OIKOS 2:2 1950

THE TORRENTIAL INVERTEBRATE FAUNA

BY

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The torrential fauna is the animal community of swift-flowing water. The term swift-flowing water may be defined on the basis of the table below, compiled from various authorities, which shows the ratio between stream velocity and the size of mineral particles which the current can transport. By stream velocity is meant the velocity in the water layer near the bottom. In deep water-courses there may in this respect be a considerable difference between the lower and the upper layers, the former being the slower. It will be seen that at a velocity of 50 cm/sec. the current will remove all particles less than 5 mm in diameter. At this and higher velolocities there will therefore be a stony bottom, and hence I shall designate 50 cm/sec. as the lower limit of swift-flowing water. It might perhaps seem to be rather a low limit. At a rough judgement, however, most people are inclined to considerably overestimate stream velocities. In a waterfall water moves at about 6 m/sec.; at this velocity, air-resistance and acceleration due to gravity are in equilibrium. 6 m/sec. is thus the theoretical upper limit for flowing water, but in proper water-courses — and even in rushing mountain streams — velocities over 3 m/sec. rarely occur. By comparison it should be borne in mind that the mechanical effect of the current is not proportional to the velocity itself, but to the square of the velocity. Thus a current of 3 m/sec.

Stream velocity	Diameter
10 cm/sec.	0.2 mm
25 ”	1.3 ”
50 ”	5 ”
75 ”	11 ”
100 ”	20 ”
150 ”	45 ”
200 ”	80 ”
300 ”	180 ”

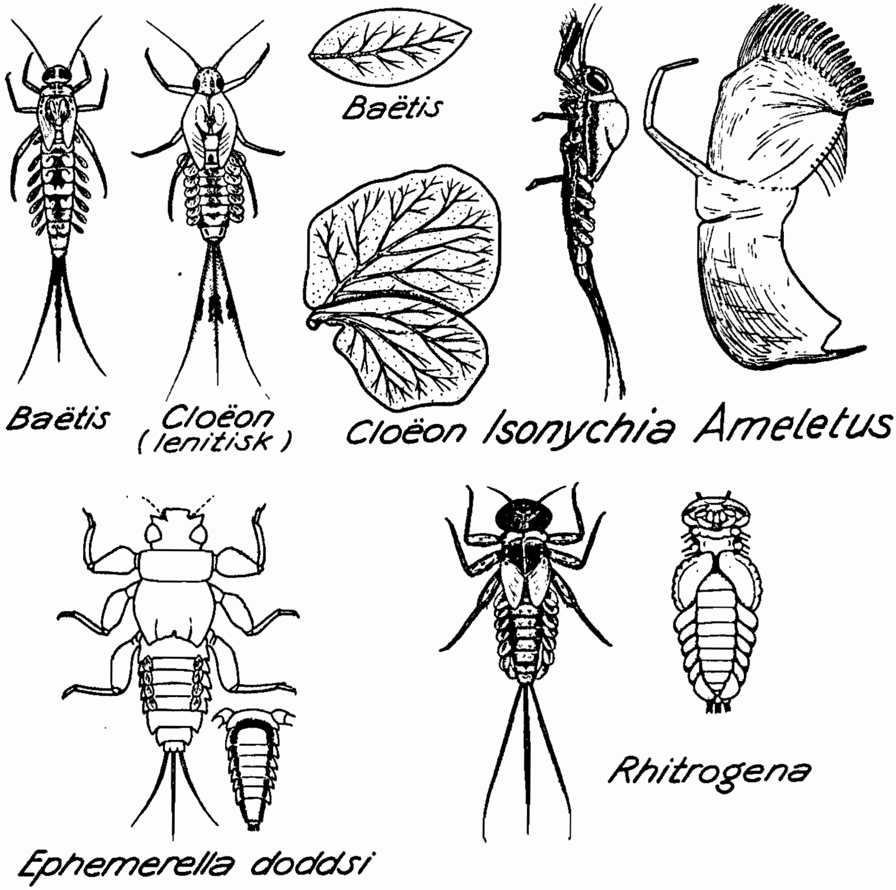
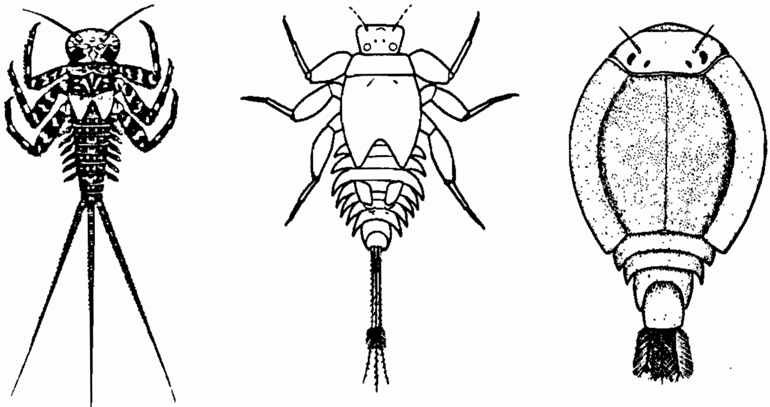


Fig. 1. Mayfly nymphs. Above: centre: gill lamellae; right: maxilla.

is not 6, but 36 times as strong as one of $^1/_2$ m/sec. With a velocity of 3 m/sec. the current exerts a pressure of nearly 500 mg per sq. mm, an exceedingly severe strain on animals which live in it.

On the stones there may be growth of robust algæ (especially *Cladophora*) and mosses (e. g. *Cratoneuron*), and at velocities up to 100 cm/sec. phanerogams may take root in the sand and gravel underlying the stones. (100 cm/sec. is the velocity at which pure water begins to foam). It is especially plants with linear leaves, such as *Potamogeton pectinatus*, or with finely divided leaves, such as *Batrachium* and *Myriophyllum*, which may occur in patches in swift-flowing water. In this paper, however, the term torrential fauna refers only to the animal life on the naked, smooth stones themselves. Animals



Heptagenia sulphurea *Ephemerella hecuba* *Prosopistoma*

Fig. 2. Mayfly nymphs.

living in other habitats of flowing water, e. g. in vegetation, we shall, together with the torrential fauna, include in the term rheophilous fauna.

The torrential fauna is not very rich in species. It is mainly composed of insect nymphs and larvæ, and among these caddis fly larvæ play the most important rôle. Mayfly nymphs are also well represented, and Chironomid larvæ of the subfamily Orthocladiinæ are usually present. In addition, nearly all the orders which have representatives in freshwater are found. From Asia and North and South America even torrential lepidopterous larvæ are known. Besides Trichoptera and Ephemeroptera there may, in the North European fauna, be reason to mention the coleopterous larva *Helmis maugei* Bedel (fig. 8) and the dipterous larvæ *Simulium* Latreille (fig. 10) as typical and common representatives. The nymphs of Plecoptera, with few exceptions, live in running water. However, — in North Europe at least — they are especially found in the vegetation, so they do not play an important rôle in the torrential fauna. It is especially members of the family Perlidæ which may be encountered here, and probably more often as occasional stragglers. Among non-insects there are some small water-mites, a few snails (in this country *Ancylus fluviatilis* Müller), and a few Turbellaria (in North Europe *Planaria gonocephala* Dugès and *Polycelis cornuta* Johnson, whereas *Pl. alpina* Dana would seem to tend towards a hygropetric life. Most likely, there are also Protozoa characteristic of this habitat, but nothing is at present known about this.

Like most other animal communities the torrential fauna is not sharply limited. *Simulium* larvæ, e. g., are also very often found in stream vegetation.

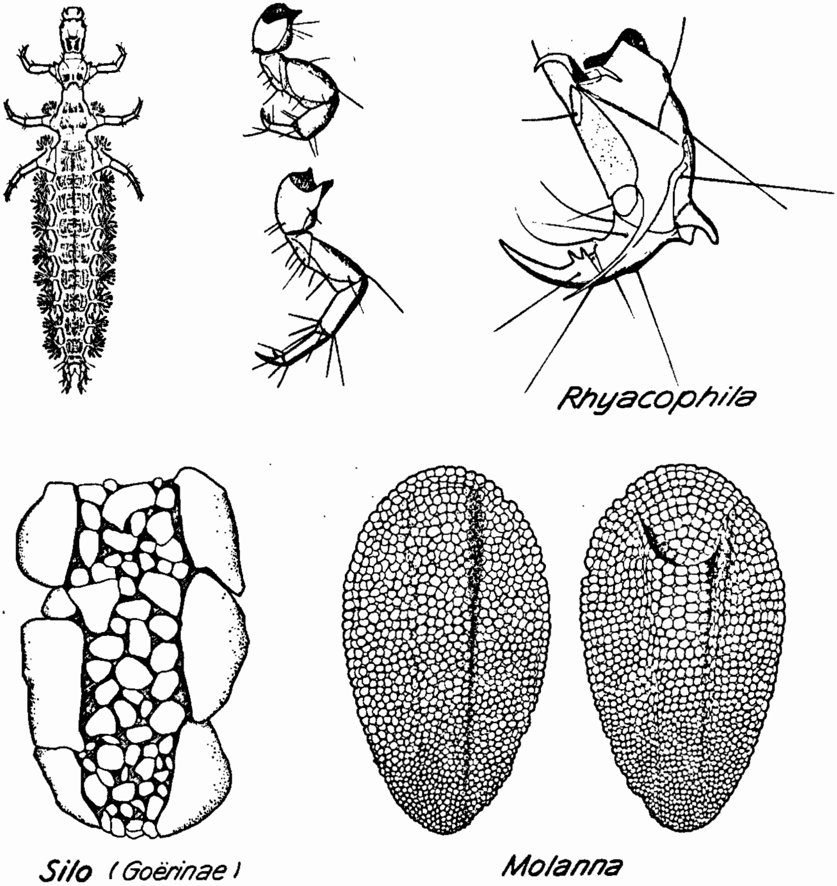


Fig. 3. Caddis fly larvae. Above: Rhyacophila septentrionis MacLachlan; larva in dorsal view; right anterior and posterior leg seen from behind; left anal proleg in lateral view. Below: cases.

Still, there are a great many forms which live exclusively upon stones in swift-flowing water. The question arises therefore as to why they are bound to this extreme habitat.

It might be supposed that it is because they require water of high oxygen contents. Swift-flowing water is in very lively gas exchange with the atmosphere, and hence the oxygen tension will never fall much below saturation, not even at night when carbon dioxide assimilation by plants ceases. This at least holds good if we look at other than heavily polluted waters. It is certainly also true that many, perhaps most (but by no means all!), torrential animals require a high oxygen tension. Morphologically this is expressed in a reduction of the respiratory apparatus. In the torrential mayfly nymph

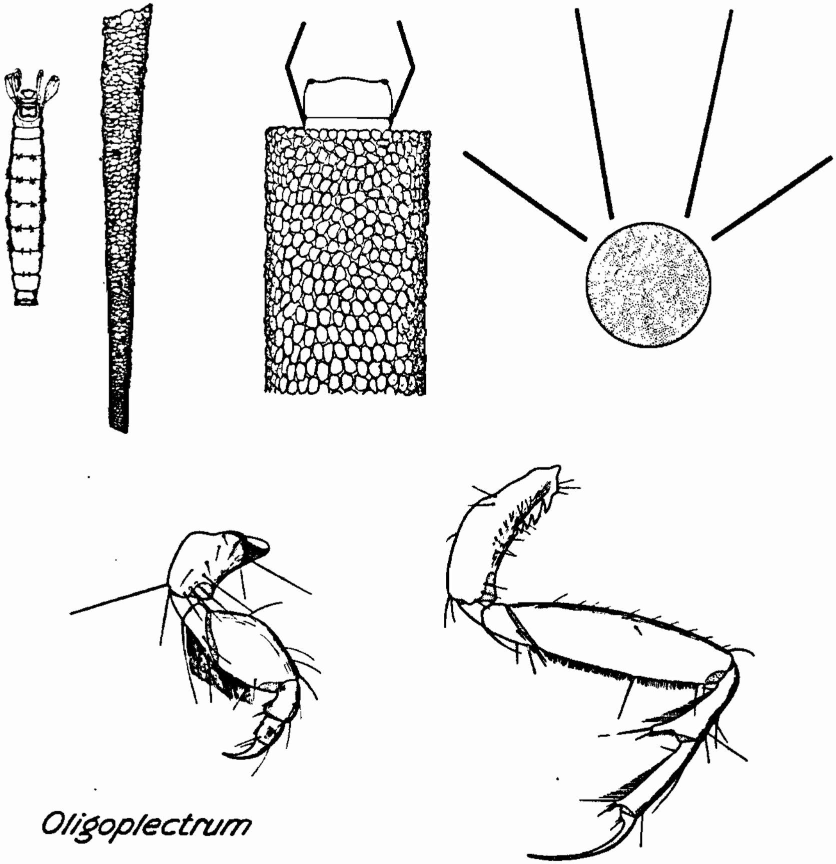


Fig. 4. The torrential caddis fly Oligoplectrum maculatum Fourcroy. Above: larva; case; diagram showing position of anterior legs during feeding; same of middle and posterior legs; (the two diagrams have been drawn in different scales). Below: right anterior and middle leg in posterior view.

Baëtis Leach, e. g., it will be seen that the so called gill lamellæ (which are not true gills; cp. 17) are much more weakly developed than in its near, lenetic relative *Cloëon* Leach (fig. 1). In *Baëtis* the lamellæ are moreover motionless, since water renewal is carried out by the current. This reduction, however, of the respiratory apparatus is, no doubt, a secondary phenomenon, and the abundance of oxygen is a quality which the torrential habitat shares with some other habitats, such as the vegetation of swift flowing waters and the littoral zone of lakes. We must therefore look for other explanations. In my opinion, competition is the most fundamental reason for the existence of torrential forms: animals which can live in the torrential habitat are protected against competition from animals which cannot.

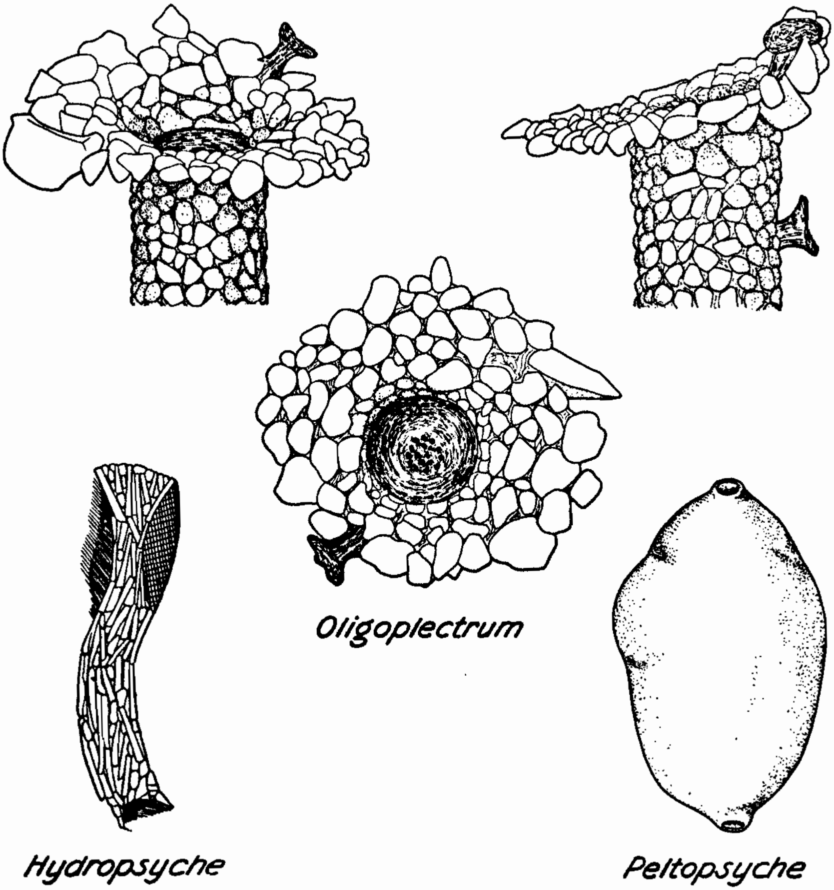


Fig. 5. Caddis flies. Above and centre: Oligoplectrum; anterior end of pupal case in dorsal, lateral, and anterior view.

And here we arrive at the first problem which faces torrential animals: they must be able to cling to stones in swift currents. They are robust forms with strong legs as a prominent characteristic. Special organs of retention have often been developed. The caddis fly larva *Rhyacophila* Pictet (fig. 3), in contrast to all other caddis fly larvæ, builds no abode of any kind, but roams freely over the stones. Proximally on its anal prolegs there is a hook, which together with the strong anal claw forms very efficient tongs, used by the larva to grasp small irregularities on the stones. In creeping it first lengthens then shortens its body, clinging to the stone alternately with the anal prolegs and the short, stout thoracic legs. (8, p. 354). *Simulium* larvæ have a circlet of rows of outwardly directed hooks on the posterior end of

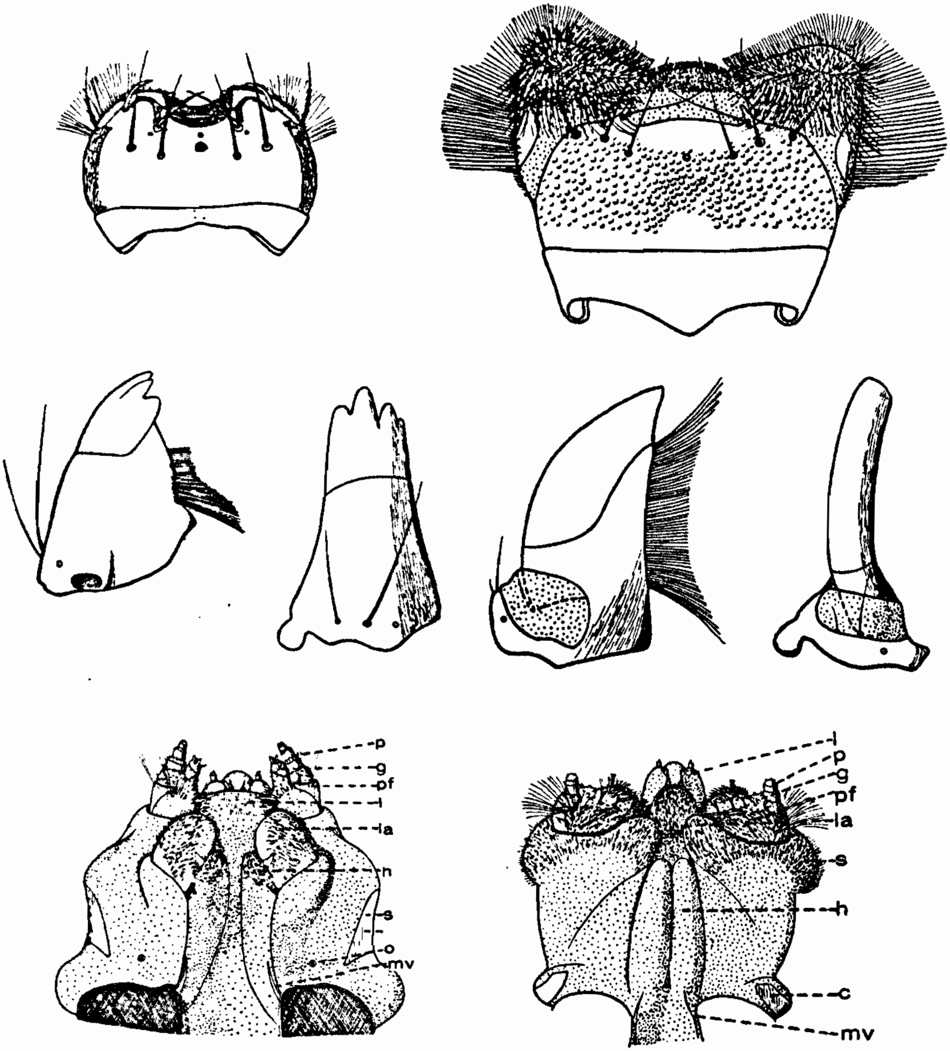


Fig. 6. Caddis fly larvae. Left: typical mouthparts of a phytophagous Limnophilid (Stenophylax nigricornis Pictet). Right: mouthparts of a torrential Limnophilid (Silo nigricornis Pictet). Above: labrum; middle: mandibles; below: maxillolabium. In Silo the maxillolabial plate described in the text is formed by the larva bending the labial lobe (the central of the three distal processes) backwards, so that the pad-like anterior side of this lobe is turned downwards.

the body (fig. 11). Strong muscles are attached to the centre of this circlet. Their contraction pulls the hooks inwards. When the muscles are relaxed, the hooks again move outwards and hang on to a small lump of silk web, previously placed on the stone by the larva. (3, pp. 214—15.)

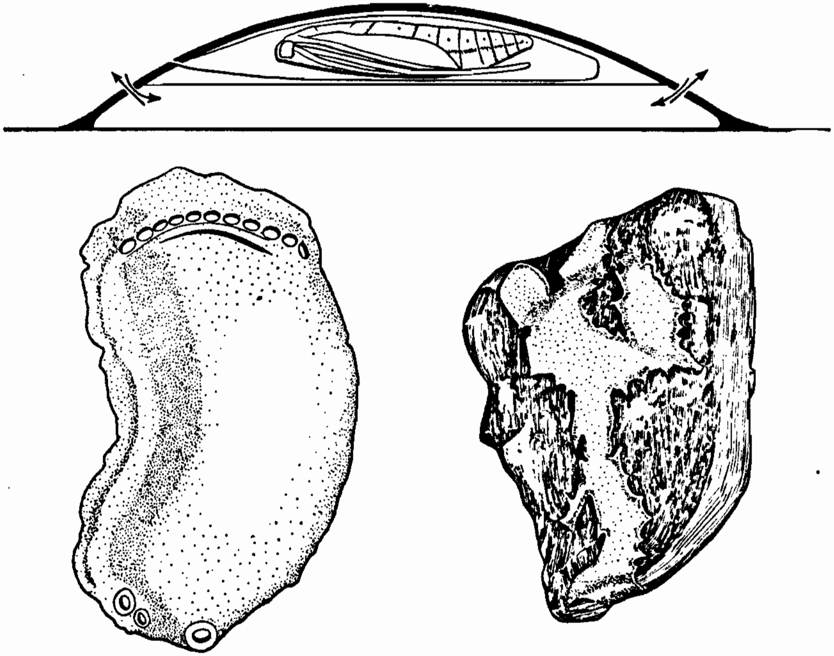


Fig. 7. The torrential Lepidopteron Aulacodes periboscalis. Above: diagrammati longitudinal section through the pupal cocoon. Below left: pupal cocoon from abov Below right: larval dwelling.

Suckers would of course form particularly efficient retention organ Typical suckers are, however, only found in the larvæ of the dipterous famil Blepharoceridæ (fig. 9), which is not represented in the North Europea fauna. They have six unpaired suckers on the ventral side. Their importanc in the biology of the larva is so great that the original segmentation has bee almost entirely obliterated and replaced by a secondary segmentation, corresponding to the number of suckers. A sort of forerunner of the Blepharoceri suckers is found in the larva of the Asiatic and American Psychodid *Maruin* FRITZ MÜLLER. *Maruina* belongs, however, to the fauna hygropetrica and thu is not torrential. It has been asserted (11, p. 51) that in the larvæ of th Asiatic dipterous family Deuterophlebiidæ (fig.9), the hook-covered apex o the peculiar, lateral processes function as suckers. This is, however, denie by Hora (3, p. 228) and, as far as I can see, rightly so. They probably act i the same way as the Simulid circlet of hooks.

A peculiar form of adhesive disc is found in some mayfly nymphs, wher the whole ventral side of the abdomen is used for such a purpose. In th North American *Emphemerella doddsi* NEEDHAM (fig. 1) the adhesive disc i

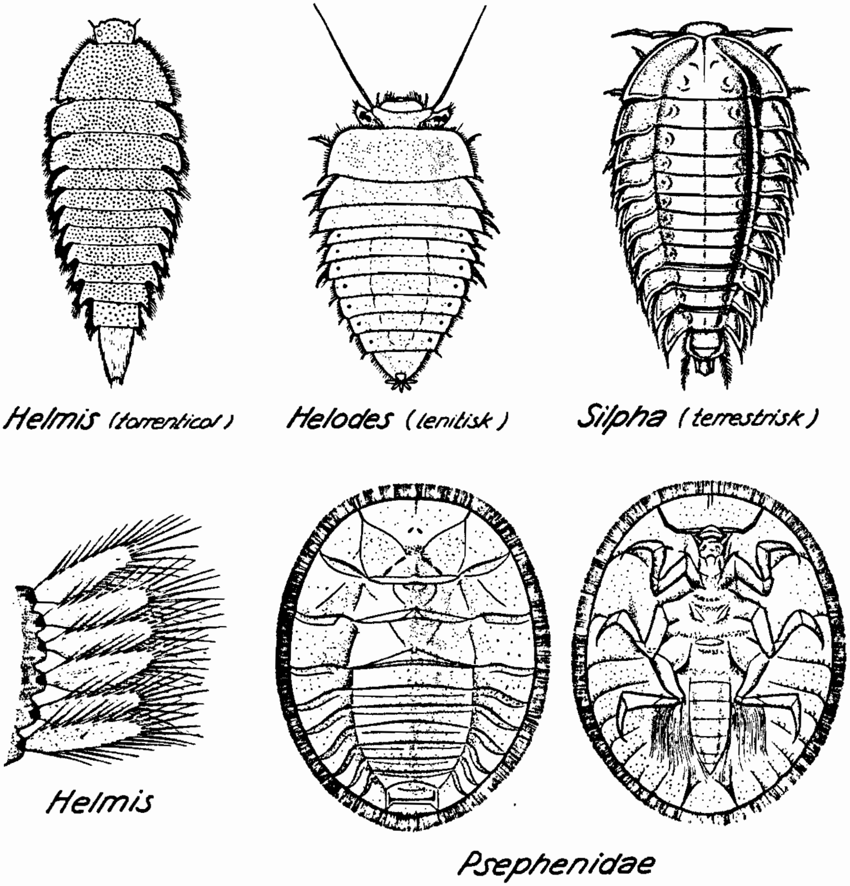


Fig. 8. Beetle larvae. Below, left: "marginal contact" of Helmis larva.

bounded by a setaceous cutaneous fold (7, p. 7); in the genus *Rhithrogena* Eaton (fig. 1) the characteristic gills form the boundary (7. pp. 12—13). The latter apparatus would seem to be still better developed in the genera *Epeorus* Eaton and *Iron* Eaton, where the lateral margins of the gill lamellæ are thickened. It has been asserted that the peculiar mayfly nymph *Prosopistoma* Latreille (fig. 2) can use the ventral side of the whole body as an adhesive disc. Something similar has been described in the larvæ of the non-European coleopterous family *Psepheniidæ* (fig. 8). They are some very flat creatures, called "water-pennies" by the Americans. By arching the body they are, supposedly, able to adhere to the substratum. About the two latter forms, Prosopistoma and Psepheniidæ, however, opinions vary (3, p. 203). Both forms live beneath stones, where one should imagine adhesive discs are not of much use.

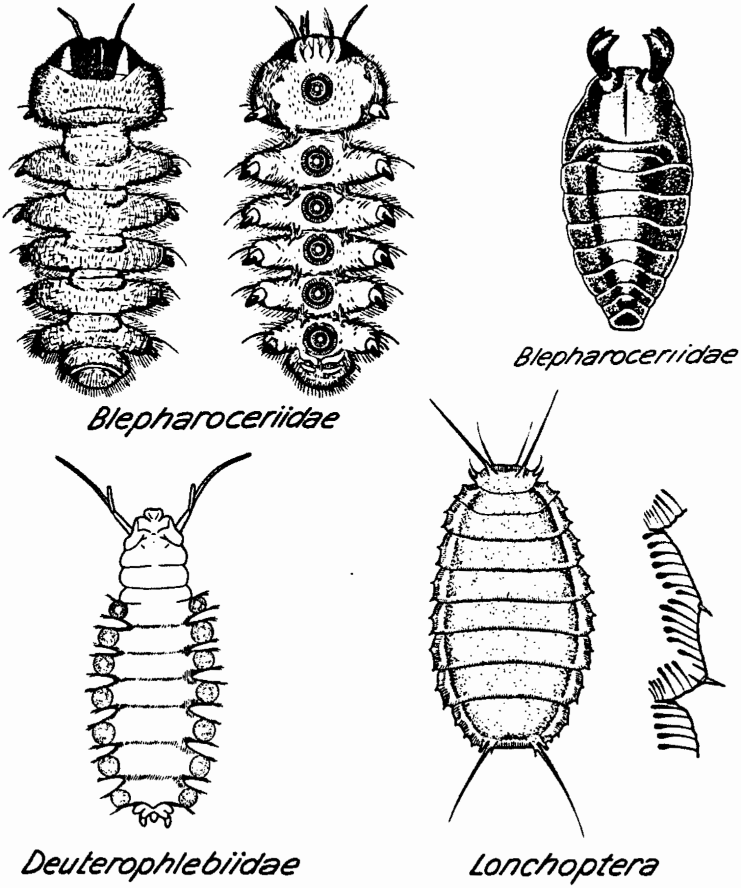


Fig. 9. Diptera. Blepharocerid larva in dorsal and ventral view; Blepharocerid pupa: Deuterophlebid larva in ventral view; Lonchoptera larva in dorsal view and "marginal contact" of same.

A reduction of appendages which increase friction is also characteristic of torrential animals. Thus, comparing *Baëtis* and *Cloëon* (fig. 1), the tail filaments and especially the antennæ are much shorter in the former than in the latter. In those *Baëtis* species which live in particularly fast-flowing water, the middle tail filament is still further reduced and sometimes entirely lacking. The reduction of the gill lamellæ may of course be considered from the same point of view.

Case-bearing caddis fly larvæ have at their disposal a special means for withstanding current-action. By increasing the weight of the case they can increase their specific gravity. They always build the case of mineral particles. Also many lenitic forms do so, it is true, but the wall is thicker, and the case therefore heavier in the torrential forms. In addition special pieces of ballast are often placed on the case. The latter reaches its culmination in the subfamily Goërinæ, where three small pebbles are found on each side of the case; (cp. also 8, pp. 609—12).

In 1907 STEINMANN put forward the theory (13, pp. 133—35) that the most striking morphological feature in torrential animals is a dorsoventral flattening of the body, a shape said to offer two advantages: In the first place a smaller surface of attack to the current; and, secondly, since the ventral side is flat, while the dorsal side is slightly vaulted, the pressure of the current would, according to the law of the parallelogram of forces, be partly transformed into a downward directed pressure (fig. 14), which should help the animal to maintain its hold on the substratum. This theory was greeted with enthusiasm; later on it has been repeated on almost innumerable occasions in text-books and treatises, and biologists have endeavoured to find new examples of dorso-ventral flattening in torrential animals. What, however, has been almost entirely omitted is to make the theory the subject of a critical examination. This will be the aim of the following paragraphs.

First, many of those animals which have been cited as examples supporting the theory are not at all distinguished by a particularly high degree of rheophily. The mayfly nymph *Heptagenia sulphurea* O. F. MÜLLER (fig. 2), e. g., lives chiefly on the shores of large lakes. It may also be found in running water, it is true, but here it is characteristic that it avoids the more swift-flowing parts. The flattening of this nymph is probably connected with its habit of seeking shelter in narrow crevices, e. g. beneath stones or in clefts of submerged branches — just as the flat body of the cockroach is related to its habit of hiding in narrow cavities. The flattest mayfly nymph known is the North American *Ephemerella hecuba* EATON (fig. 2); about it NEEDHAM & CHRISTENSON write: "It looks as it may have been run over by a steam roller ..." (7, p. 9). This nymph lives in running water, it is true, but only in sheltered bays with a muddy bottom. The mayfly genus which has been most successful in inhabiting torrential streams is *Baëtis* (fig. 1). Together with Blepharocerid larvæ members of this genus occur in the swiftest currents known to contain animal life (1). Their nymphs, however, do not show the slightest trace of dorsoventral flattening. Thus, mayfly nymphs do not support STEINMANN's theory. DODDS & HISAW (1) have expressed exactly the same views with regard to North American mayfly nymphs.

Whilst the torrential beetle larva *Helmis* has a very flat body, a very similar body shape is found in lenitic forms, such as *Helodes* LATREILLE, and also in terrestrial beetle larvæ, such as *Silpha* LINNÉ (fig. 8). Thus, in coleopterous larvæ, flattening of the body may be considered rather as a fairly common body form than as an adaptation to torrential conditions.

As mentioned above, caddis fly larvæ play a very important rôle in the torrential fauna. However, in North Europe at least, there is no example of dorso-ventral flattening in torrential representatives. The only forms which might perhaps be so considered are the Goërinæ; but here it is a matter of ballasting and not of flattening the case (8, p. 613). The flattest case is that of *Molanna* CURTIS (fig. 3), but it is a lenitic form, which chiefly lives in not too shallow water in lakes; in fact, it extends farther out into lakes than any other caddis fly larva.

About the rheophilous water-mites the excellent specialist VIETS writes (14, p. 14): "Die dorsoventrale Abflachung des Körpers ... kommt bei den Bachmilben nicht in dem Masse und nicht so ausgeprägt vor, dass dies Merkmal als für diese Tiere typisch angesprochen werden dürfte. Die an den Bachpflanzen kletternden, z. B. in den Blattwinkeln der Laub- und Lebermoose versteckten und sich hier anschmiegenden ... sind flach gebaut ... Die Bewohner des Bachbodens und der Steine sind weniger dersoventral abgeflacht ...". The snail *Ancylus fluviatilis* O. F. MÜLLER has been quoted as a typical example of dorso-ventral flattening in torrential animals, and it ought to be admitted that for a snail it has rather a peculiar body shape. However, *Ancylus* has a near relative, *Acroloxus lacustris* LINNÉ, which is distinctly lenitic, living even in small forest ponds. From fig. 13 it will be seen that *Acroloxus* is much flatter than *Ancylus*, which hardly supports STEINMANN's theory. Finally, the few torrential Turbellaria have been mentioned as examples of dorso-ventral flattening; but they are no flatter than their much more numerous lenitic relatives.

Summarising, it appears that dorso-ventral flattening is, at any rate, no more common in torrential animals than in lenitic ones. The flattest torrential forms — *Prosopistoma* and the Psepheniidæ — are known to live beneath stones (3, pp. 187, 195, and 203). It is therefore a bit risky to state that dorso-ventral flattening is an adaptation for withstanding strong currents.

It is also open to question whether, in fact, dorso-ventral flattening can be an adequate method for withstanding current action. For it must be borne in mind that water currents are not laminar, as was supposed by STEINMANN, but turbulent. Simultaneously with the progressive movement the water particles also perform a rolling movement, thus the resulting stream-lines show an irregular wave pattern (fig. 14), as can be easily seen on the surface of swift-flowing waters. (One may easily satisfy oneself that the waves on the surface of such waters are not simply reflections of the irregularities of the bottom). From the figure it will be seen that just as often as the current exerts a downward directed pressure, it will exert an upward directed suction. It goes without saying that the suction action will have its strongest effect upon flat bodies. In this connection it is important to note that the stream-

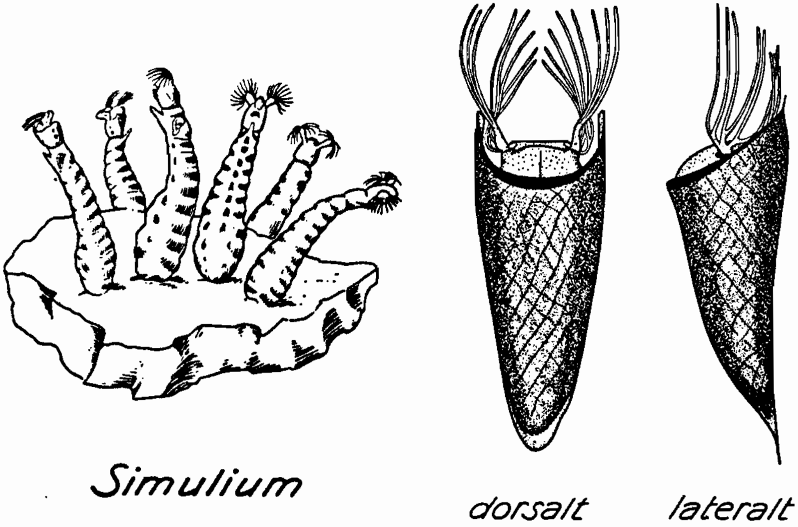


Fig. 10. Simulium. Left: larvae upon a stone. Right: pupa in its case.

line pattern is changing every moment; areas of pressure and areas of suction have no fixed position on the bottom, but are continuously shifting about. It is also a well known fact that flattened mineral particles are more easily transported by current than rounded ones. Finally, by increasing the surface of the body, dorso-ventral flattening will increase the friction between the latter and the water.

Thus dorso-ventral flattening is hardly an adequate body shape for torrential animals, at least not unless they are provided with devices by means of which, from a physical point of view, they may make themselves a part of the substratum. Such devices have also been described under the term *marginal contact*. In the *Helmis* larva, e. g., the marginal contact is said to consist of the row of close-set, vigorous, pinnate setæ found on the margins of the body (fig. 8). As to the marginal contact, however, what we said about dorso-ventral flattening applies here also: it is by no means restricted to torrential forms. A finer marginal contact than that found in the fly larva *Lonchoptera* Meigen (fig. 9), consisting of a striated lamella, can hardly be imagined. But *Lonchoptera* is not torrential; it leads a terrestrial or hygropetric life in spring swamps and similar, very quiet habitats.

Perhaps the theory of dorso-ventral flattening *and* marginal contact cannot be entirely abandoned. On the other hand, it cannot be regarded as a well established fact until it has been tested by field observations and, preferably, also by experiments in the laboratory. In my opinion, the test is most

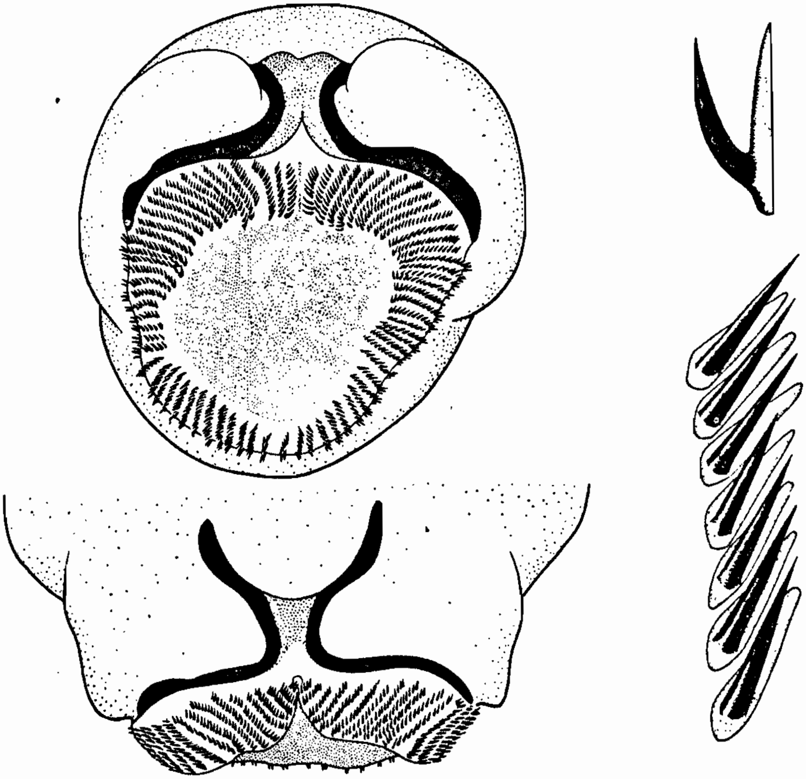


Fig. 11. Simulium larva. Left: posterior end in anal (above) and dorsal view (below). Right: hooks from the adhesive disc in "lateral" (above) and surface view (below).

likely to give negative results. In those cases where flattening actually occurs in torrential animals, the point probably is to avoid the current by seeking shelter in narrow crevices or beneath stones. Thus it may of course be said to be an indirect adaptation for withstanding current action.

Despite a robust body shape and despite retention organs it may happen that the animals are carried some distance by the current. They may compensate for this by migrating against the current. In a great many torrential animals a positive rheotaxis has been demonstrated. In fact some of them, especially the Turbellaria, spend most of their lives moving against the current. Rheotaxis also results in the animals usually orientating themselves with the head-facing the current, which of course is more advantageous than turning broadside to it. *Baëtis* nymphs may be seen sitting on stones head against the current and the tail end swinging from side to side, up and down;

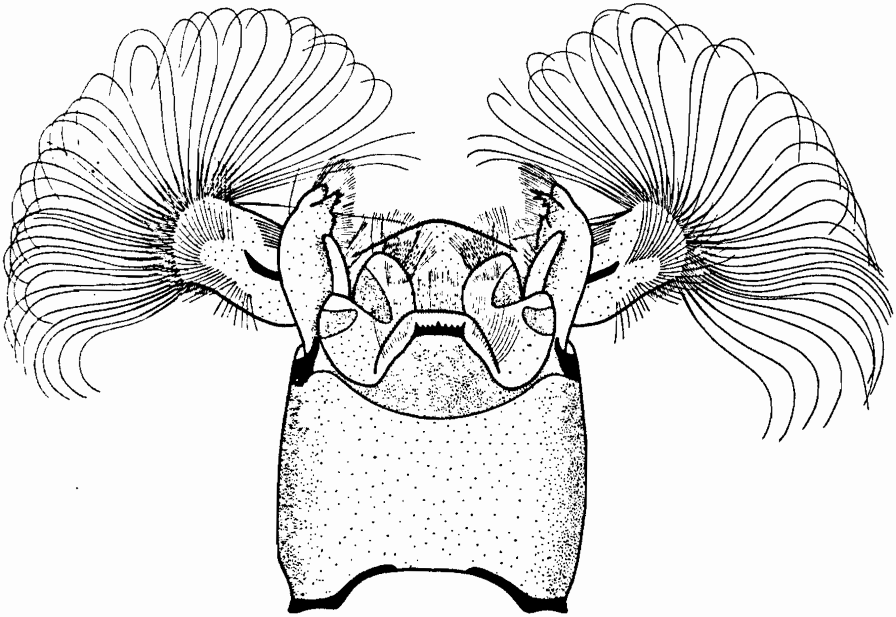


Fig. 12. Simulium larva; head with catchers stretched out in ventral view.

these movements no doubt correspond to the change in current direction due to turbulence.

Most torrential animals, however, do not move very much, but are to some extent sedentary. And among caddis fly larvæ, forms occur which have assumed an entirely stationary mode of life. The *Hydropsyche* larva builds its pretty net (fig. 5) upon the stones. Stationary nets are also found in lenitic forms, it is true, so in *Hydropsyche* the adaptation to torrential life is mainly shown in the compact and very solid construction of the net. Also within those groups, however, which usually build portable cases, sedentary representatives occur in the torrential habitat. *Oligoplectrum maculatum* FOURCROY fastens its slender case (fig. 4) to the stones with the anterior end facing the current, by preference in those sites where the latter is most rushing (9, pp. 54 and 67—70). The shape and the orientation of the case serves to diminish the effect of the current. The American Hydroptylid *Peltopsyche* MÜLLER (6, pp. 73—74; 5, pp. 117—21) also has a stationary case. It is built exclusively of silk and bears a faint resemblance to the egg-capsules of the leach *Herpobdella* (fig. 5). The torrential lepidopterous larvæ (4, pp. 145—52) must be considered as sedentary, since they live beneath a silk web, which, however, is much larger than the larva itself (fig. 7). The Orthocladiine larvæ must also be included in this ecological group, though the spinning of sedentary tubes is not peculiar to torrential Chironomids.

Another big problem which faces the torrential animal is that of feeding. Stones in swift-flowing water might appear to form a habitat very poor in food, and yet, in many streams the torrential fauna is very rich in individuals. Still, it is only apparently that the stones are poor in food. If taken out of the water, it will be found that they are smooth to the touch; they are covered with a very thin, much less than paper-thick, slimy film, consisting of microscopic organisms, the bulk of which are diatoms. Though some Protozoa occur in the film, it may be described as *microflora*. It of course also occurs on other objects in flowing water, such as the leaves of water-plants. From the point of view of productivity its rôle in flowing water is similar to that of plankton in lakes, but whereas the latter has been the subject of numerous works, the microflora of flowing water has been almost entirely disregarded. The study of its composition in various types of water-courses, as well as of its importance in productivity, offers limnologists a rich field of investigation.

Most torrential animals feed on the microflora. However, very few animal groups have mouthparts suited for the intake of food found as a thin film upon the surface of stones. Hence the mouth parts of their torrential representatives are remodelled to cope with this special type of food. These modifications have been best investigated in caddis fly larvæ (8, pp. 619—20). Left side of fig. 6 shows the typical shape of the mouth parts in phytophagous larvæ. The labrum is scleroticized on its external side, the mandibles have two toothed edges, the maxillæ, labium, and hypopharynx are partly coalesced to form a kind of lower lip, the maxillolabium; (cp. also 8, pp. 275—92). In torrential forms (fig. 6, right side) the mandibles are toothless, nail-like; they might also be compared with hollow chisels. The distal part of the labrum is broad, membraneous, and somewhat thickened, and the distal parts of the maxillolabium are also transformed into soft lobes. Thus two soft plates are formed, the labrum in front, and the maxillolabium behind, the mandibles. When the larva feeds, these plates are pressed against the substratum, and between them the naillike mandibles work, scraping the microflora off the substratum. The penicillus of the mandibles is very well developed and serves possibly as a sort of baleen, sieving the water from the scraped off material. Investigations of conditions in other groups would, no doubt, yield interesting results. In mayfly nymphs (12, p. 89) it would seem that the maxillæ form the most important feeding organs. They are provided with a kind of comb or brush by means of which the diatoms are swept off the substratum (fig. 1).

Also another sort of food is at the disposal of torrential animals. Detritus is not deposited in this habitat, it is true, but it is carried past the stones. The caddis fly larva *Oligoplectrum* (9, pp. 70—74), as mentioned above, fastens its case on stones with the opening facing the current. The larva sits with

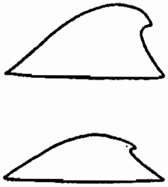


Fig. 13. Outlines of Ancylus (above) and Acroloxus (below) in lateral view. Ancylus fluviatilis varies a good deal; forms considerably higher than that figured may be found, also in very swift streams.

the foremost part of its body protruding from the case. The anterior legs are stretched forward, the middle and posterior legs outward, so that they radiate from the mouth of the case like the spokes of a wheel (fig. 4). Their median edge is turned against the current: it is furnished with a row of fine spines to which detritus will adhere. At intervals now one, now another of these four legs is folded up like a clasp knife and moved towards the mouth. Here the anterior legs, which have a great brush of hair-like spines on the median side, sweep off the collected material and mould it into a ball. The legs are also used to trap the sand grains from which the case is built. The mayfly nymph *Isonychia* EATON (=*Chirotonetes*; 7, p. 12) catches detritus with its anterior legs. It sits head facing the current and its anterior legs stretched forward and outward. They are covered with fringes of long setæ, which act as a sort of filter (fig. 1). In *Simulium* larvæ a pair of fan-like organs on the labrum form the food catching device. The larva sits on a stone attached by its posterior end, with the body stretched in the direction of the current, and the catching organs spread out. Each of these structures (fig. 12) consists of a fan of long, curved setæ, placed distally on a short shaft. At rapid intervals the larva alternately folds up the two fans and moves them to the mouth; here, the collected material is swept off by the mandibles, which are furnished with various combs and brushes. The catching organs of *Simulium* larvæ are well suited for collecting very finely divided detritus. Pollution increases the amount of such microscopic detritus in water-courses, and I have observed that pollution leads to a considerable increase in the number of *Simulium* larvæ. The imagines are blood-suckers of mammals and may seriously damage live-stock. An increase in their number is thus unwelcome and another reason for not contaminating streams.

As regards feeding habits, two types can thus be distinguished among phytophagous forms: microflora eaters and filter feeders. Finally there is a third possibility: the carnivorous habit. It is realized both in free-living and sedentary forms. A well marked example of the former is the *Rhyacophila* larva, which might be called the tiger of the torrential fauna. The *Hydropsyche* larva is an example of the sedentary type. Its dwelling (fig. 5) consists of a barrel vault and a somewhat more spacious vestibule. In the latter there are two openings, one facing the current and another pointing away from it and closed by a comparatively coarse net. The larva sits with its abdomen in the barrel vault and the forepart of its body in the vestibule. Small animals carried by the current into the vestibule are caught in the net and devoured by the larva. Useless materials, such as sandgrains, the larva will throw beyond the border of the vestibule, where they are carried away by the current.

We shall now consider some adaptations in torrential insect pupæ. The coleopterous larvæ leave the water before pupation and spend the pupal stage on land. This is a general rule in aquatic Coleoptera and not a special adaptation in torrential forms. The caddis fly pupæ spend the pupal stage in a case (or shelter), fastened to the substratum. So all caddis fly pupæ do, and the case of torrential forms does not differ in principle from that of lenitic forms. The pupal shelter of Rhyacophilidæ, which is freely exposed to the current, is distinguished by an especially solid construction. Most other larvæ prior to pupation seek shelter beneath loose-lying stones. In *Oligoplectrum* (9, pp. 74—76 and 82), however, the case of the old larva is so firmly attached to the substratum that it is impossible for the larva to move. The pupa is therefore found in the same place as the larva, with the anterior end of the case facing a very strong current. When the pupa before emergence leaves the case, it thus must creep out against the current, which perhaps may be difficult enough. To overcome this difficulty a very interesting adaptation is seen in the pupal case (fig. 5): Before pupation the larva enlarges the opening of the case with a trumpet-like collar. This collar must necessarily cause strong eddies in the water, so that a sort of "dead space" will arise in front of it. The latter will of course highly facilitate the creeping out; perhaps it is only the "dead space" which makes it possible for the pupa to creep out at all.

Simulium larvae before pupation spin sedentary cocoons (fig. 10), which bear some resemblance to the wind-shelters built by primitive people. The pointed end of the cocoon faces the current; the other end is open, and through this opening the peculiar gills of the pupa are stretched out and float in the water. In the Diptera Blepharoceriidæ (fig. 9) and Deuterophlebiidæ the obtect pupa is glued to the substratum by means of a cement, which is said to be produced by the salivary glands of the larva (3, p. 257).

The torrential lepidopterous larvæ (10 a) before pupation spin a cocoon (fig. 7), which is much larger than the pupa itself. The cocoon is a flat dome and very thick-walled. Internally it is divided into two floors by means of a thin

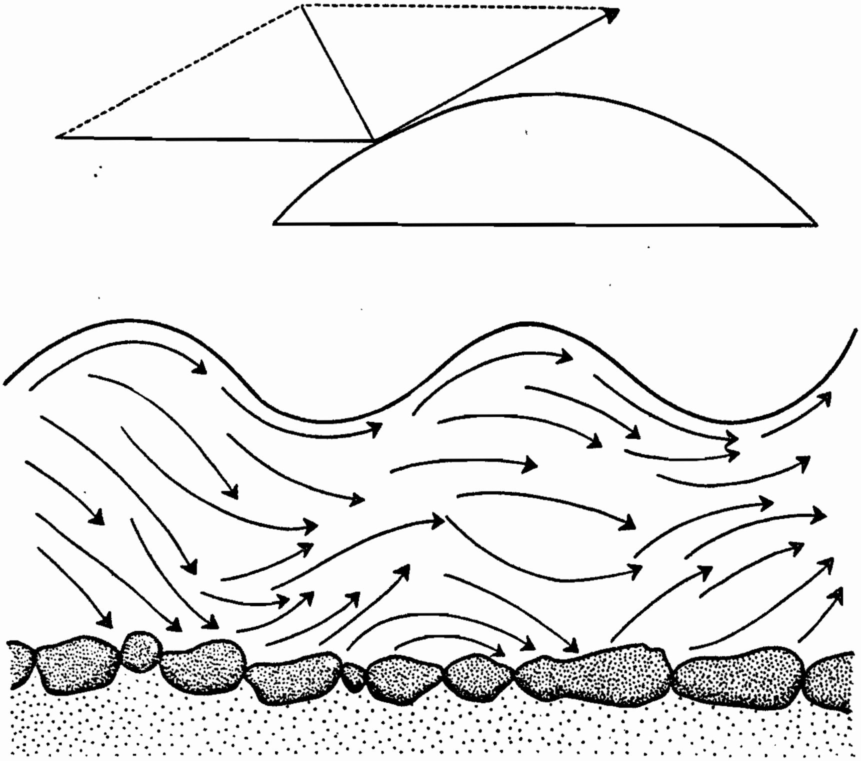


Fig. 14. Above: diagram showing action of the current upon flattened animals according to Steinmann's theory. Below: Diagrammatic longitudinal section through a stream. The figure shall give a rough idea of conditions in running water, but does not pretend to be an exact picture of the water-movement.

and delicate septum. The pupa lies in the upper floor, enclosed again in a very thin-walled cocoon. The latter is filled with air of unknown origin; at the anterior end it is connected with a narrow cleft in the outer cocoon, through which the imago eventually creeps out. The cocoon very effectively protects the pupa against the current and the sand grains carried by the latter, but it would appear to make respiration difficult; the exchange of gas through the thick wall is of course very slow. There is, however, remedied for this, the lower floor being connected with the surroundings by a number of small holes, which allow for water circulation. Thus the respiration of the pupa takes place through the two thin silk walls. This is one of the most ingenious cocoons occurring in the animal kingdom.

Some torrential Coleoptera, e. g. *Helmis,* also live as imagines in running water, though not in the torrential habitat, but in the vegetation. The imagines of all the other forms mentioned above are terrestrial. In contrast to the Trichoptera,[1] the pupæ of Lepidoptera and most Diptera have no power of locomotion, so the last moult occur in the place where the pupæ spend their lives, and the animals must make their way from the bottom to the surface as imagines. In the Lepidoptera the pupa, as mentioned above, is surrounded by air. When the imago leaves the cocoon, it carries some of this air with it and reaches the surface in an air-bubble, which immediately bursts, whereupon the imago flies away in a dry condition. In *Simulium*, Blepharoceriidæ, and Deuterophlebiidæ air is secreted between the imaginal and the pupal cuticle just before the final moult. Hence these animals also reach the surface surrounded by an air-bubble. Nevertheless, it is of course a very critical period in the life of the animals, and many perish during emergence.

Also the change from aerial to aquatic life offers certain problems. Some insects lay their eggs on land and the newly hatched larvæ have to seek the water themselves. Others lay their eggs in the water, but in quiet parts of the water-courses, from which the larvæ migrate to the torrential habitat. There are also many forms, however, which go out into the torrential habitat and oviposit there. It might seem that many of them, e. g. the mayfly *Baëtis*, are very little suited for such an excursion. And yet, *Baëtis* can do it and even reach the shore again in safe condition. It lays its eggs in several turns (2, p. 11; 16, p. 171).

It has been asserted (15, p. 606) that there is a very great similarity between the fauna of swift-flowing waters and the fauna of stony lake shores. This statement needs a little modification. Actually, the torrential habitat and the lake shore have very few animal forms in common, whereas there may be a considerable similarity between the faunas of more slow-flowing waters and the lake shore. In North European lowland water-courses with a great seasonal variation in water volume the swifter winter current erodes a stony bottom in many places where the more moderate summer current would be unable to do so. The fauna of such stretches is to a very great extent composed of the same elements as that of the lake shore. (10, p. 141.)

I have already said that most probably it was the competition factor which, so to speak, had forced the animals into the torrential habitat. During the ages, however, many of these animals have become so specialized for the torrential habitat, in feeding biology (e. g. *Oligoplectrum*), respiration (e. g. *Baëtis*), etc., that they are now unable to live elsewhere. For such animals it is an advantage that there is always a fresh current, also in periods when the water volume has its minimum. Whether this demand is fulfilled depends on the constancy of the water volume. Also the amount of food — microflora

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[1] Strictly speaking, trichopterous pupæ do not swim. It is the imago in pupal cuticle that swims.

and detritus — is important, and this depends on the water's contents of dissolved matter, especially nitrate, phosphate, and bicarbonate. Both these factors are again dependent on the geological structure of the drainage area.

The figs 1—5, 7—12, and 14 have been redrawn by Mr. Preben Gross, partly from the papers quoted, partly from original drawings.

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