and bending their bodies in various directions, whereas from the very beginning the larvae of *L. flavicornis* (FABR.) and *P. nigricornis* (PICT.) showed locomotor activity consisting in roaming over the bottom of the vessel. In this connection larvae of *Limnephilus flavicornis* (FABR.) were used as representatives of the third group of caddisflies for a study on locomotor activity on the horizontal plane in contrast illumination.

Divested of their cases, the larvae of *L. flavicornis* (FABR.) behaved like those of *Rh. septentrionis* McLACH. and *H. angustipennis* (CURT.), i. e., they turned away and contracted and stretched their bodies, but performed the same movements of legs as when moving on a horizontal plane. If, however, they happened to meet a flat surface, they travelled in a normal way, as if they had retained their cases, but only for a short time, and next they relapsed into disorderly, incoordinate movements. This fact indicates that the satisfaction of tactile reguirements and gravitational orientation, in which they are directed by the weight of their cases, formalize their locomotion by means of legs and, in consequence, their movements become symmetrical and compensatory.

Observation of the travelling larvae of *L. flavicornis* (FABR.) non-divested of their cases showed that at increases in the illlumination of the light fields up to 3 lux they moved incessantly on the bottom of the vessel, passing unconcernedly from dark fields to light ones and vice versa. On the other hand, at differential illuminations above 3 lux (up to 10 lux) the larvae were observed to hesitate at the passage from dark fields to light ones, and at an increase in the illumination of the light fields above 10 lux they entered the light fields only partly and immediately returned or travelled to the nearest dark squares. Practically, in this case they most frequently wandered along the lines connecting the dark squares.

At continuous uniform illumination, after the extinction of response owing to adaptation, the stimulative luminosity (B_o), retaining the same value, turns to the adaptive luminosity (B_t). In this connection the thresholds of differential and contrast sensitivities will have different values, conditioned by the values of B_t, at each increase in the illumination of the background.

At contrast illumination (experiments with black squares) the larvae moved continuously for the whole period of 30 minutes and therefore the light that acted on their photoreceptors varied in strength with time. If a larva stayed in a dark field before the light was switched on, this field formed an adaptive background, B_t, and the illumination of the nearest light field was a stimulative luminosity, B_o. As soon as the larva had entered the light field, its background became, in turn, the adaptive luminosity and the nearest dark field the stimulative luminosity. Thus, during the motion of the larva the times of the action of both luminosities, B_t and B_o, overlap each other.

Previous experiments showed that motor responses do not begin simultaneously with the onset of the stimulus, but after the lapse of a definite time. Neither do the responses stop immediately after the extinction of the light stimulus. If the responses were immediate, it was so owing to the increased strength of the stimulus. It may however be supposed here that the time of acquirement of visual information would not have reached the zero mark, if the next stimulus had followed, because its reception would have been delayed by the time of inertia caused by the stimulation and adaptation connected with the previous stimulus. In addition to the strength of light, 3 agents have an effect on the formation and maintenance of a visual sensation: the time of acquirement of visual information, the time of fixation of information or adaptation, and the time of inertia or subsidence of the action of the stimulus. The sum of the time of acquirement of visual information and the time of adaptation makes up the time of stimulation, and the sum of the time of adaptation and the time of inertia is the time of duration of the response. The time of stimulation and that of duration of the response overlap. A diagram showing the relationship and overlap of the agents that act on the formation and maintenance of a visual sensation is given in Fig. 32. This diagram, greatly simplified and linear in form, is constructed on the basis of the data obtained chiefly from the experiments with continuous uniform light, and it illustrates the course of a single visual sensation. Naturally, the lengths of individual sections do not represent the mutual relations between the time values, because they vary according to the successive stimuli. If there follows another light stimulus, the time of acquire-

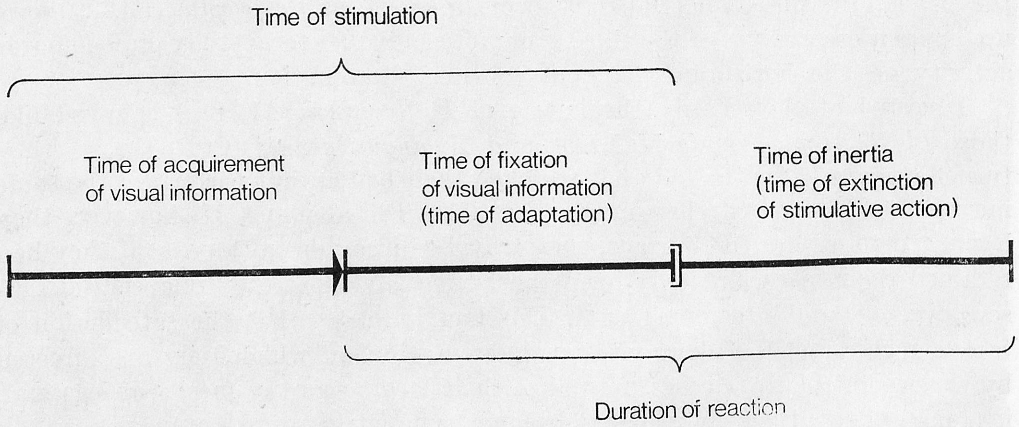

Fig. 32. A diagram showing the relation between and the overlap of time parameters acting on the formation and maintenance of a visual sensation

ment of new visual information depends not only on the strength of this stimulus, but also on the time of inertia conditioned by the strength of the preceding stimulus. In other words, the new information is checked by the inertia following the preceding visual sensation.

The time of fixation of visual information is a secondary parameter of the time of adaptation at a continuous uniform illumination. It results from adaptation time interrupted during the action of kinetic contrasts. If the locomotor reaction is to proceed in a possibly continuous manner, the adaptation to the stimulative luminosity must be continually interrupted. The occurrence of the response is thus conditioned by the rhythmically repeated action of kinetic contrasts.

The particular time parameters are closely connected, variable, and show a rhythmic pulsation, the amplitudes of which depend on the frequency and strength of consecutive stimuli and the individual receptive capacities of the larvae. The fact that the perception of a light stimulus takes a definite time to appear indicates the formation of a physiological excitation, which, having attained an appropriate threshold value, elicits the phenomenon of vision and next a motor response.

The problem of physiological excitation is well known, but in physiological optics the authors generally treat the process of formation of the phenomenon of vision as a direct result of the action of a light stimulus. This is probably due to the fact that physiological optics is concerned chiefly in studying the parameters of vision of such an efficient sight organ as the human eye is, whose time parameters are very short and difficult to manifest in isolation, because they fuse together and overlap each other. The fact that the visual sensation originates from a physiological excitation and adaptation, set up in time, was emphasized for the first time in the theory of sight feeling (Fidos, 1967, 1968), which was put forward out of need of more detailed studies on the efficiency of the human eye.

However, only comparative studies of a systematic unit which is characterized by evolutionary phases represented by both the forms which are ethologically and morphologically relatively primitive and those more specialized for attainment of a higher degree of autonomy can throw light on the evolution of vision or that of the efficiency of photoreceptors.

A given efficiency of photoreceptors, consisting in the lowering of the time parameters owing to the evolution of vision, certainly cannot be an indication of the evolutionary stage of the organism. The development of the efficiency of photoreceptors is nothing but a result of the adaptive evolution of animals to their living conditions.

In order to find the thresholds of sensitivity of the photoreceptors in the larvae of *Limnephilus flavicornis* (Fabr.) at other adaptive illuminations, experiments with chequer were repeated, the black squares being replaced with layers of white paper of the same size so as to make it possible to regulate the relative illumination of the darker and lighter fields optionally. The differences in illumination between the squares of the chequer were calculated, after the light penetrating through the layers of paper had been measured separately for light and dark fields. Illumination was measured after each experiment, the same lighting conditions being repeated by the use of the recorded numbers of layers of white paper.

Dark adapted larvae were used for the first experiments. Since in the previous experiment with contrast illumination of the "light-dark" type, the larvae moved continuously throughout the time of observation (30 minutes), the occurrence of a locomotor response owing to an increase in luminosity of the squares of the chequer was an indication of the threshold perception here. The results of these experiments are given in Table XVI, which also confirms the results of the previous studies, that is, the threshold values of differential sensitivity of the photoreceptors in the larvae adapted to dark.

The experiments were carried out so that if the highest increase in illumination of the light squares ΔB (Table XVI) that caused motion was 0·25 lux, the luminosity of the dark squares with $B_t = 0$ was adjusted to 0·25 lux, or the stimulative luminosity, to make them the adaptive background for the next experiment. After the extinction of locomotor activity owing to the adaptation to the background, the luminosity of the squares designed as stimulative fields was raised up to the occurrence of a response, the illumination of the dark squares being left unchanged. If in the next phase of experiments the highest illumination releasing motor responses was 1 lux, the illumination of the dark squares, being 0·25 lux, was raised to 1 lux so that they should become an adaptive background again and stop the movements of the larvae examined.

The figures in the columns of Table XVI marked with the symbol B_o represent the illumination of the light squares in lux at the given adaptive luminosity B_t of the darker squares. The ΔB column gives the differences between the stimulative illumination B_o and the adaptive background B_t, which are at the same time the thresholds of differential sensitivity of the larvae examined, whereas the ε column lists the thresholds of contrast sensitivity expressed by the ratio of threshold of differential sensitivity to adaptive luminosity.

Table XVI shows a clear dependence of the thresholds of differential sensitivity and those of contrast sensitivity on the luminosity of the adaptive background. The threshold of contrast sensitivity rises, as the adaptive illumination increases, which means that the larvae adapted, e. g., to the background luminosity $B_t = 77$ lux do not perceive objects of a luminosity lower than $\bar{x}\Delta B = 445$ lux at stimulative illuminations $\bar{x}B_o = 542·5$ lux. In this case the contrast between the adaptive illumination (77 lux) and the differential increase in stimulative illumination must be nearly sixfold (5·8). Hence it follows that at relatively low illuminations, e. g., below 10 lux, the larvae perceive more light changes in the environment than they do at illuminations above 10 lux, and the adaptation to stronger and stronger illuminations decreases the sensitivity of the photoreceptors because the thresholds of contrast sensitivity rise.

Table XVI

Thresholds of differential and contrast sensitivity of larvae of *Limnephilus flavicornis* (Fabr.) at gradually increased adaptive illuminations B_t — adaptive luminosity of background, B_o — stimulative luminosity, ΔB — thresholds of differential sensitivity, ε — thresholds of contrast sensitivity

Larva No.	B_o at $B_t = 0$	ΔB	ε	B_o at $B_t = 0{\cdot}25$	ΔB	ε	B_o at $B_t = 1$	ΔB	ε	B_o at $B_t = 3$	ΔB	ε	B_o at $B_t = 12$	ΔB	ε	B_o at $B_t = 77$	ΔB	ε
1	0·125	0·125	∞	0·75	0·50	2	2·50	1·50	1·50	12	9	3	60	48	4	550	473	6·1
2	0·25	0·25	∞	1	0·75	3	1·50	0·50	0·50	10·50	7·5	2·5	56	44	3·7	495	318	4·1
3	0·125	0·125	∞	0·75	0·50	2	2	1	1	9·50	6·5	2·2	49	37	3·1	460	383	5
4	0·25	0·25	∞	1	0·75	3	2	1	1	10	7	2·3	51	39	3·2	470	393	5·1
5	0·125	0·125	∞	0·75	0·50	2	1·50	0·50	0·50	13	10	3·3	67	55	4·6	540	463	6
6	0·125	0·125	∞	0·75	0·50	2	1·75	0·75	0·75	12·50	9·5	3·2	71	59	4·9	590	413	5·4
7	0·25	0·25	∞	1	0·75	3	3	2	2	11·50	8	2·8	53	41	3·4	510	433	5·6
8	0·25	0·25	∞	0·75	0·50	2	3	2	2	11·50	7·5	2·5	65	53	4·4	550	473	6·1
9	0·125	0·125	∞	0·75	0·50	2	2	1	1	10	7	2·3	72	60	5	610	533	6·9
10	0·125	0·125	∞	0·75	0·50	2	1·50	0·50	0·50	9·50	6·5	2·2	77	65	5·4	650	573	7·4
$\bar{x}$	0·175	0·175	∞	0·82	0·57	2·3	2·07	1·07	1·07	10·9	7·9	2·6	62·1	50·1	4·2	542·5	445·5	5·8

The photoreceptors seem to be most sensitive at adaptive illuminations below 3 lux, because the thresholds of differential sensitivity show a distinct increase starting from this value upwards. The immediate motor responses at stimulative luminosities from 10 lux upwards under the conditions of continuous uniform illumination (Tables V and VI) may rouse doubt as to the soundness of this conclusion. However, it should be kept in mind that in those experiments the adaptive background was darkness, to which the larvae had been adapted during the night and so for a relatively long time. Thus, the responses may have been of the nature of a shock.

Like the time parameters determined under the conditions of continuous uniform illumination (time of acquirement of visual information, time of adaptation and time of inertia), the thresholds of differential and contrast sensitivity are individual characters of specimens examined. The numerical range of the thresholds indicates also their selective value. The larvae whose photoroceptor sensitivity is best suited to environmental conditions undoubtedly have a chance of better development, because their better spatial orientation owing to the more efficient reception of information facilitates both the intake of substances from the surroundings and the avoidance of unfavourable conditions. Photoreceptors are not the only factors that contribute to spatial information. Other receptions may play and probably play a more important part. Nevertheless, the parameters of these receptions, like those of the photoreceptors, are characterized by the individual properties of the specimens, and within a population have certainly selective values.

In the experiments in which round vessels were used in contrast illumination, i. e., with a chequer of black and light squares placed and lighted up under the bottom, the larvae were observed to mowe incessantly right along the circumference of the vessels, starting from as low an increase in the illumination of light fields as 0·25 lux. Observations were made for a definite time, not exceeding 30 minutes, for it was not the purpose of this study to examine the tiredness of larvae. If however the experiments were continued longer, no breaks in the movements of the larvae were noted before the lapse of about one hour. Since the locomotor movements along the circumference of the vessel practically lasted longer than the designed time of observation, it may be stated that contrast illumination releases the peripheric reaction in the travelling larvae.

At illuminations of the light fields up to 10 lux the larvae moved along the circumference of the vessel without any inhibitions at a mean rate ($\bar{x}$ from 10 measurements) of 25·14 cm, that is, the circumference length, in 4 minutes 8 seconds or about 6 cm/minute, whereas at illuminations above 10 lux the larvae were observed to hesitate and linger before passing from a dark field to a light one, and so the time they took to travel all round the vessel was lengthened to 8—10 minutes. Frequently however, especially at illuminations of 50, 100 and 200 lux, the preipheric reactions were interrupted by excursions towards the centre of the vessel. Thus, the responses to light stimuli were of the nature of a shock under these conditions.

In order to examine the influence of the time of adaptation on the reactions of this sort, a half of the vessel bottom was covered with black paper instead of the chequer used in the previous experiment. In this way longer periods of adaptation to light and dark were established for the travelling larvae. It appeared that at as low increases in illumination as 1 lux the larvae behaved in the same manner as they did at illuminations above 10 lux with a chequered background, i. e., their motion was characterized by moments of lingering and turning along the boundary between the dark and the light field (Fig. 33) before entering the latter. At illuminations above 10 lux the larvae did not leave the dark field at all. This proves that the shock nature of the response is influenced not only by the stregth of the new information, but also by the time that the larvae have for adaptation to the preceding information. The normal course of reaction is thus conditioned by the shorter and therefore interrupted time for adaptation. The frequency of interruptions is certainly not indifferent and has its threshold limits, because it is connected with the rhythm of the action of kinetic contrasts in natural surroundings and the adaptation of the organism to this rhythm.

On the other hand, the shock nature of stimulation, which cannot be ruled out in a natural environment, may either provide lethal conditions or cause slight mutations in the genetic apparatus, which sorted out in the adaptive process through natural selection, may prove useful for the further evolution of the organism in changed living conditions.

The thresholds of differential and contrast sensitivity were not examined in the larvae of the first and second groups of caddisflies in gradually increased adaptive illuminations, because then it would have been necessary to apply other methods of examination in connection with the different manifestations of their motor activity. The methods used were only fit for larvae exhibiting locomotor reactions in the horizontal plane, and comparative studies demand standarized methods. The results obtained from the investigation carried out

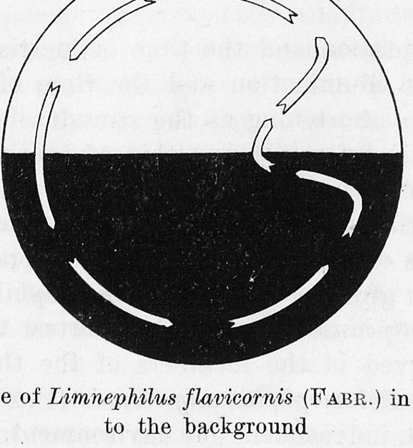

Fig. 33. Movements of larvae of *Limnephilus flavicornis* (FABR.) in relation to their adaptation to the background

in both continuous uniform and contrast illuminations are of some significance in the comparative aspect and may be used as the basis for conclusions concerning the evolution of the efficiency of photoreceptors in the larvae of caddisflies.

The thresholds of differential and contrast sensitivity of the larvae of the first and second groups of caddisflies in gradually increased adaptive illuminations will undoubtedly differ from those in the larvae of *Limnephilus flavicornis* (FABR.), which is evidenced by their relatively high time parameters at continuous uniform illumination. The sensitivity thresholds of the photoreceptors of these larvae will certainly be higher, especially in stronger illuminations.

4. Results and conclusions

The results obtained from the studies on the photoreception of the larvae representing the particular groups of caddisflies and the conclusions drawn from them are as follows:

1. Light induces optomotor reactions in caddisfly larvae and these reactions make it possible to examine the sensitivity and efficiency of their photoreceptors.

2. The time parameters having an effect on the formation and maintenance of visual sensations and demonstrated under the conditions of continuous uniform illumination are the time of acquirement of visual information, the time of adaptation and the time of inertia. The sum of the time of acquirement of information and that of adaptation corresponds with the time of stimulation, and the sum of the time of adaptation and that of inertia covers the duration of the response. The time of stimulation and the time of response fuse together and overlap each other (Fig. 32).

3. The time parameters depend on the strength of stimulative illumination and individual properties of specimens. The most differentiated of them is the time of adaptation, which shows the widest range within the series of larvae of particular species. The time of inertia is also variable, though to a lower degree, whereas the time of acquirement of visual information is a relatively constant parameter.

4. The time of adaptation and the time of inertia grow with differential increases in stimulative illumination and the time of acquirement of visual information undergoes a shortening as the stimulus increases.

5. The range of the time parameters within 10-specimen series of individual species suggests the occurrence of a similar range within specific populations. It is therefore of selective importance to the adaptive process.

6. The longest times of adaptation and inertia were found in the most primitive larvae of the first group of caddisflies, *Rhyacophila septentrionis* MCLACH. and *Hydropsyche angustipennis* (CURT.). The shortest times of adaptation and and inertia were observed in the members of the third group, *Limnephilus flavicornis* (FABR.) and *Potamophylax nigricornis* (PICT.), which are travelling forms and so the most independent on environment.

7. At particular values of stimulative illumination (0·125, 0·25, 0·50, 0·75, 1, 3, 10, 50, 100 and 200 lux) used for examining the responses of larvae, the time parameters were found to decrease in the members of individual groups of caddisflies in connection with their transition from passive to more active ways of life.

8. This decrease in the time parameters of vision is associated with the development of motor activity and the transformation of asymmetrical uncompensatory movements into symmetrical compensatory ones. They consist in the larvae's ability to move over a horizontal surface, and this ability developed owing to their detachment from the substrate and the presence of protective structures which condition the appropriate orientation of the larvae in relation to gravity and facilitate their travelling mode of life.

9. The detachment of the larvae of the third group of caddisflies together with their cases from the substrate has resulted in the development of the positive geotaxis, and the travelling way of life has contributed to the improvement of their photoreception. The decreased time parameters of vision are a manifestation of their efficiency.

10. The evolution of the efficiency of vision thus consists in the reduction of the time parameters of vision.

11. There is also some improvement in the efficiency of photoreceptors in individual development, as can be seen from the time parameters of vision in the second larval instar of *Limnephilus flavicornis* (Fabr.) in comparison with those in the fifth instar of the same species. Since the fifth instar attains the highest photoreceptive efficiency, the particular instars will have varying selective values in this respect, because this is related to the development of spatial orientation.

12. The time parameters of the second larval instar of *Limnephilus flavicornis* (Fabr.) resemble the parameters of the fifth larval instar of *Hydropsyche angustipennis* (Curt.), which belongs to the most primitive group of caddisflies. This indicates that the parameters of the second larval instar of *L. flavicornis* (Fabr.) are traces of a function of its ancestors, and their diminution is conected with the development of cenogenetic adaptations.

13. At contrast illumination, during the action of kinetic contrasts caused by the movement of the surroundings in relation to the organism or that of the organism in relation to the surroundings, the time of acquirement of visual information and the time of inertia fuse and overlap, and so do the time of stimulation and the time of reaction. This results in a specific pulsation of the time parameters owing to the rhythm of the action of kinetic contrasts.

14. During the action of kinetic contrasts the time of acquirement of visual information depends on the time of inertia induced by the action of the preceding stimulus. Acquirement of visual information is checked by inertia in this case.

15. Kinetic contrasts interrupt adaptation to light stimuli, which is evidenced by the incessant motor activity of the larvae examined throughout

the designed time of observation at contrast illumination, whereas during the same time at continuous uniform illumination adaptation leads to the decline of the response. Discontinuous adaptation is therefore the condition of the occurrence of response, and kinetic contrasts which act in a natural environment, that is, illumination changing with time, release optomotor responses.

16. The cylindrical shape of the vessel releases the peripheric reactions in travelling larvae only at contrast illumination.

17. The thresholds of differential sensitivity at the sort of light used for all the examined larvae, adapted to dark at night, lie within a range of 0·125—0·25 lux.

18. The thresholds of differential and contrast sensitivity depend on the luminosity of the adaptive background. As the adaptive illumination increases, the threshold of contrast sensitivity rises, which means that the larvae adapted to a definite luminosity of the background do not perceive objects of luminosity lower than the thresholds of differential sensitivity, and their adaptation to stronger and stronger illuminations decreases the sensitivity of photoreceptors.

19. The photoreceptors of the larvae of *Limnephilus flavicornis* (Fabr.) are relatively most sensitive at adaptive illuminations below 10 lux. At illuminations above 10 lux the responses assume a shock nature. It is so because above 10 lux light begins to have a dazzling action on these larvae.

20. The sensitivity of photoreceptors is also dependent on the time of adaptation to adaptive luminosity, for in the experiments in which the adaptive background had a larger area (Fig. 33) than the adaptive areas of chequer squares at contrast illumination the responses assumed a shock nature at as low increases in stimulative illumination as 1 lux, whereas when a checkered background was used, it happened from 10 lux upwards.

21. A shorter time of adaptation, i. e., discontinuous adaptation of frequency certainly suited to the informative capacity of photoreceptors, conditions a normal course of optomotor reactions.

22. The thresholds of differential and contrast sensitivity are characterized within series by a range which widens as the stimulative illumination increases. They are therefore, like the time parameters of vision, of selective importance to the process of adaptive evolution.

FINAL CONCLUSIONS AND INTERPRETATION OF THE ADAPTIVE PROCESS

The course of adaptive process of caddis larvae in their historical development has been presented in the first part of this paper. A relationship of the new cenogenetic adaptations to the palingenetic adaptations in the adaptive evolution of the insects mentioned has been demonstrated. This relationship consists in the cenogenetic modification of palingenetic adaptations under the influence of the controlling action of environment. Šmalgauzen's (1966) theory about the relative nature of adaptations, which are conditioned and restricted by the historical development of the organism finds its justification here.

A diversity of adaptations both in function and in structure indicates the multiformity of the adaptive process, and the mutal supplementation of individual adaptations its complementarity.

The adaptive evolution of caddis larvae includes the phases of transition of the larvae of their ancestors from life on land to life in cold running waters and next that of the caddis larvae from flowing to stagnant waters and their return through flowing waters to the land environment. Individual phases can be regarded as adaptations to definite living conditions. The particular adaptations were therefore interrupted in their adaptive evolution by the next phases. The discontinuity of adaptations is thus the condition of the maintenance of the morphogenetic adaptive process just as the discontinuous adaptations to light in the process of photoreception are the condition of the optomotor reactions and, in consequence, photoreception itself. The receptive reactions and adaptive processes connected with them, resulting from the processes of reception of information from the surroundings, proceed in microintervals of time, which can be observed by man and recorded by the apparatuses applied. On the other hand, the morphogenetic reactions resulting from the adaptive process in the historical development proceed in macro- and megaintervals of time. We learn about them on the basis of the conclusions from comparative studies. It is probably in this connection that these two processes are generally interpreted differently, the adaptive process in the phylogenetic aspect and the adaptations associated with the process of reception of information from the surroundings. It seems that these processes can be reduced to a unity, because they are of the same nature but occur in different intervals of time.

A biological system is a reactive system characterized by the phenomenon of inertia. This phenomenon is caused by the share of the genetic apparatus in the adaptive process, which apparatus is responsible for the fixation of adaptive characters through natural selection. Remane (1956) put forward the rule that "if an animal changes its environment, the characters of the previous ways of life are often retained far longer than it would suited the ecological requirements of the new environment". Inertia is therefore a consequence of a fixed adaptation just as it is connected with adaptation in the process of vision. The time of adaptation in the process of photoreception is an individual character and within a series of specimens it is marked by the zone of selection. It is thus of importance to the adaptive process. Adaptations formed in the historical development are also related to the properties of the individual genetic apparatus. Within populations they must therefore have their selection zones connected with the various degree of tolerance and of accomodation to variable and cyclically changing environmental conditions. Otherwise natural selection could not act and there would not be any morphogenetic processes.

In the historical development the time of adaptation has certainly its limits and, if it is not interrupted at an appropriate stage by the next phase of adaptation to changed living conditions, it probably leads to the ageing of the evolutionary line of the genotype similarly to how the time of adaptation to light, if not interrupted, leads to the decline of phototactic and photokinetic reactions.

Steady conditions have a preserving action on the function and structure of a biological system in the same way as a continuous stimulus leads to adaptation. However, the living conditions, e. g., in stagnant waters, to which many forms of caddisflies have adapted themselves, cannot be regarded as steady. Nevertheless, full adaptation to such conditions completes the adaptive process. If the process taking place in an environment did not provide conditions for accomodation, which begins each adaptive process (ROTHSCHUH, 1959) and is possible owing to the tolerant properties of the organism, which properties form selection zones within the population, the caddis larvae would represent only the phase of adaptation to stagnant waters. The preservation of a few relatively primitive caddis families is due to the steadier living conditions provided by mountain-brooks (ROSS, 1956).

The phenomenon of inertia arising from the multiform adaptation to definite living conditions resists new adaptations in the adaptive evolution, just as in the process of photoreception it delays the acquirement of visual information. The formation of new adaptations in the historical development is connected with the fact that the resistance resulting from the preceding adaptations abates, as the new adaptations are improved by natural selection. The resistance is therefore morphogenetic, for it never vanishes in the adaptive process.

There occurs an analogy to the resistance of the biological system to information from the surroundings. It is inconceivable that this system should be absolutely "transparent" to information (SEDLAK, 1968), for then it would not be reactive. This resistance is due to the piezoelectric characteristics of cells and tissues of animals (ATHENSTAEDT, 1960) and is connected with the semi-conductive properties of organic compounds (GARRETT, 1962) and the existence of a piezoelectric effect in DNA and RNA as well as in nucleoproteids and proteins (DUCHESNE et al., 1960). Owing to such properties of biological systems, external information induces a change in electricity inside the system (SEDLAK, 1967). Internal information is an internal state which resists external information. The reception of external information is therefore differential, since it is achieved by comparison. The existence of an internal signalling system causes that the biological system is not only a store of information, but also its active and responding receiver. Thanks to internal information the automatic regulation can act inside the biological system by means of feedback loops in the signalling system. The state brought about by internal information is adaptation, though it does not come to a full adaptation, because new information interrupts the preceding adaptation, as in the photoreceptive process. Neither do the responses to the signals running along the feedback channels allow this state of adaptation, for they act on the changes in an inhibitory or stimulative way. It may be stated that the biological system is partly of ambivalent nature, because if the feedback is negative, it receives changes, guarding itself against them at the same time.

The same is probably true also of the duration and dynamics of the adaptive process in the historical aspect. As a result of the action of natural selection adapted or inadaptive specimens get eliminated. The process continues owing to the fact that adaptations to definite living conditions are inhibited and interrupted by stimuli to new adaptations. If the interruption does not occur at the appropriate point of the evolutionary line of the genotype, then the prolongation of the time of adaptation probably leads to the preservation of the function and a narrow specialization, and so an adaptive specialization. In this case the unadapted specimens are eliminated by natural selection.

Although the phenomenon of adaptation to a stimulus in reception processes proceeds in time, it never reaches its limits, because the biological system is continually disturbed by information.

Feedback is a relatively well known phenomenon in natural sciences, especially in biophysics and neurophysiology. In physiological optics it is demonstrated in the block diagram of the sight analyzer (FIDOS, 1967). The sight analyzer is a system of automatic regulation with a loop of negative feedback.

The negative feedback also seems to act in the adaptive process in the historical development. According to ŠMALGAUZEN'S (1966) theory, the only possible adaptations are those to the conditions in which the given organism evolved historically or which occurred frequently in its history as local or temporary phenomena. This is also indicated by the process of adaptive evolution of caddis larvae, i. e., by the relationship of new adaptations in particular phases to the original adaptations of the larvae of the ancestors of caddisflies. Each phase or evolutionary stage arises from the preceding one, and the characteristics of the phase representing the return to life on land are also related to the initial phase. ŠMALGAUZEN (1966), as has already been mentioned in the first part of this paper, defines these phenomena as adaptive modifications, which mark out the course of the evolutionary process of the given organism. This suggests the existence of a "historical inheritance" in the genetic apparatus and its inhibitory and restrictive action on the direction of the adaptive process, which it controls simultaneously. WINKLER (1959) also paid attention to such a "historical inheritance" in the modes of behaviour displayed by the organizations of many organisms.

The phenomenon of automatic regulation and steering is defined in the cybernetic language as the action of the output of the system on its input. The biological system is historically conditioned. Each of its evolutionary stages, or relatively terminal state, is related to the preceding stages. If the model of a biological system were presented in the form of an evolutionary line and its particular stages, which may be represented by a species or another systematic unit, in the form of blocks, each of them would have to be provided with loops of negative feedback going to the preceding blocks. The adaptive process is therefore characterized by feedback.

The adaptive evolution of caddisflies, in addition to the phases in the adaptive process, presents also a cycle from the land phase of the larvae of their ancestors to the land phase of the caddis larvae themselves. Cycles and phases are properties of rhythms. The adaptive evolution of caddis larvae therefore includes a segment of the biological rhythm in the megaintervals of time. The interrupted adaptations to individual living conditions confirm the existence of this rhythm. The adaptive process is thus characterized by biological rhythms.

Biological rhythms are peculiar to living organisms. They occur at all the levels of biological organization. This is evidenced by the existence of the hereditarily conditioned circadian rhythms (Sollberger, 1960; Bünning, 1963) maintained within the 24-hour rhythms of the physical surroundings. They are physiological rhythms connected with the rate of physico-chemical changes occurring in the organism and are adaptive in character, because they must be adjusted to the cosmic rhythms. The biological rhythms are observed starting from the molecular level, where the reccurrence of chemical cycles and the doubling of molecules of DNA acids appear, throughout the levels of climax organization, which betray the 24-hour, monthly, seasonal, annual and solar rhythms and probably those of still greater time intervals, because they are characterized by the ageing of climax formations and their renewal through the serial stages (Clements, 1936). The fact that a constituent of a biological system fails to keep the rhythm peculiar to it is a pathological phenomenon and the system must strive against it. If at higher levels of organization, e. g., that of population or multi-population organization, the rhythm of specimens is not synchronized with the rhythms of the surroundings (e. g., the reproduction cycle, in which this is connected with the development and acquisition of food), they will be eliminated from life by natural selection; they may be preserved only if their rhythm is better suited to the new conditions, e. g., while passing to a new niche. The adaptive process is therefore marked by rhythms of various lengths of cycles. The rhythm of adaptation in the processes of photoreception originated from both the rhythm of the action of interrupted stimuli and the appropriate internal rhythm of the biological system.

In biological philosophy the so-called PCT theorem has been introduced (Rensch, 1968) as a general rule of life based on the principles of symmetry. It is characteristic of all known elementary life processes. The constant P represents the existence of the parity of the right and left sides, which arise like mirror reflections. The constant C expresses the law of contrast, according to which each elementary molecule has a corresponding anti-molecule with the opposite electric charge. These molecules exchange each other and substitute for each other. Finally, the constant T indicates that there must also be a symmetry in the time arrangement. Rensch (1968) does not discuss the problem of biological rhythms, yet symmetry is an essential character of rhythms.

The adaptive process is therefore characterized by symmetry in time.

Summing up the foregoing considerations based on the conclusions and results of the studies reported in both parts of this paper, it may be stated that the adaptive process is marked by the following characters: the universality, for it occurs at each level of biological organization, multiformity, complenetarity, feedback and symmetry. These characters are closely related to each other, intermingle, and result from each other. This interpretation of the adaptive process allows the reduction of the adaptive processes in the historical development and the adaptations connected with the reception of informaton from the surroundings to unity.

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STRESZCZENIE

W pierwszej części pracy autor omówił pochodzenie i rozwój ewolucyjny chruścików. Na podstawie analizy morfologicznej larw i budowanych przez nie konstrukcji ochraniających oraz zachowania się związanego ze sposobami zaspokajania potrzeb życiowych wyróżniono 3 grupy biologiczne chruścików, które określają następujące po sobie, kolejne fazy procesu przystosowawczego tych owadów: przejście z życia lądowego larw przodków chruścików do wód zimnych, bieżących, następnie larw chruścików z wód bieżących do wód stojących i powrót poprzez wody bieżące do środowiska lądowego.

Do pierwszej grupy autor zaliczył podrząd *Annulipalpia* oraz rodziny *Rhyacophilidae* i *Glossosomatidae* z podrzędu *Integripalpia*, do drugiej — rodzinę *Hydroptilidae*, a do trzeciej — pozostałe rodziny *Integripalpia*.

Fazowość procesu przystosowawczego uzasadniają ślady dawnych funkcji, ukryte w aktualnym zachowaniu się larw chruścików. Ślady te, ujawnione w doświadczalnie wywoływanych reakcjach przedstawicieli poszczególnych grup są pozostałością funkcji, które w pewnych etapach rozwoju historycznego larw stanowiły podstawę ich egzystencji.

Każda faza w ewolucji przystosowawczej larw chruścików, polegającej na wzroście autonomii, nawiązuje do poprzedniej i reprezentuje względnie

końcowy stan, który jest determinowany przez warunki początkowe, ponieważ powrót z wód stojących do wód bieżących i na ląd odbywa się w tej samej drodze co przejście do życia wodnego larw przodków chruścików i przystosowanie się cenogenetyczne chruścików do wód stojących. Powstałe w tej drodze zmiany przystosowawcze są wynikiem modyfikującego sterowania przez środowisko procesu przystosowawczego. Zostały one utrwalone przez dobór naturalny i zachowały się w postaci śladów dawnych funkcji, które ujawnione w doświadczalnie wywoływanych reakcjach stanowią, jakkolwiek utajone, aktualne cechy charakteryzujące rozwój historyczny.

Druga część pracy obejmuje badania nad fotorecepcją larw chruścików. Obiektem badań były larwy reprezentujące wyróżnione grupy chruścików. W doświadczeniach ujawnione zostały parametry czasowe działające na powstanie i utrzymywanie się wrażenia wzrokowego: czas osiągania informacji wzrokowej, czas adaptacji i czas inercji widzenia. Suma czasu osiągania informacji wzrokowej i czas adaptacji obejmuje czas stymulacji, a suma czasu adaptacji i czasu inercji stanowi czas trwania reakcji. Czasy stymulacji i trwania reakcji zlewają się z sobą i zachodzą na siebie (rys. 32). Autor zwrócił uwagę na rozpiętość liczbową parametrów czasowych w obrębie serii badanych osobników, która ma w procesie przystosowawczym wartość selekcyjną. Stwierdził również proces skracania się tych parametrów u przedstawicieli poszczególnych grup chruścików w związku z przejściem z biernego do bardziej aktywnego trybu życia.

Skracanie się parametrów czasowych widzenia jest wyrazem ewolucyjnego rozwoju sprawności widzenia i wiąże się z rozwojem aktywności ruchowej i przekształcaniem się ruchów asymetrycznych, niekompensacyjnych w ruchy symetryczne, kompensacyjne, polegające na zdolności poruszania się po płaszczyźnie poziomej w związku z oderwaniem się larw od podłoża i stosowną budową konstrukcji ochraniających, warunkujących odpowiednią ich orientację względem siły przyciągania ziemskiego i ułatwiających wędrowny tryb życia.

Oprócz wykazania zwiększania się sprawności fotoreceptorów w drodze filogenetycznego rozwoju autor stwierdził również proces skracania się parametrów widzenia w rozwoju osobniczym larw *Limnephilus flavicornis* (Fabr.) i w związku z tym wysunął wniosek, że poszczególne stadia rozwoju larwalnego mają różną wartość selekcyjną w procesie działania doboru naturalnego, gdyż wiąże się to z rozwojem orientacji przestrzennej.

W oświetleniu kontrastowym podczas działania kontrastów kinetycznych wynikających z ruchu otoczenia względem organizmu lub organizmu względem otoczenia, czasy osiągania informacji wzrokowej i inercji zlewają się z sobą i zachodzą na siebie, podobnie jak czas stymulacji i czas trwania reakcji. Sprawia to swoistą pulsację parametrów czasowych, wywoływaną rytmiką działania kontrastów kinetycznych. Ponieważ kontrasty kinetyczne przerywają adaptację do bodźców świetlnych, przerywana adaptacja jest warunkiem występowania reakcji optomotorycznych. Natomiast w oświetleniu ciągłym, jednolitym, nie przerywana adaptacja prowadzi do zaniku reakcji.

Badanie progów czułości różnicowej i kontrastowej wykazało, że zależą one od luminancji tła adaptacyjnego. Cechuje je także rozpiętość liczbowa w obrębie serii osobników w miarę wzrostu oświetlenia stymulującego. Mają więc one, podobnie jak parametry czasowe widzenia, wartość selekcyjną w procesie ewolucji przystosowawczej.

We wnioskach końcowych autor wysunął tezę, że podobnie jak przerywane adaptacje w procesie fotorecepcji są warunkiem występowania reakcji optomotorycznych, proces przystosowawczy w rozwoju historycznym trwa dzięki temu, że przystosowania do określonych warunków bytowania są hamowane i przerywane wzbudzaniem do nowych przystosowań. Jest to warunek kształtotwórczego procesu w rozwoju historycznym.

Stałe warunki działają w sposób konserwujący na funkcję i strukturę układu biologicznego tak samo, jak bodziec ciągły prowadzi do adaptacji. Zdaniem autora czas adaptacji w rozwoju historycznym powinien mieć także swoje granice i, jeśli nie zostanie na odpowiednim etapie przerwany następną fazą przystosowawczą do zmienionych warunków bytowania, prowadzi prawdopodobnie do starzenia się linii rozwojowej genotypu, podobnie jak nie przerywany czas adaptacji do światła prowadzi przez adaptację do zaniku reakcji fototaktycznych lub fotokinetycznych.

Porównując proces przystosowawczy w rozwoju historycznym z procesami adaptacyjnymi związanymi z odbiorem informacji otoczenia autor wykazał wspólne ich cechy: powszechność, wielopostaciowość, komplementarność, sprzężenia zwrotne i symetria w czasie. Cechy te pozwalają na sprowadzenie tych procesów do jedności.

РЕЗЮМЕ

В первой части своей работы автор обсудил происхождение и эволюционное развитие ручейников. На основании морфологического анализа личинок и построенных ими защитных конструкций и их поведения, связанных со способами удовлетворения их жизненных потребностей, были выделены три биологические группы ручейников, которые определяют последовательные очередные фазы процесса приспособления этих насекомых: переход из наземной жизни личинок предков ручейников в холодные текущие воды, следовательно переход личинок ручейников из проточных вод в стоящие и возврат через проточные воды в материковую среду.

К первой группе автор отнёс подотряд *Annulipalpia* и семейства *Rhyacophilidae* и *Glossosomatidae* из подотряда *Integripalpia,* ко второй группе семейство *Hydroptilidae,* а к третьей — остальные семейства *Integripalpia.*

Фазы процесса приспособления доказывают следы прежних функций, сохраняющиеся в настоящем поведении личинок ручейников. Эти следы, обнаружены в опытно вызванных реакциях представителей отдельных групп, являются остатками функций, которые в определённых этапах исторического развития личинок были основой их существования.

Каждая отдельная фаза в процессе приспособления личинок ручейников рассчитана на рост автономии, навязывает к предыдущей фазе и представляет относительно, конечное состояние, которое зависит от начальных условий, так как возврат из стоящих вод в проточные и на материк происходит по тому же пути, что переход к водяной жизни личинок предков ручейников и ценогенетическое приспособление ручейников к стоящим водам. Возникшие на этом пути изменения приспособления являются результатом модификационного управления средой приспособительного процесса. Они были укреплены естественным отбором и сохранились в виде следов прежних функций, которые были обнаружены экспериментальным путём вызванных реакций и представляют собой, хотя скрытые, настоящие черты, характеризующие историческое развитие.

Вторая часть работы охватывает исследования фоторецепции личинок ручейников. Предметом исследований были личинки, представляющие выделенные группы ручейников. В экспериментах были обнаружены временные параметры, действующие на возникновение и сохранение зрительного впечатления: время получения зрительной информации, время приспособления и время инерции зрения. Сумма времени для получения зрительной информации и время приспособления охватывает время стимуляции, а сумма времени приспособления и времени инерции даёт время продолжительности реакции. Время стимуляции и продолжительности реакции сливается и накладывается друг на друга (рис. 32).

Автор обратил внимание на числительный диапазон временных параметров в кругу серии иследованных особей одного вида, который имеет значение селекции в процессе приспособления. Автор тоже сконстатировал процесс сокращения этих параметров у представителей отдельных групп ручейников в связи с переходом от пассивного к более активному образу жизни.

Сокращение временных параметров зрения является выражением эволюционного развития точности зрения и связано с развитием двигательной активности и преобразованием асимметрических и некомпенсационных движений в симметрические, компенсационные, которые дают возможность движения по вертикальной плоскости в связи с оторванием личинок от почвы и подходящим построением защитных конструкций, обусловливающим, соответственно, их ориентировку в отношении к земному притяжению и облегчающим активный образ жизни.

Кроме доказательства увеличения исправности фоторецепторов путём филогенетического развития, автор сконстатировал также процесс сокращения параметров зрения в онтогенезе личинок *Limnephilus flavicornis* (Fabr.) и в связи с этим выдвинул предложение, что отдельные стадии личиночного развития имеют различную селекционную стоимость в процессе естественного отбора, так как это связано с развитием пространственной ориентировки.

В контрастном освещении во время действования кинетических контрастов, исходящих из движения окружения по отношению к организму или организма по отношению к окружению, время получения зрительной информации и инерции сливаются и накладываются друг на друга, подобным образом, как время стимуляции и время продолжительности реакции. Это вызывает свойственную пульсацию временных параметров, вызванных ритмикой действования кинетических контрастов. Так как кинетические контрасты прерывают приспособление к световому стимулу, прерванное приспособление является условием проявления оптомоторических реакций. Зато в постоянном монолитном освещении не прерванное приспособление доводит к исчезанию реакции.

Исследования порогов дифференциальной и контрастной чувствительности доказали, что зависит они от иллюминации адаптационного фона. Характеризует их тоже числительный диапазон в кругу серии особей по мере роста стимуляционного освещения. Таким образом они имеют, как и временные параметры зрения селекционную стоимость в эволюционном процессе приспособления.

В конечных итогах автор выдвинул тезис, что похоже как разорванные адаптации в процессе фоторецепции являются условием существования оптомоторической реакции, приспособительный процесс в историческом развитии продолжается благодаря тому, что приспособления к определённым условиям существования бывают заторможены и прерваны возбуждением к новым приспособлениям. Это является условием формирующего процесса в историческом развитии.

Постоянные условия действуют, как консерваторы на функцию и структуру биологической системы так же, как постоянный стимул доводит к адаптации. По мнению автора, время адаптации в историческом развитии должно иметь тоже свои пределы и, если они не будут на соответствующем этапе прерваны последующей фазой приспособительной к изменённым условиям существования, доводит, вероятно, к старению линии развития генотипа, так как не прерванное время адаптации к свету доводит через адаптацию к исчезновению фототактических или фотокинетических реакций.

Сравнивая процесс приспособления в историческом развитии с адаптационными процессами, связанными с приёмом информации окружения автор доказал их общие черты: всеобщность, многообразие, комплементность, возвратную связь и симетрию во времени. Эти черты разрешают привести эти процессы к единству.

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