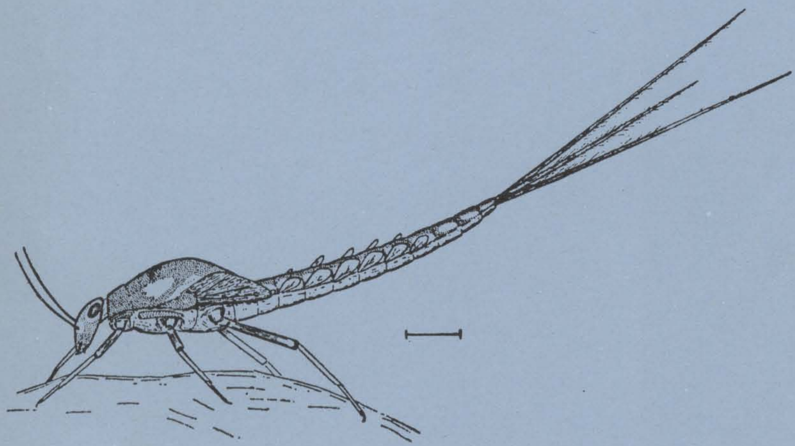
THE STUDY OF MAYFLIES

(EPHEMEROPTERA)

T. T. Macan



AES

LEAFLET No. 31

AES PUBLICATIONS AGENT
137 Gleneldon Road
Streatham, London, S.W.16.

AES Leaflet 31. The Study of Mayflies (Ephemeroptera)

CORRIGENDA

The cover illustration and text figure 4 show the nymph of *Baetis rhodani.*

Text figure 5 shows the nymph of *Centroptilum pennulatum.*

In the section on "Anglers' names" (page 2) a word has been transposed. Lines seven to nine of this section should read as follows:

"Some of their names apply only to one sex at one stage; for example the Iron Blue Dun is the subimago of both *Baetis pumilus* Burmeister and *B. niger* Linn., and the images of the two are . . ."

THE STUDY OF MAYFLIES (EPHEMEROPTERA)

Introduction

It is often stated that the day of the amateur naturalist as a serious contributor to knowledge is over. The argument, when the statement is proffered as an arguable point and is not one of those doleful assertions about the passing of the Good Old Days in which some elderly folk delight, is that today anybody with a taste for Natural History gets a job as a scientist, and that advances in science are possible only with the aid of apparatus that private individuals cannot afford to buy. There is some force in the first point. Obviously we shall not return to the conditions of a century ago when there were hardly any paid posts and when science was pursued by those who had sufficient money not to need a paid post. However, the probability is that, in the future, the working week will shorten and everybody will have more leisure to devote to something that interests him or her. The second point has no force at all, and indeed can be used to support the opposite point of view. Because laboratory apparatus is now complicated, there is a tendency to look down on the biologist who does not use it and, as nobody wishes to be looked down on, few professionals now make direct observations of animals in their usual surroundings to explain problems to which an answer is sought. Some problems, however, are more likely to be solved by observation in the field than by experiment in the laboratory. Many have tried to explain the distribution of a particular species in terms of the chemical composition of the medium in which it lives, although in fact the creatures occur where they do because that is where the female chooses to lay her eggs. Unless the present trend is reversed, amateurs are more likely to solve these problems than professionals. 'Solve' perhaps is a pretentious word to use, for the explanation of any biological observation usually poses further questions and opens up further fields of investigation. To revert to oviposition: observation of the egg-laying female may explain why larvae of a certain species are restricted to a certain type of place but it poses the further problem of what determines the female's choice. This may prove a problem for the biochemists. But at least it may be said that amateurs are likely to formulate the problems and provide the basic information without which the professional can easily waste his time.

One of the fields to which amateurs have made a notable contribution in the past is the description of species. The group under discussion was monographed with professional competence by one of the Victorian naturalists already mentioned, the Reverend A. E. Eaton. Biology owes a great deal to country parsons of that era. Eaton's descriptions are still referred to today, but a modern key to the adults has been written by the well known British Museum expert, Mr D. E. Kimmins (Freshwater Biological Association Scientific Publication No. 15). Descriptions of the species of most groups were completed during the last century but they were generally of the adults only. Keys to the immature stages, often of more importance to the freshwater naturalist, are generally much more recent. The nymphs of the British species have all been described and a key to these has appeared in the same series (No. 20). The student of the Ephemeroptera, therefore, can lay his hands at once on up-to-date keys to both immature and adult stages, and he should have no difficulty in naming species.

Anglers' names

The scientific names of the group, thanks to the sound pioneer work of Eaton, have been subjected to little change, and the beginner is not likely to be confused, as are students of some other groups, by the finding of the same species referred to by different names in different works. On the other hand he will not find any suitable English names. Anglers have a nomenclature of their own designed for their particular purpose. Some of their names apply only to one sex at one stage; Burmeister, for example the Iron Blue Dun is the subimago of both *Baetis pumilus* and *B. niger* Linn., and the imagines of the two are Jenny Spinners if male and little Claret Spinners if female. Not one of these names is applicable to the species as a whole, which makes them unsuitable for general use. Moreover anglers fall foul of the entomologists over the use of the term 'mayfly' to cover the whole group. They apply it to certain stages of the genus *Ephemera* only. Here, therefore, only Latin names are used. It is strange to find that some people shrink from a Latin name (more properly latinized, for often only the termination is Latin), fearing that it is something learned and obscure designed to withhold knowledge from all but a circle of the élite, like the medieval Latin that a doctor writes on a prescription form. Strange and unreasonable, because such people have no difficulty with friends of Celtic origin whose difficult names are derived from a language with far less affinity to English than Latin.

Life cycles

There is a widespread belief, which the writer has seen repeated in the most reputable journals twice within the last few weeks, that mayflies live for but one day. They must, therefore, have 365 generations in a year, a logical deduction from the first statement that a moment's reflection will reject as ridiculous. In fact, of course, although the adult life is short—it has to be because the mouth parts are atrophied and no feeding is possible—the nymphal life may be comparatively long by insect standards. The unique feature of the group is not the short adult life, but the fact that, after a large number of moults in the aquatic stage, the winged form that emerges is not the adult, and there is yet one more change of skin before this stage is reached. Scientists refer to subimago and imago, anglers to dun and spinner. A misconception, repeated in several current books, is that the cast subimaginal skin retains its form, so that the naturalist who has boxed a subimago is astonished to find that he has apparently two specimens when next he looks in his box. In fact the wings of the subimaginal skin shrivel, and nobody has ever been astonished in this way.

The life histories are intriguingly different not only from species to species but within one species at different places. This means that there is endless scope for study, and that, if two naturalists are studying the same species in different places, the result is likely to be, not a useless duplication of effort, but an instructive comparison. For example, the present writer was studying the life history of *Rhithrogena semicolorata* Curtis in a stream in the Lake District when he received an account of a similar study in South Lancashire from Dr Janet Harker. Being second in the field proved an advantage. The first account could do no more than present the facts, the second could make comparison and draw deductions. *Rhithrogena semicolorata* is a winter species that grows all through the winter and emerges in the Lake District in late May and early June. The eggs do not hatch till August. Dr Harker recorded a longer emergence and earlier hatching. She also recorded a lower water temperature. A correlation was postulated. Further studies of the life history of this species in warmer and in colder water would be worth making. Ultimately the exact way in which temperature influences life history can be discovered only by experiment, but the more extensive the field observations the more precisely will it be known what experiments should be carried out.

There are two other aspects of the life history of *Rhithrogena semicolorata* that deserve mention. Adults are on the wing for six, perhaps eight, weeks and egg-laying must, therefore, be restricted to this period, yet the smallest nymphs occur throughout a period of nearly six months. There are two possible explanations: either some eggs take much longer to incubate than others, or the incubation period varies little but some nymphs do not start to grow until several months have elapsed. That the first explanation is valid for *Baetis* sp. has been demonstrated by the German scientist, Professor J. Illies, and it has been shown that the second possibility is the reason for the persistence of tiny nymphs in other groups. Larger specimens may inhibit the growth of small ones either by means of a secretion or by occupying the relatively few vantage points from which sufficient food for growth can be obtained. This, however, remains a field in which a great deal of work remains to be done. The other noteworthy point about the life history of *R. semicolorata* is the waiting period which large nymphs enter. Those that are first to hatch grow at a rate which appears to be steady and independent of temperature and they may reach full size by Christmas. Growth then stops. Some tiny nymphs are still present at this time and their growth starts soon and proceeds at a rate similar to that of nymphs developing at the end of the previous year. Some may not reach full size till normal emergence time is reached and then they and those that reached full size much earlier emerge within a short time of each other.

Few insects fly in winter, because, it is supposed, the air temperature may be too low for a cold-blooded animal to be active. Whatever the explanation, many aquatic insects have some means of avoiding emergence during the winter. One of them is known as diapause and a good example is provided by the dragon-fly *Lestes sponsa* Hansemann. The eggs are laid in summer, and the embryo starts to develop because the temperature is above the threshold at which this process ceases. At a certain stage, however, development stops even though the temperature is above the threshold and it continues only after the egg has been subjected to low temperature. This ensures that the eggs of *Lestes* cannot hatch until the following spring. The rate at which the days are growing longer or shorter determines whether certain other species continue development or enter a resting phase. This is the kind of discovery that intrigues the scientific mind. Sometimes the enthusiastic search for a complicated solution, and diapause can be much more complicated than the bare outline given above might suggest, leads to the overlooking of more simple explanations. Sometimes growth stops because food is in short supply.

Rhithrogena was referred to as a winter species. It is convenient to group together all species with a similar life history; science would founder in a slough of detail if such generalizations were not made. There is, however, a danger that must not be lost sight of. A nice scheme of classification is sometimes mistaken for a scheme of explanation, and the possibility that one goal may be obtained by different routes is overlooked. In contrast to the winter are the summer species, of which the most striking example is *Ephemerella ignita* Poda, whose subimago is known to anglers as the Blue-Winged Olive. In several small stony streams that have been investigated nymphs (fig. 1) are first found in late May or early June and by September only a few stragglers remain. Development is completed in a month or so and the rest of the year is spent as an egg. This life history, however, is far from universal; in south-country chalk rivers nymphs are to be found in every month and even adults have been recorded the year round. Whether this is produced by more than one generation a year, or by a single generation developing at different times only careful observation in a number of places will show. Then the question of an explanation will be posed.

Some species in the genus *Baetis* belong to this group, though possibly they achieve more than one generation in a summer. Two of the commonest, however, *B. rhodani* Pictet and *B. pumilus* have two generations, one that grows slowly throughout the winter and one that grows quickly during the summer. The elucidation of this life history is complicated by the delayed hatching of the eggs, already mentioned, and might have defied analysis but for the fact that the adults appearing during the first part of the summer are upwards of twice the size of

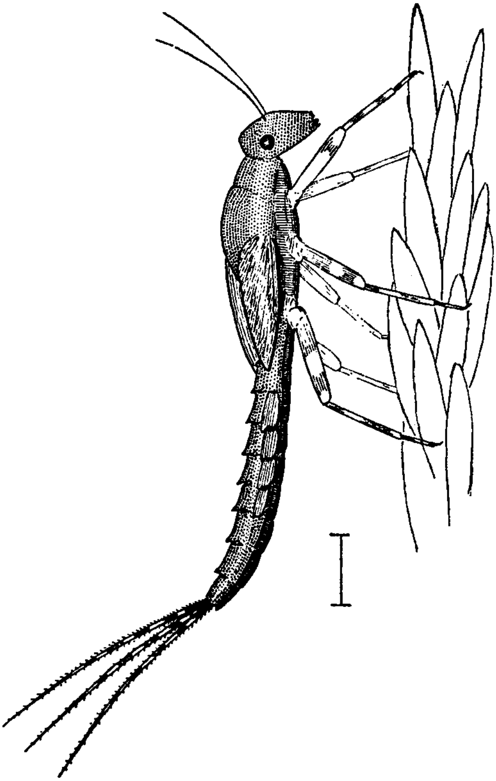


Fig 1 Ephemerella ignita.

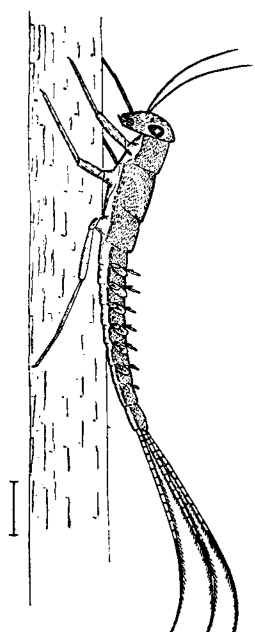


Fig. 2 Cloeon dipterum.

those appearing in the second part. The assumption was made that the former are derived from the slow-growing winter generation and the latter from the quick-growing summer one.

Cloeon dipterum Linn. (fig. 2) may have a superficially similar life history but there is not much growth in winter and the emergence periods are shorter. Dr D. S. Brown has found that there may be more than one summer generation, the number rising with increasing temperature, and in the north there is often only one generation in a year.

Whether *Ephemera* takes more than one year to complete development has been disputed. There seems no reason why both sides should not be right. More observations will be interesting.

The study of life histories involves frequent and regular collecting from the same place, and measurement of the specimens caught. It will not appeal to those for whom natural history is a good reason for exploring new countryside. For these the study of ecology and distribution will be more attractive. One regrettable fact must, however, be stressed; the most agreeable time for exploring the countryside is the worst time for collecting Ephemeroptera. Some of the commonest species are winter growers, and they are present only as eggs or tiny nymphs during the usual holiday months. The writer receives a few letters each year from parties of naturalists, generally students, who are making a long-vacation expedition to some out-of-the-way place and who hope that he will be interested in the resulting collection of mayflies. The reply has to be that such collections will be too incomplete to be of interest; if the expedition could return in February, March or April, it would be another matter.

Ecology

In productive ponds of the type common in the south and east of England, the only species often encountered is *Cloeon dipterum*. The other species in the genus, *C. simile* Eaton, also dwells among weeds but in deeper water, which means that it is absent from the smaller ponds, but may, on the other hand, inhabit much larger bodies of water than *C. dipterum*. In the north and west, where ponds are generally in an unproductive peaty basin, the species are *Leptophlebia marginata* Linn. and *L. vespertina* Linn. Nobody has ever sought out a series of ponds extending from one extreme with *Leptophlebia* only to the other with *Cloeon* only, with a view to finding something with which the change might be correlated. At present it is possible to do no more than speculate. *Leptophlebia* grows in winter, *Cloeon* in summer, but the significant point may well be that the eggs of *Cloeon* hatch very soon after they are laid, and those of *Leptophlebia* do not. Some of the productive ponds where *Cloeon* is found have very little oxygen, at least near the bottom, at times during the summer, and it is possible that these conditions are lethal to the eggs of *Leptophlebia*, immobile throughout the critical time, but not to *Cloeon* which passes so rapidly from this vulnerable stage to a mobile one in which unfavourable local conditions can be avoided. This could be the reason why *Leptophlebia* is barred from one end of the range but not why *Cloeon* is barred from the other. It is often stated that peaty water contains humic acids which are toxic to many organisms, though this remains to be established definitely. If it be assumed to be true, there remains the question of whether the nymphs of *Cloeon* are affected directly, or indirectly through their food.

Food as a factor affecting distribution is not easy to study. All British Ephemeroptera, as far as is known, feed either on vegetable matter or on the detritus that accumulates in any piece of fresh water. It is simple to ascertain what they eat, far less simple to discover from what they derive their nourishment. Dr H. B. N. Hynes believes that the chief source of food for animals in a stream is the dead leaves blown in from the land, but, he has suggested, the animals cannot digest dead leaves, and utilize only the bacteria and fungi that are in the process of breaking down the vegetable tissues. The problem, therefore, passes into the field of microbiology. Dr Hynes and his team, now operating in Canada, are working on this problem at the present time.

The reader will have noticed that in both genera mentioned there are two species. According to what is inappropriately known in Britain as Gause's hypothesis, two species with the same way of life cannot live together. The two species of *Cloeon,* as already noted, are not identical, because they occupy different habitats. Moreover, they are separated in time, nymphs of one species being small when those of the other are large. For example in a moorland fishpond studied by the writer, most nymphs of *Cloeon simile* are 5–6mm long during the winter and the adults are on the wing in April and May. The next generation appears in September. Those of *Cloeon dipterum* are 3–4mm long during the winter and emergence takes place in June and July. On the other hand the habitats of both species of *Leptophlebia* appear to be identical. Here too, however, there is temporal separation. *L. marginata* is bigger than *L. vespertina,* and emerges about a month earlier. It probably hatches earlier, also, and is, therefore, always larger. If it be assumed that nymphs of different size have a different diet, *Leptophlebia* also proves to be no exception to Gause's hypothesis.

More species of Ephemeroptera are found in a lake than in a pond. Anyone turning over stones near the edge of, for example, a lake in the Lake District will soon come across *Ecdyonurus dispar* Curtis and *Heptagenia lateralis* Curtis. Both belong to a family whose nymphs are highly modified; the body, particularly the head and the femora, is flat and the legs project sideways. The whole is adapted to life on a flat hard surface and the animals can progress with considerable speed while remaining closely pressed to the rock or stone. Stones and rock are found only where current or waves have enough force to remove finer particles and it is not surprising, therefore, to find that the inhabitants of this substratum have evolved a form which prevents their being removed too. It is probably difficult also for a predator to pluck them off. Another species of the stony shore is *Centroptilum luteolum* Mueller. It is not flattened and can swim rapidly by means of the short tails, which are closely beset with hairs down the sides. It is much smaller than the ecdyonurids, and doubtless takes refuge beneath the stones when waves are beating on the shore. It is one of the most easily distinguished nymphs. Its tails are marked with narrow black rings but no broad bands, as are those of *Cloeon*. Its gills are simple plates ending in a point. It matches a sandy bottom and a characteristic pattern is discernible under a microscope.

Large calcareous lakes are rare in England, Scotland and Wales, but common in Ireland. On a stony bottom in one of these, two common species are *Heptagenia sulphurea* Mueller and *H. fuscogrisea* Retzius. The latter is known to the writer only from one locality in England, the River Kennet near Reading, where it is found on the stems of such plants as Iris and Burr-reed. There seems no reason why a nymph adapted to live on a flat surface should not cling to plants of this type as well as to stones, but this is the only place where I have ever seen one of them doing this. It is perhaps a matter of behaviour, a hypothesis which could be, but has not been, tested by a simple experiment.

Leptophlebia also inhabits the stony shore but, in the Lake District lakes, it is hardly ever taken except near the time of emergence. A visit to Windermere by the Newcastle University Sub-Aqua Club provided evidence that this is because at other times of year it is at a depth beyond the reach of a collector who, working from the shore, cannot sample the bottom in water deeper than the length of his arm.

Where there is less water movement, either in deeper water or in a bay, sand and finer particles floor the lake. Here may be found nymphs adapted for burrowing. *Ephemera danica* Mueller is one of the largest species and, with its short broad legs and feathery gills arched over the back, one of the most distinctive. The legs recall those of another burrowing animal, the mole. The feathery gills form a tunnel supporting the substratum above it and keeping it away from the back of the animal along which their beating maintains a flow of water. *E. danica* inhabits sands, *E. vulgata* Linn. mud (fig. 3). The third species, *E. lineata* Eaton, is rare.

A more deeply indented bay will be colonized by reeds, in which *Leptophlebia* is abundant. Also to be found is *Siphlonurus lacustris* Eaton, a swimming nymph like *Cloeon* and *Centroptilum,* but bigger when full grown. This species occurs also in streams, generally high up in the Lake District, where these run sluggishly over a flat area of land. In Brown Cove, to the north west of Helvellyn, there is a small tarn, not much over a foot deep, dammed to supply water to a mine. The bottom is sandy. *Siphlonurus* is abundant here and when the nymphs flee at the approach of an observer, they appear at first sight like a swarm of shrimps. *Siphlonurus* has an inexplicably sporadic distribution. *S. lacustris* is generally, but not always found in places of the type mentioned and occasionally in slow rivers. The records

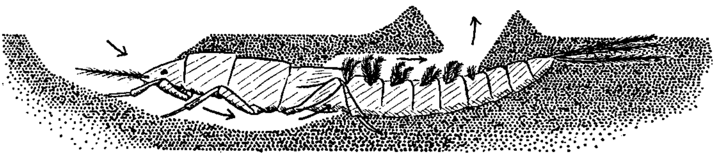


Fig. 3 Nymph of *Ephemera vulgata* in its burrow.

of *S. armatus* are from more calcareous waters, but it is difficult to make out a significant difference between the few places where it does occur and the many where it does not. *S. linneanus* is widespread in northern Europe but the number of records is small in all countries except Ireland, where it may be encountered frequently.

The fauna of small stony streams is now comparatively well known. Streams on Dartmoor, in Shropshire, in the Lake District and in the Pennines have been studied and there has been much work done in Wales and Scotland also. The common species are:—

Baetis rhodani Pictet	*E. venosus* Fab.
B. pumilus	*Heptagenia lateralis* Curtis
Rhithrogena semicolorata	*Ephemerella ignita* Poda
Ecdyonurus torrentis Kimmins	

Two of these genera, both flat stone-clingers, have been encountered already on the stony lake shore, but it will be noticed that the species in the genus *Ecdyonurus* there was not the same. Also belonging to this family is *Rhithrogena*. Neither species in this genus occurs outside running water, a distribution of which the explanation falls within the sphere of physiology rather than field observation. The gills of *Rhithrogena* are modified to form a sucker for adhesion to the substratum, whereas those of *Ecdyonurus* and *Heptagenia* are free to beat and maintain a current of water over the body. A Swiss scientist, Dr. H. Ambühl, imprisoned nymphs in an apparatus through which water could be passed at a known speed, and he measured the uptake of oxygen at different current speeds. *Rhithrogena* used more oxygen the faster the current. The other two did not. *Rhithrogena* evidently depends on a continuous flow to bring sufficient oxygen for active life, but *Ecdyonurus* and *Heptagenia* in still water can create a sufficient current for this purpose by beating their gills.

Nymphs of *Baetis* are swimming forms but their gills are smaller than those of genera already mentioned and almost immovable, which is likely to be the reason why this genus also is confined to running water. *Ephemerella* is characterized by the position of the gills, which lie on the back and do not project from the sides as do those of most genera. It cannot swim actively and reaches its greatest abundance in the vegetation of productive rivers. Nevertheless it is often fairly

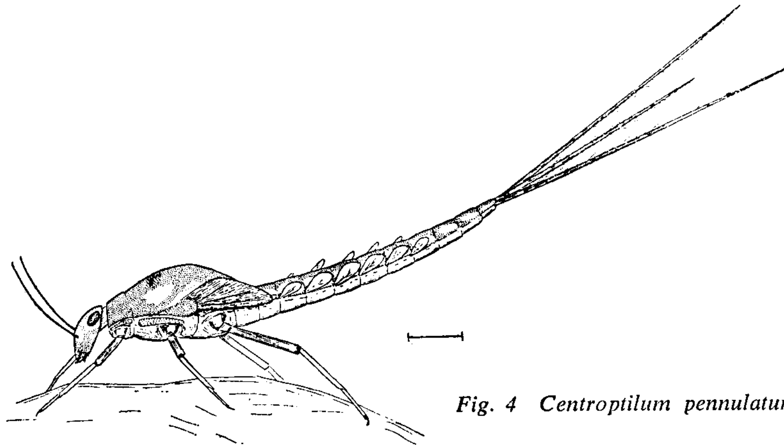


Fig. 4 Centroptilum pennulatum.

numerous in stony streams even in reaches where very few of the stones are covered with moss.

Once a definite association of species of this kind has been discovered, the naturalist will seek varying environmental conditions to see whether corresponding variations in the animal community can be

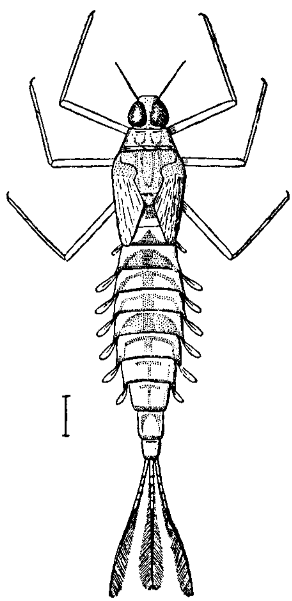


Fig. 5 Baetis rhodani.

observed. The student of stream faunas will move upstream and downstream, and pass to waters with slower flow. With increasing altitudes, *Ecdyonurus* tends to drop out, and stoneflies become more numerous relative to mayflies. At about 1,000 feet, *Baetis tenax* Eaton and *Ameletus inopinatus* join the community. It is tempting to suppose that species confined to high altitudes are intolerant of the higher temperatures lower down, but this temptation must be resisted. A competitor may keep a species out of a region in which, alone, it would flourish. A tentative correlation has been made between temperature and the distribution of *Heptagenia lateralis*. The writer and his colleagues found this species to be abundant in many small Lake District streams, but absent or scarce in others. In the hope that light might be thrown on this, maximum and minimum thermometers were concealed in a number of streams, by good fortune during a long fine summer. Most streams reached a maximum in late May and thereafter in every sunny spell until mid-September reached a level that rarely differed from it by more than a degree or two. The range of maxima was found to be surprisingly large – from 16 to 28°C. The highest temperature was in a stream that originated from a sheltered swamp and flowed slowly in a channel not shaded by trees. The coldest stream sprang from a thick deposit of soil in a valley facing north and flowed through a wooded gorge. *H. lateralis* was generally found where the maximum did not exceed 18°C and rarely in streams that were warmer. No experimental confirmation of these field observations has been made.

Small stony streams run together to form rivers which may retain the same general character if the slope is steep enough. There must, however, be certain differences; in the first place the water is more productive because it is receiving the debris and the drainage from a larger area; secondly everything is on a larger scale, which may mean that some small local feature, such as a sand-floored bay, reaches at a certain point downstream a size at which it can support a viable population of a species that dwells on such a substratum. Though little more than speculation of this kind can be offered as explanation, the fact that increasing size goes hand in hand with more species is well established. *Centroptilum pennulatum* Eaton, *Procloeon pseudorufulum* and *Baetis scambus* Eaton are probably associated with bays where flow is less, because they are found also in small streams whose flow is slow enough to permit sand and gravel to settle. Less easy to explain are changes within genera typical of swift conditions. *Ecdyonurus torrentis* is confined to small streams; *E. venosus* occurs in small streams and rivers; *E. dispar* Curtis has been recorded only from rivers, and the change to *E. insignis* Eaton may be associated with change to calcareous conditions. In other genera the stream species persists and is joined by a river species: *Ephemerella notata* and *Rhithrogena haarupi* Petersen. *Heptagenia lateralis* is replaced by *H. sulphurea*. Two extremely rare species known only from large rivers are *Ephemera lineata* and *Potamanthus luteus*.

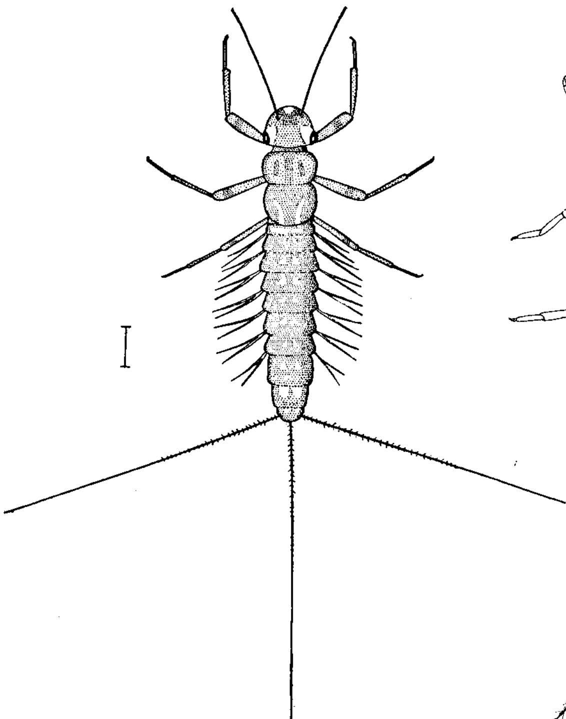


Fig. 6 Paraleptophlebia submarginata.

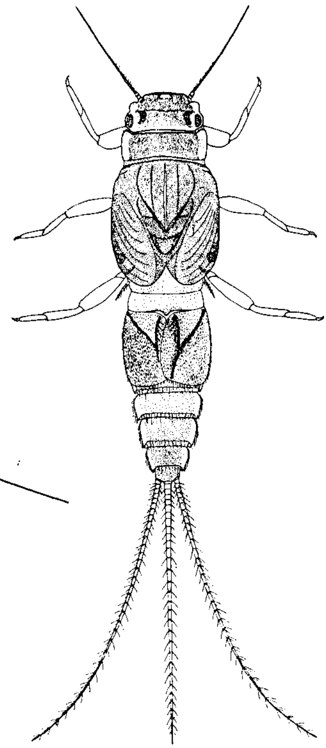


Fig. 7 Caenis rivulorum.

The starting-point of this story is well established, but the rest is based on a very limited number of records and requires confirmation. It is no accident that small stony streams have been studied and stony rivers ignored; sampling is so much easier. This is a pity because there are likely to be small stony streams in much the same condition as to-day for many years to come, whereas all kinds of covetous eyes are cast on rivers. To the water engineer it is so much good water rushing to waste at a time when finding sufficient to satisfy the ever-growing needs of an industrial society is proving harder and harder. To the electrical engineer it is an untapped source of power. To the drainage engineer its alternating deeps and shallows, its curves, its backwaters, its shingle spits, in short those features which the angler, the naturalist and the lover of the natural scene prize, are encumbrances whose removal would achieve the desirable effect of speeding the passage of flood water to the sea. The agriculturalist as well as the industrialist may see a precious commodity in the passing water, and for long all sorts and conditions of men have esteemed running water for the way it takes out of sight, and therefore out of mind, anything they happen not to want. All this has been going on for a long time, but we cannot do more than guess at its effect on the fauna because so many old records do not mention a precise place nor describe exact conditions. If a determined effort could be made today to find out what inhabits our big rivers and to record the observations carefully, we, or our successors, will be able to follow more accurately the inexorable impoverishment of our fauna as the urbanization of the country marches on.

If the flow of a small stony stream falls to a rate at which sand settles, tufts of such plants as Milfoil occur. In them the nymphs of *Baetis niger* are generally found. Other species typical of such stretches are the two species of *Centroptilum* and *Procloeon pseudorufulum*. *Paraleptophlebia submarginata* (fig. 6) is another species that occurs when flow is not too fast; possibly it is joined or replaced by *P. cincta* in rivers, but the number of records is too small to warrant a definite assertion.

When a river becomes slow enough to allow rooted plants to colonize the bottom, great number of *Ephemerella* occur, and *Baetis vernus*, *B. atrebatinus* join *B. rhodani*, *B. pumilus* and *B. niger*. With increasing sluggishness the mayfly fauna may consist largely of *Cloeon*, the pond species.

The genus *Caenis* has received little notice so far. Its nymphs are small and burrow in the substratum. The first pair of gills is reduced to a thread-like appendage on each side. The second pair is large and covers the rest, which are feather-like, as are those of the other burrower, *Ephemera*. *C. rivulorum* (fig. 7) is found in the slower parts of small stony streams. *C. moesta* was added to the British list during the war by Mr D. E. Kimmins, who found it inhabiting gravelly parts of Windermere. *C. horaria* occurs in muddier places in lakes and ponds. *C. macrura* appears to be confined to large rivers. *C. robusta*, the largest, was first recorded in Britain by Dr H. B. N. Hynes and the writer during the course of a summer meeting of the Ecological Society in The Norfolk Broads. After the nymph had been described, it was recorded from several other places, all productive localities with a bottom of rich black mud. Possibly the adult had escaped observation because it emerges early in the morning and then mates, lays eggs and dies before most naturalists are afoot.

Predation

It may be stressed again that much of this account is based on scanty data. Much more careful collecting is required before the habitat of each common species, and the distribution of those species that are rare, or are thought to be rare, can be defined. Nonetheless it seems clear that each species is confined within a limited range of conditions. How this comes about is a fascinating problem. A few of the factors have been mentioned. The work of Ambühl on oxygen is one of the few comprehensive studies of a single factor. The influence of the rest is largely speculation based on field observation unconfirmed by experiment; temperature is a good example of this. Clear examples have been described in other groups of the limitation of the range of one species by another, generally a close relative, and further work will probably disclose it in the Ephemeroptera also. Behaviour has been mentioned, so has food though only in the most nebulous way. Another factor, until recently ignored by professional scientists obsessed with their measurements of physical and chemical factors, but now coming to the fore thanks to the work of Dr T. B. Reynoldson and his school on flatworms, is predation. It is probably responsible for the distribution of Ephemeroptera that has recently been described in Windermere. Most of the shallow water in this lake lies over a stony substratum. On this, in the middle of the north basin, Plecoptera, and Ephemeroptera of the species mentioned above, are numerous, and few animals that are not insects occur. The collector travelling north or south finds a steady diminution and eventual disappearance of stoneflies and mayflies and a corresponding increase in the number of flatworms and various crustaceans. The abundance of these appears to be associated with the enrichment of the lake by sewage effluent. The nature of the relationship is unknown; probably small worms, and other animals on which the large ones mentioned feed, are much more abundant in the richer water. Once they have become numerous in the regions where the food supply is good, these animals, it has been suggested, exterminate the mayflies and stoneflies. Possibly they eat most of their eggs, which are laid in a haphazard way. It is unlikely that there is anything toxic in the sewage effluent for it is well purified and greatly diluted.

The distribution of the young of some groups is brought about by the habits of the egg-laying female, but this is unlikely to be true of most Ephemeroptera because the eggs are laid in such a haphazard way. Many seem to be unable to distinguish between water and any other shiny surface such as a wet road or even a polished car. It seems scarcely likely that they select a particular kind of water. However, some species of *Baetis* crawl down into the water and glue their eggs to some solid object. These certainly appear to select a site for their eggs. The whole subject of egg-laying is worth much more careful study. So also are the dancing swarms of the males. A good account of these is given by J. R. Harris (1952) in 'An Angler's Entomology' (London: Collins. New Naturalist No. 23), almost the only recent book in English to devote an appreciable amount of space to the Ephemeroptera. The significance of these dances is unknown. They are common among insects. Certain species of mosquito will assemble only in certain conditions, and no mating takes place unless the dance is performed. In contrast a male and female of some other species, which may be closely related, will mate at once within the confines of a test-tube. Whether dancing is always an essential preliminary to mayfly copulation has not been investigated. Many anglers are convinced that a poor season for *Ephemera* is due to the prevalence of wet and windy conditions during the period when the eggs were laid, but this is largely an armchair surmise unsupported by systematic observation. Several questions immediately pose themselves. How many days can the adults survive if they happen to emerge during unfavourable weather? What is the relation between number of eggs laid and number of adults subsequently emerging? It may be slight, for a female lays several thousand eggs, and therefore a small number could repopulate a large area. At what stage does the main mortality take place and what is the chief cause? Probably it is extremely high in the early stages, and many nymphs die because the eggs have fallen in unsuitable places. How far is overcrowding alleviated by migration of nymphs to less thickly populated areas? This is an important question, and a difficult one particularly in running water, which must be answered before reliable figures for mortality at successive stages of one generation can be obtained. The writer once spent a night camping beside Lough Sheelin in pursuit of the nymphs of *Heptagenia fuscogrisea.* The evening was sunny but there was a cold and strong wind. On the exposed side of a wooded peninsula not a mayfly was to be seen. Under the lee of the trees the air was thick with them. What is the result of such circumstances if weather conditions remain unchanged throughout the flight period, which, in view of its brevity, must sometimes happen?

Recording

The compilation of lists has long been an activity favoured by natural history societies, and sometimes the purpose of it has been vague. A bare list which fails to distinguish the species that abounds everywhere from the one that would not have been recorded but for the determination of some naturalist to take it within the prescribed bounds is of limited value. A list with some indication of relative abundance is better. A list with detailed descriptions of where each species was found is better still. The identification must, of course, be reliable. One collector, who, ranging far afield, misnames his captures will make nonsense of any distribution map which includes his records. To obviate this difficulty certain societies, for example the Botanical and the Conchological Societies, recognize no new record that has not been confirmed by an appointed recorder, even though the person making the capture may be the authority. It is not easy to find for a less popular group somebody who is competent to act as recorder, and who is willing to accept the view that knowledge will accrue more rapidly if he is prepared to take time off from his own work to check the collections of all and sundry. It is to be hoped that the activities of the Nature Conservancy based on Monk's Wood will put the whole question of recording on a more satisfactory basis.

Much recording has been founded on the idea that light might be thrown on the origin of the species taken. The popularity of explaining present distribution in terms of recolonization after the Ice Age fluctuates widely. Sometimes those who enjoy speculation unhindered by too many facts are widely followed. At other times they are discredited by the hard-headed pragmatic types who point out that much has happened in the last 2,000 years, let alone the 20,000 or so since the ice retreated. Britain has been largely deforested during that period and then drastically modified by industry, agriculture and drainage. Moreover, the distribution of many species is imperfectly known and the identification of some earlier records open to doubt.

In the past the distribution of species has generally been recorded by counties, or vice counties though political boundaries have little to recommend them. More valuable are records of what occurs in some uniform area. The Natural History of Wicken Fen (ed. J. Stanley Gardiner 1932. Cambridge: Bowes & Bowes) may be taken as an illustration of this point and of several others. The village of Wicken lies some twelve miles from Cambridge and near it there is an area of fenland that escaped the drainage operations of the seventeenth and nineteenth centuries. It was one of the earliest properties to be acquired by the National Trust. After the first World War the fauna and flora were studied extensively. A future Professor of Botany laid the foundation of his reputation there and several of his students made it the subject of their Ph.D. theses. At that time, however, field work had ceased to attract professional zoologists and many of the reports on the fauna were written by amateurs, among whom one must place the undergraduates. One can sense a certain frustration in many parts of the book. The chief zoological attraction at that period was the Swallowtail Butterfly, abundant in but almost confined to Wicken Fen. Students of other groups clearly expected to find something comparable and were disappointed that their lists contained only common and widespread species. No new vistas were opened up; few contributions to general theory were possible. However, in the years that followed the writer has often noted what they took and where they took it and what they did not collect, and found it valuable when making comparison with some other relatively uniform area. The pioneer can do little more than record but his records may prove an essential platform from which advances in the future can be launched.

T. T. Macan.

(Reprinted from The Bulletin of the Amateur Entomologists' Society No. 283, May 1969)

Printed by Ellis & Phillips Ltd., East Side Press, Rye Street, Bishop's Stortford and published by the Amateur Entomologists' Society, 335 Hounslow Road, Hanworth, Feltham, Middlesex. 1969

LEAFLETS

Numbers not included are out-of-print or replaced by others.

3. Rearing Silkworms. (The Mulberry Silkmoth). 4pp., 2 figs.
4. Collecting Sawflies. 12pp., (incl. 2pl.), 26 figs.
5. Collecting Flies (Diptera). 8pp., 1 fig., 8pl.
6. Collecting Beetles associated with Stored Food Products. 9pp., 6 figs., 3pl.
7. Some Improved Devices for Rearing Hymenoptera. 7pp., 3 figs.
9. Collecting Caddises. 5pp., 4pl.
10. Experiments with Bees. 12pp., 3 figs.
13. Collecting Microlepidoptera. 4pp., 1 fig.
14. Setting Microlepidoptera. 4pp., 5 figs.
15. Collecting Het-Bugs (Hemiptera-Heteroptera). 12pp., (incl. 2pl.), 5 figs.
18. Collecting Clearwings. 12pp., (incl. 2pl.), 4 figs.
20. Preserving Caterpillars. 14pp. (incl. 6pl.), 9 figs.
21. Collecting Psocoptera. 4pp., 10 figs.
22. Collecting Lacewings. 9pp., 8 figs., 5pl.
24. Entomology of Bird Pellets. 8pp., 4pl., 1 map.
25. Collecting Bumble Bees. 20pp., 83 figs.
26. Collecting Collembola. 6pp., 4 figs.
27. A Study of the Insects Living on the Wayfaring Tree. 20pp., 4 figs., 1 diagram.
28. Killing, Setting and Storing Butterflies and Moths. 13pp., 10 figs.
29. Collecting Fleas
30. Rearing Stick Insects
31. The Study of Mayflies
32. The Study of Leafhoppers

PAMPHLETS

4. Label List of British Macrolepidoptera. 32pp.
5. Check List of British Macrolepidoptera. 32pp.
6. Label List of British Butterflies. 2pp.
7. Directory of Natural History Societies. 155pp. published 1948, of considerable historical importance.

7a. First Supplement to Directory. 44pp. published 1949.

10. Glossary for the Young Lepidopterist. 6pp., 2 figs.
11. Label list of the Butterflies of North, Western and Southern Europe. Set in 10pt Times type.

Other Leaflets are in preparation

These publications are obtainable from AES Publications Agent, 137 Gleneldon Road, Streatham, London S.W.16, England. Do **not** send remittance with your order as an invoice will be sent with the publications and will include the correct postal charge.