STUDIES ON THE FAUNA OF A SHROPSHIRE HILL STREAM

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With a prologue and a general discussion
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A prologue reviews the main factors affecting invertebrate animals living in small stony streams. Four contrasting stations on the stream in Ashes Hollow (on the Long Mynd, Shropshire, Great Britain) are described. Methods of collecting aquatic invertebrates and emerging adults are dealt with. The results of the collections are presented and discussed. It is concluded that despite greater diurnal temperature fluctuations and a generally higher nutrient status than is normal in streams of this type, the only unusual features in the fauna were the abundance of *Dinocras cephalotes* by contrast with other large plecopteran carnivores, and the apparent restriction of *Polycelis felina* to the spring.

PROLOGUE: SOME GENERAL NOTES ON SMALL STONY STREAMS

THE study of plant ecology started when plants had been named and their identification facilitated by the publication of floras. Communities were then distinguished and described, and now interest centres on physiological experiments designed to explain the field observations. The study of animal communities has proceeded in a less orderly way, and few communities have been delimited and described. The motility of animals is one reason for this but the main one has been the large number of species and the difficulty of identifying them. This applies particularly to fresh water, in which the main components of many of the communities are the immature stages of insects, and these were ignored in the heyday of systematics. Only within the last two decades have keys to all the species of Plecoptera and Ephemeroptera become available, and the immature stages of some important groups, notably the Trichoptera and Diptera, are still unknown. The worker who wishes to put reliable names to species in these groups must either rear the larvae to the adult stage or trap the adults as they emerge.

It is important that more should be known about animal communities, for it is difficult to obtain reliable figures for production, a popular line of study at the moment, without a knowledge of the life histories of the various species, their numbers at different times, and their position in the food web. Moreover, the environment is changing at the hands of man. It has been for centuries, but the process has recently accelerated with the discovery of innumerable new pesticides. This process cannot be checked or ameliorated unless it can be measured, and it can only be measured from the base line which general surveys provide.

Studies of small stony streams in moorland areas have been popular. Yet another may be justified on two counts. Only when a number have been surveyed will it be possible to discern whether biotopes of this kind are occupied by a characteristic community, or by a varying assemblage of species brought together by chance invasion. If there is a characteristic community, as there appears to be, each survey will reveal differences between parts of one stream and between different streams. It may prove possible to correlate these differences with differences in the environment and formulate explanations that can be tested experimentally.

At this point, where the discussion becomes less general, the kind of place under discussion must be described more fully. The word "stony" indicates that the current is swift enough to remove sand and finer particles, but it is not entirely accurate, as in places the substratum may be solid rock. The word "small" is less definite and for present purposes it is taken to be a width less than about 2 metres. Streams gradually merge into rivers and any distinction between the two is a matter of convenience and of temporary convenience at that. The nature of the substratum can vary considerably, and the most important difference is probably whether it is stable or unstable. An unstable bottom is composed of stones which, rounded by the action of ice or water, tend to shift when current speed increases. As a result there is no more than a covering of algae. A stable bottom consists of larger more angular stones, or rock, and it withstands all but exceptional floods and presents an upper face sufficiently long for colonization, often dense, by bryophytes. The water is well oxygenated. Few observations have been made since those of Hubault but it is a fair assumption that a thin layer of water flowing over an uneven bottom is rarely deficient in oxygen. The concentration of other substances may vary widely. Generalizations about temperature have been made but have been shown to be invalid. Water emerging from deep soil is likely to be cold, but a stream that originates in a shallow basin of peat, for example, may be warm. A stream warms rapidly in the sun and may cool rapidly in shade such as may be provided by a wood. Hynes (1961) has suggested that the basis of the food chain is detritus most of which is washed in from the surrounding land. Whether the herbivores can digest vegetable fragments, or whether they derive their nourishment from the bacteria or fungi which are breaking them down, is a line which he has under investigation at the moment. If detritus is the main source of food streams will, in general, become progressively richer with increasing distance from the source.

It is at present possible to relate the occurrence of some species and the conditions found in stony streams, and the purpose of the next few paragraphs is to review this subject briefly.

An animal requires food, and shelter from its enemies and from unfavourable features of the environment. It may have peculiar requirements of, for example, temperature or oxygen. Success depends on a complicated balance of these various requirements and discussion of the factors one by one tends to lead to over-simplification. It would be preferable to take the species one by one, but this is not possible in the present state of knowledge as all the requirements of any one species have not yet been investigated.

Food

Jones (1950) and Hynes (1961) have made important studies of what is found within the guts of animals living in streams. As already noted this does not necessarily indicate what are the main sources of nourishment, nor have the difficult subjects of how much is available and how much is required yet been investigated. In streams leaving lakes the fauna consists largely of net-spinning Trichoptera and *Simulium*, feeding on the rich supply of plankton and detritus. Another example of how food supply can affect the composition of a community is provided by polluted streams.

Sewage enriches water with organic matter the decomposition of which may use up all the dissolved oxygen. If it does not, the fauna may consist largely of snails, leeches and *Asellus*, a community found in the zone where purification has started in rivers that have been grossly polluted. It is difficult to separate the effects of reduced oxygen and increased supply of nutrients. The first might be responsible for the disappearance of the species typical of the pure stretches, but could not be responsible for the appearance of a different community, unless the newcomers could not normally survive in the presence of the others. As it is argued in the next section that the reverse is true, the conclusion is that the existence of a new community depends on the rich supply of food.

Predation

On the stony shores of Windermere, Ephemeroptera and Plecoptera predominate along a stretch that is remote from any source of sewage. Elsewhere these insect groups are often absent and flatworms and *Asellus* are the common animals. The main sources of sewage are two purification plants one of which is modern. The effect must, therefore, be a question of enrichment rather than pollution, though the links between the enriched water and the flatworms and *Asellus* remain unknown. It has been suggested that the *Ephemeroptera* and *Plecoptera* disappear because they are eaten; possibly their haphazardly laid eggs are particularly vulnerable to predation. The present writer also surveyed a stream which, towards the end of the work, was affected by the overloading of a septic tank. This was followed by a tremendous increase in the number of *Polycelis felina* and then by a reduction of the number of certain Ephemeroptera and Plecoptera. It is argued that the decrease was due to predation by the flatworms, because had it been due to a poison in the effluent it would have taken place sooner and more abruptly.

Competition

That flatworms occur in zones in a stream, and that one will extend its range should the species normally neighbouring it not occur, has been known for a long time. Hynes (1952) records that the stonefly *Diura bicaudata* is found near the sources of streams and on lake shores. In between *Perlodes microcephala* occurs. In the Isle of Man, however, the streams are inhabited by *Diura* throughout their length for *Perlodes* has apparently never reached the Isle. It is, of course, unusual to find an area where one species is absent because it has failed to reach it, and therefore there may be plenty of other examples of range restricted by competition which nobody has detected.

Shelter

How far the size, the shape or the texture of the surface of the stones influence the animals clinging to them remains to be investigated. The main contribution to the study of the importance of substratum is still that of Percival and Whitehead (1929). The largest number of species and individuals is found in moss, which no doubt provides cover and by trapping particles being washed downstream, also provides food. *Ephemerella* is neither flattened, as are the mayflies in the family Ecdyonuridae, nor streamlined and able to swim rapidly as are members of the genus *Baetis*. Anyone inspecting its form and structure might deduce that these insects would be common in the moss, but might be surprised to learn that they are also common on a bottom of unstable and therefore mainly bare stones. *Ancylus* is absent from this substratum and the obvious explanation is that it cannot move fast enough to avoid being crushed when the stones start to move. A discovery which more than one ecologist has made is that experiments do not always confirm that the obvious explanation is the correct one. The whole field of the relations between species and substratum needs re-examining not only experimentally but in the light of the advances in taxonomy made since Percival and Whitehead's day. For example, a simple experiment that has not been carried out, as far as I know, would be to test the reactions of *Ancylus fluviatilis*, the limpet, to various substrata. It is one of the most tolerant of the snails and is widely distributed, but it is found only where stones or rock offer a hard surface. There is no apparent reason why it should not sit on flat leaves as the other limpet, *Ancylus* (*Acroloxus*) *lacustris*, does. In the absence of experimental observation, it might be deduced that it moves off soft substrata and keeps moving until it comes to a hard one. Similarly the Ecdyonuridae are confined to stones and rocks, except for *Heptagenia fuscogrisea*, which clings to leaves.

Dinocras cephalotes, one of the largest stoneflies, is generally found in streams and rivers where the stones are stable and covered with moss, whereas the similar *Perla bipunctata* is generally found on an unstable bottom (Hynes, 1941). Here again there is no work which might explain how this comes about.

Current

Since current is an environmental factor whose intensity can be varied easily in an experimental trough, several workers have turned their attention to it. A simple experiment is to expose various species to an ever-increasing current and note at what speed they are washed away. Unfortunately this approach takes no account of the fact that nearly all the animals that dwell in fast streams occur under stones where the current is slight. Not only is it slight under stones but Ambühl (1959), in an ingenious and important contribution, has demonstrated that current speed falls off greatly in the neighbourhood of a surface and that even a large invertebrate on the top of a stone is exposed to a current much slower than that obtaining a centimetre or two higher up. He showed this by putting into a tank particles that reflected light and then photographing their movement. The negative was exposed for a comparatively long time but light was intermittent because the electric current was alternating. Each particle appeared as a series of lines in the photograph, and the length of each line indicated the speed at which the particle was travelling.

Current is, of course, an important ecological factor on account of its effect on the substratum. As soon as it is slow enough to allow sand or mud to settle, species adapted to live in such a substratum, and in the rooted plants which colonize it, largely replace the species found in the stony reaches. Within the stony zone, however, there are some species which are confined to the least rapid stretches. One of these, *Baetis scambus*, may possible be adapted in some way to life on a predominantly gravelly substratum. It is important to make the point here that an area of gravel in a small stream may not be large enough to support a population, whereas lower down the course, where everything is on a larger scale, comparable conditions may produce one that is. Scott (1958) concludes that certain species of Trichoptera occur in zones of slower current because that is where the detritus on which they feed falls to the bottom.

Animals whose distribution is clearly related to current velocity are the net-spinning Trichoptera, which have been studied in a series of instructive experiments by Edington (1965). They require a certain minimum speed to make the nets function and there is a maximum speed above which the nets are washed away.

Temperature

The upper reaches of many streams are always colder than any other part of the region in which they lie. Some species are found there and nowhere else, and of these a certain number occur because they cannot tolerate the higher temperature lower down. The best known example is *Crenobia* (*Planaria*) *alpina*. A great deal has been written about this flatworm, sometimes by workers unfamiliar with what others had done; this has led to a number of contradictory statements. However, it has been established by careful experimental work that it is a true cold-water species. It does not breed in water warmer than 12° C. and at about this temperature a change of behaviour tends to take it back into cooler conditions. It can tolerate 25° C. provided it is not exposed to it for too long. There is some disagreement about the highest temperature at which it can be kept alive indefinitely, which is not surprising since Dahm (1958) showed that there is a considerable amount of genetic differentiation among the various populations, all of which are isolated. There can, however, be no doubt that its observed distribution is due to the fact that its optimum temperature is low.

A series of maximum and minimum thermometers left in various streams during the fine summer of 1959 and read at intervals showed that the maximum temperature reached ranged between 16° C. and 28° C. *Heptagenia lateralis* was abundant in streams in which the maximum did not exceed 18° C. and generally absent in the rest, which appeared to explain a distribution that had been puzzling up till then. However, this interpretation of the field observations has not been confirmed by experiment.

Not every species found only in cold water is restricted to it by a low optimum temperature. *Diura bicaudata*, for example, might be thought to be a cold-water species by anybody who has not looked for it in lakes. As described already, it is competition that confines it to the higher reaches. It is likely that other species find a niche in springs and the upper part of streams because, in warmer water, which may suit their physiological requirements better, they cannot maintain a population in face of competition or predation.

Chemical factors

Determination of the concentration of the eight ions which constitute up to 99 per cent of the inorganic solutes in water is a favourite activity among ecologists, though frequently an unfruitful one. Whether an examination of the trace elements or of the composition of the organic matter in solution would be more profitable, it is impossible to say.

Gammarus pulex is one of the commonest species in some streams and is unknown in others. There is some evidence to connect its occurrence with the concentration of calcium, but whether the relationship is a straightforward physiological one or whether the calcium level has its influence through the food is unknown. The concentration below which an animal cannot take up an essential ion from the water is difficult to establish, because it varies according to the concentration of the other ions present at the same time. Pearsall showed long ago that calcium was an important agent in the decomposition of plant remains in a lake, and could affect the community considerably through this property, but whether a comparable process takes place in running water has not been investigated.

Thanks, again, to the work of Ambühl it is possible to make more definite statements about oxygen as an ecological factor. Ambühl imprisoned various animals in an apparatus in which he could alter the speed of the current flowing over them and, at the same time, measure the amount of oxygen they were using. He found that the consumption by *Rhithrogena* (Ephem.), *Rhyacophila* (Trichopt.) and *Baetis* (Ephem.) rose considerably as current speed increased up to 7 cm./sec. Thus, in still water, or in a slow current, these species are likely to be handicapped considerably by a shortage of oxygen. They are, in fact, found only in running water. In contrast the consumption of oxygen by *Ecdyonurus* (Ephem.), *Ephemerella* (Ephem.), *Anabolia* (Trichopt.) and *Hydropsyche* (Trichopt.), animals found in still as well as running water, did not rise or scarcely rose with increasing current speed. *Rhithrogena* and *Ecdyonurus* are similar in structure but *Rhithrogena*'s gills are modified to form a sucker by means of which the nymph can adhere to a flat surface. The gills of *Ecdyonurus* are not modified and can be waved in such a way as to cause a current of water to flow over the surface of the body. *Baetis* cannot move its gills effectively whereas *Ephemerella* can. *Hydropsyche* can create a current for itself by waving its abdomen and it can easily be observed to increase the rate of undulation as oxygen concentration falls.

Behaviour

Nymphs of *Agrion* (formerly known as *Calopteryx*) are confined to running water, though to streams slower than those under consideration. They cannot create a current and it has been shown that the oxygen requirements of the nymphs are such that they cannot live in most still waters in temperate latitudes. However, their distribution is brought about by the behaviour of the adults at the time of oviposition. Whether there was a selection of adults that chose streams to lay their eggs in because the nymphs required more oxygen than is available in still water, or whether, because they always find themselves in flowing water, the nymphs have lost the ability to take enough oxygen from standing water, is a question that will probably never be answered.

Adaptation of behaviour rather than adaptation of form has probably been more effective in enabling animals to colonize swift water. *Gammarus*, for example, has no clinging organs and cannot swim rapidly, two features which, possessed by other stream animals, must obviously facilitate life in a current. It has, however, a reaction to swim against a current and to get out of it under a stone as quickly as possible and this behaviour has, no doubt, enabled it to colonize streams as successfully as it does.

Morphological adaptations

The British organism that shows most morphological adaptations to life in a current is the larva of *Simulium*. It can produce silken threads, which it lays over the surface of stones, here and there sticking down a little mat which serves as a firm anchorage. At the end of the abdomen, and on the thoracic prolegs, it has areas beset with many hooks, by means of which it can attach itself to its web. It attaches first one end, then the other, progressing after the manner of a looper caterpillar. At the end of a journey it attaches itself to one of its anchorages by the abdominal pads and then hangs, often in the swiftest part of the current, straining floating particles of debris out of the water by means of highly modified mouthparts.

The flat spread-eagled form of the Ecdyonuridae is an adaptation to life on the surface of a stone rather than to life in running water, though the modification of the gills of *Rhithrogena* to serve as a sucker would probably not be of value in still water.

Plastron respiration is an adaptation to a good and continuous supply of oxygen and, as running water provides these conditions, animals that have developed it are frequent in streams and rivers. Most water beetles and water bugs take down a bubble of air on some part of the body. In water in which plenty of oxygen is dissolved, this functions for a limited period of time as a gill. If the tension in the water is high enough, oxygen will diffuse from it into the bubble to replace that which the body has used. Carbon dioxide diffuses rapidly from the general surface of the insect and is not important in the present context. The largest constituent of a bubble of air, nitrogen, generally disappears into solution in the water. If it could be prevented from doing so, a bubble of air would be a permanent gill, and this is what the plastron does. It is a pile of hairs set so close together and so water repellent that considerable force is needed to drive water into it. The hydrostatic pressure at the depths at which the possessors live is insufficient and therefore the air, once secreted, remains; there is constant diffusion of oxygen into it, to make good that used in respiration. This method of respiration is convenient in running water, first because there is a good supply of dissolved oxygen and secondly because the method whereby a bubble has to be renewed from the air presents a problem of counteracting the displacement downstream at each visit to the surface. It is found in *Aphelocheirus*, a water bug that lives in rivers larger than the one under discussion and in various beetles of the family Elmidae (or Helmidae, or Helminthidae). These small animals are often to be found crawling over the bottom in numbers, but they occur on stony lake substrata as well.

It may be stressed once more that the eventual distribution of a species is the result of a complex interaction of some of the factors just discussed and probably others too. The discussion has not attempted so far to separate two distinct though intertwined questions; first, why is a particular species found in rapid streams, and second, why is it confined to certain parts of those streams or at least why is it more abundant in some than in others.

Simulium is so highly modified in form to obtain its food by filtering the water that flow past it, that its absence from still waters is no matter for surprise. The net-spinning Trichoptera also depend on the current to bring them their food, though a few species occur in still water. The Ecdyonuridae and, to a lesser degree, *Ancylus*, are modified to live on the surface of flat stones. This type of substratum is common in streams but is found also in lakes where the shallow regions are exposed to waves and some of the animals are found here also. *Crenobia alpina* is confined to streams by its requirements of a low temperature. In Britain it is thought of as a stream species, but high up in the Alps it is much more widespread and abounds in the cold lakes. Other species are confined to streams because only in flowing water can they obtain sufficient oxygen. Further experimental work will, no doubt, make it possible to assign to one or other of these categories many species about which at present it is not possible to make a definite statement. Some species, however, are not modified structurally and not restricted by physiological requirements. They tend to be widespread species whose colonization of running water has been made possible by appropriate modifications of behaviour.

Details studies of behaviour will probably throw light on the second question also. Dr. Malcolm Elliott observes stream animals in a tank with a glass bottom and can see what is going on beneath the stones, which is where most of the animals are by day. Even so the exact nature of the place where a species tends to rest, and the extent to which it wanders or to which it falls a prey to some carnivore if it does not find a resting place, will not be easy to observe in the complex structure of a stony substratum. More precise information about the nature of the food, the extent to which two similar species exploit a particular source of food, and the extent to which the requirements of a good feeding place must be balanced against the requirements of safety from predation are all problems to which little attention has so far been devoted. In summary it may be said that work has reached the stage where the precise habitat of a few species has been defined but not the stage where the distribution can be explained.

Two further lines of work on streams merit notice. Elliott (1967), to quote a recent contribution to a line of investigation that has been pursued by several workers, finds that almost all stream animals are caught in nets through which stream water is flowing. All except the mites begin to come to the surface of stones soon after dusk and large numbers are dislodged and carried downstream. Probably most do not travel far before regaining the shelter of the bottom. The proportion of a species adrift increases as total numbers increase. At the present time this is one of the growing points in the study of stony streams.

Some small animals spend their lives in the interstices between the fine material beneath the stones flooring a stream, and may extend beyond the confines of the stream itself into the ground water on either side. The smallest nymphs of some Plecoptera and Ephemeroptera are found here too. Much more must be discovered about this community before accurate assessments of the productivity of a stream can be made. In particular it is important to know whether some of the larger animals can penetrate deep enough to exploit this source of food. It is possible that the tiny nymphs can remain very small for a long time, and do not grow unless they can find a place among the larger stones. They may be a source from which losses of larger specimens is constantly being made good. The present writer has observed a comparable phenomenon in a pond and has pointed out how large an error it can introduce into a calculation of production if the method of collecting does not sample all the tiny as well as the large specimens.

BACKGROUND TO THE AREA

The stony hill streams of the Long Mynd have been used as teaching ground for biology students at Preston Montford since 1958. Although accounts have been published on the invertebrate fauna of several other hill streams in the British Isles there has been none on that of the streams in this region.

The present paper was written with two objects in view: first, to act as a background guide for biology students at Preston Montford; and secondly, to compare the invertebrate fauna of the Long Mynd streams with that of similar streams in other parts of Britain.

The Long Mynd

Shropshire is a county of varied geology and landforms (Dineley, 1960). The Long Mynd (Fig. 1) lies near the centre of the hill country in South Shropshire. Within the county it is a conspicuous feature, but it is small by comparison with a range such as the Cambrian Mountains of Wales.

In plan the Long Mynd is a triangular upland area about 12 km. long from base (north) to apex (south), and 6 km. wide at the northern end. The rocks are Pre-

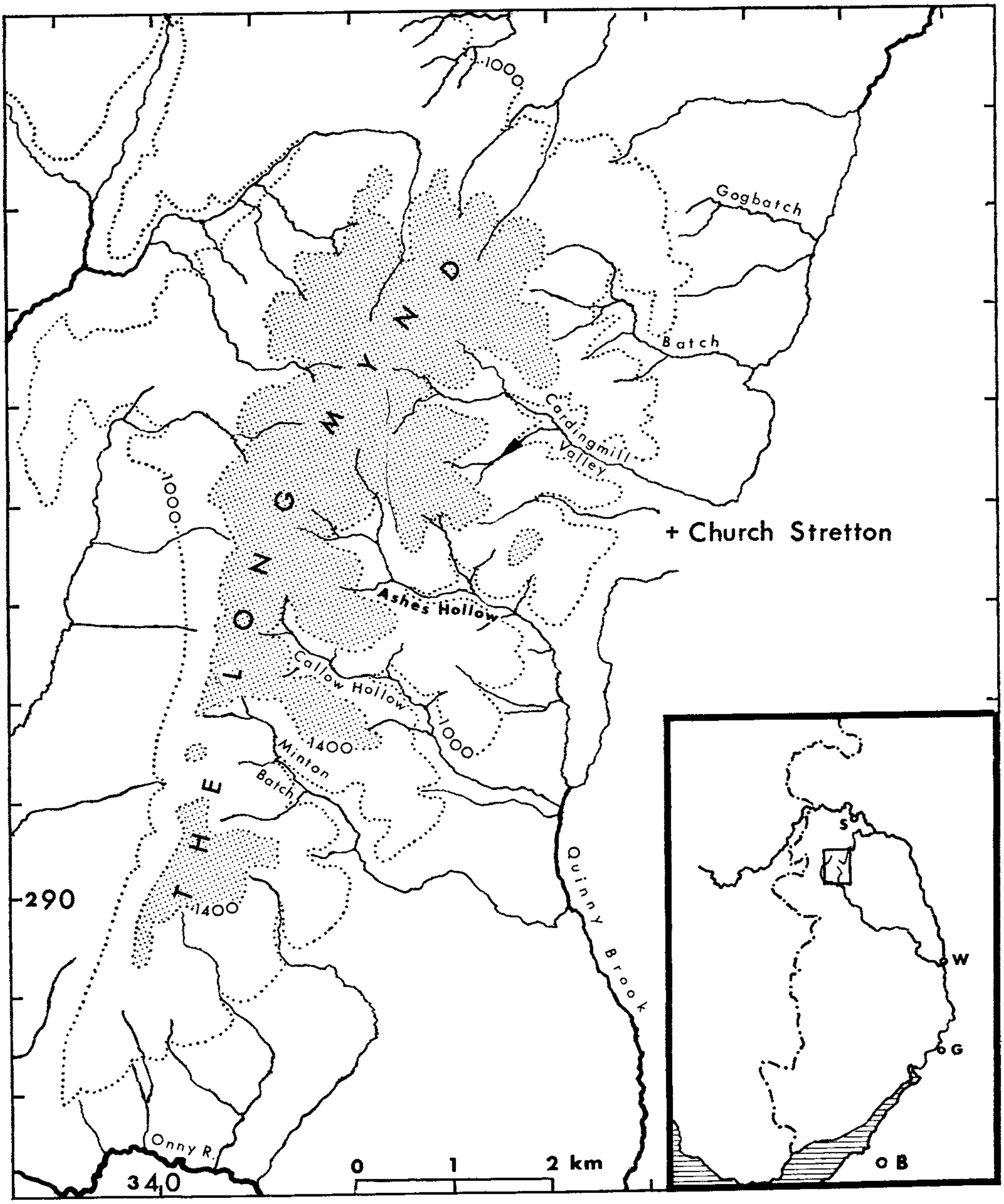

FIG. 1.
Map of the Long Mynd and its drainage pattern (inset shows location related to course of R. Severn. B: Bristol. G: Gloucester. S: Shrewsbury. W: Worcester.)

Cambrian in age, with shales, siltstones and sandstones predominating (Wright, 1968). They have been strongly folded (strike NNE-SSW) and indurated, with the result that they weather and erode relatively slowly.

The main part of the upland is an irregular plateau at approximately 450 m. (1,500 ft.) rising to a subdued summit at 518·3 m. (1,695 ft.) and flanked to the east by remnants of successively lower, almost level, surfaces. The watershed is near the western edge of the plateau and the main streams flow south-eastwards traversing this stepped relief and dissecting it deeply into steep-sided valleys which are known locally as "batches" or "hollows" (Plate I). The north and north-west flanks are less deeply dissected and the stream pattern is irregular. The southern half of the west flank is a steep fault-line scarp unbroken by large streams and terminated to the south by the gorge of the River Onny. All the drainage eventually reaches the River Severn by a variety of routes (Fig. 1, inset).

Ice-sheets more or less surrounded the Long Mynd during at least one of the Pleistocene glaciations, but the plateau and its valleys apparently remained free from ice. Although glacial drift is therefore absent, over large parts of the plateau the bedrock is deeply buried beneath a mantle of weathered rock material (head), and similar stony debris occupies the wider valley floors where it has been partly re-worked by the streams.

The soils of the Long Mynd vary considerably with slope and drainage (Burnham and Mackney, 1964, 1966), but are for the most part poor and stony with a top soil of acid raw humus. The rainfall is rather low (about 1,250 mm.): the general absence of a blanket of hill-peat not only leaves the waters free from the brown stain of humic colloids so characteristic of mountain streams in the north and west of Britain, but also means that there is no natural buffer against the variations in discharge between spate and drought.

The vegetation today is a patchwork of mountain heath and rough grassland: heather (*Calluna vulgaris*) and bilberry (*Vaccinium myrtillus*) predominate on the plateau and the north-facing valley sides, grasses (*Festuca ovina*, *Agrostis canina*, *A. tenuis*, *Nardus stricta*, etc.) occupy the shallower soils especially on ridges and south-facing slopes, while bracken (*Pteridium aquilinum*) forms extensive patches wherever the soils are deep and freely drained; widely scattered hawthorn bushes (*Crataegus monogyna*) grown on the valley sides, and there are small trees of various species along the banks of the streams themselves. There is no natural woodland on the open parts of the Long Mynd, and improved grassland is confined to a few fields round the small farms at the lower ends of the valleys.

Most of the hill is unenclosed common land, as it has been for many centuries. It is heavily grazed by hill sheep, and—especially since its recent acquisition by the National Trust—generally treated as a public open space; its management includes regular burning of certain areas as grouse moor. No doubt the high density of sheep and of tourists at certain times and places has an affect on the chemical characteristics of the water, but there is no evidence of serious pollution.

The streams and their valleys

The south-east-flowing streams in the Long Mynd are all fairly similar in their general pattern (Fig. 2). Some rise on the summit plateau between 400 m. and 450 m. Others rise on steep hillsides in the upper parts of the valleys. In either case the sources of the streams may be wet spring flushes supporting abundant growth of

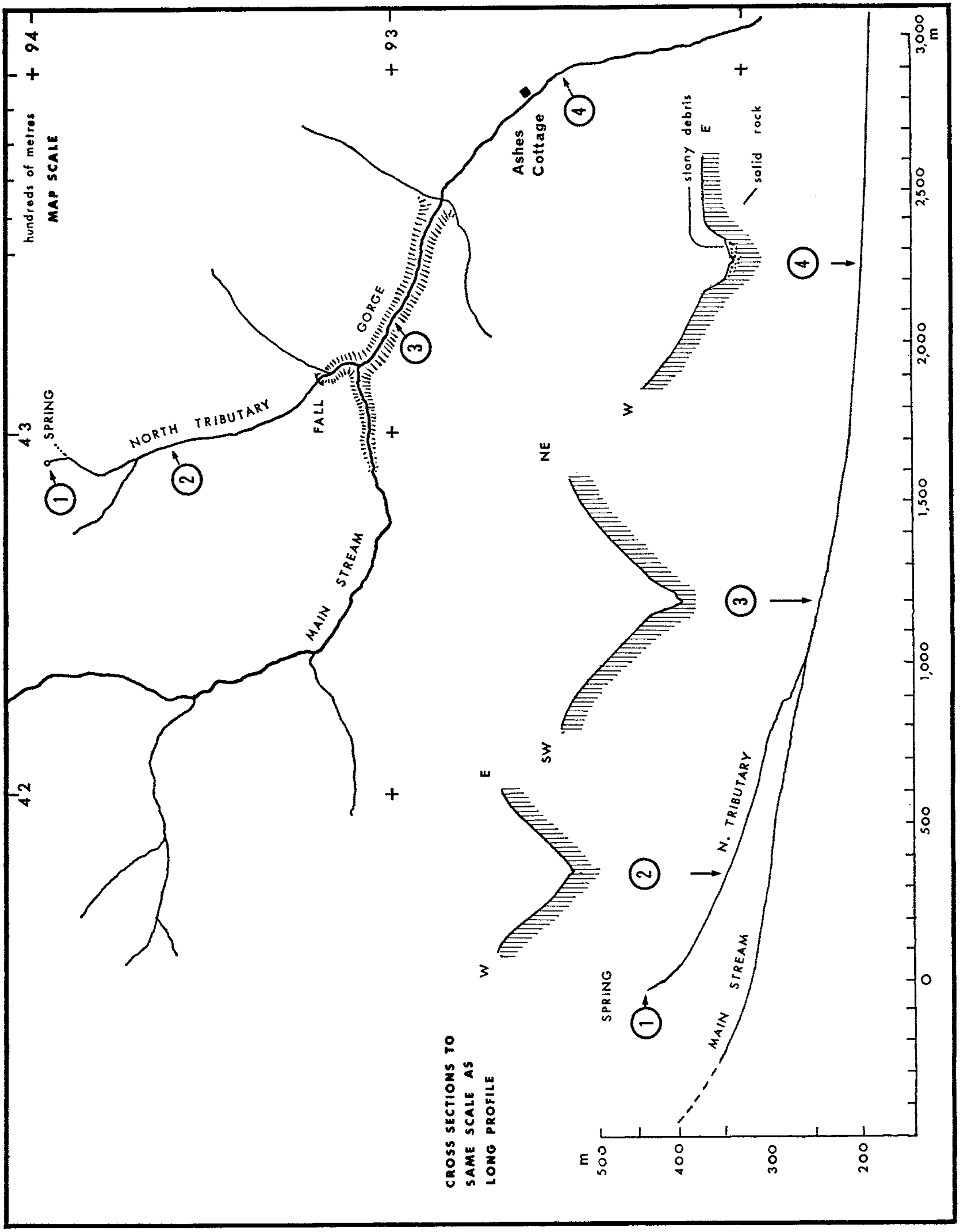

FIG. 2.
Map of main stream and tributaries in Ashes Hollow, with long profile of course studied and schematic cross sections at collecting stations 2, 3 and 4.

mosses and liverworts, or they may be definite rocky or stony springs. Examples of definite springs are found at the head of the New Pool Hollow (a tributary of the Carding Mill Valley), the Boiling Well at the head of Ashes Hollow, and one at the head of the next tributary to the east in that valley. Several of the tributaries of The Batch have definite springs, though these are subject to drying up in the summer. This type of spring far more easily yields a clean, mud-free sample than does the mossy spring flush. The definite springs often run immediately downstream into seepage areas. Spring flushes and seepages of varying size are found draining into the streams at many points well below their sources. These seepages usually support a type of flora which indicates a fairly high base status in the water.

The streams which rise on the summit plateau flow over a very gentle gradient for 50 to several hundred metres before plunging into the upper parts of the steep-sided valleys. Those which rise within the valleys plunge steeply almost at once; this steep part only stretches for one or two hundred metres.

The next part of the stream course is on the floor of an open, upland valley, where it flows moderately swifty over a bed of solid rock and large stones. The stream width varieties from 0·3 m. to 0·7 m. and its depth from 75 mm.–225 mm. Rushes, bracken, grass and heather overhang the banks, and in places dead plant debris is caught up in the stream.

After 1 km., in which there is a drop of 65 m., the stream plunges abruptly over a waterfall or a series of falls. This waterfall stage is well marked in the northern tributary of Ashes Hollow and in the Carding Mill Valley, owing to one or another of the more resistant bands of rock crossing the valleys at right angles to the stream courses. The waterfall in the Ashes Hollow north tributary is only about 10 m. high and is broken into two separate drops with a pool between them. That in the Carding Mill Valley (the Lightspout) is a single drop of about 23 m. In other valleys these resistant bands of rock cross the stream courses more obliquely and the waterfall stage is spread out into a series of smaller cascades over a distance of a hundred metres or more.

Below the waterfall stage is a narrow, steep-sided gorge through which the Ashes Hollow stream flows for about 1 km. Here the stream is 0·6 m.–1·0 m. wide, and its bed consists of solid rock whose varying resistance has given rise to alternating falls and pools. At the sides of the pools small stones and gravel accumulate. Some of the falls are only 0·1 m.–0·3 m. high, often with large stones resting on them. Others are up to 1·0 m. high and on bedrock. Many of the falls support a rich growth of moss, mostly *Eurhynchium riparioides*, particularly in the parts which are subjected to a swift current only in times of spate. In the middle of the falls where there is always swiftly flowing water the rock is devoid of mosses. Similar growth of moss is found in the upper reaches above the waterfall; in both these reaches there is a considerable seasonal growth of the blue-green alga *Nostoc verrucosum*, and of the red alga *Lemanea mamillosa* whose robust filaments like tufts of seaweed cover many of the stones in spring. All the stable but moss-free stones and rocks in shallow water are covered with a growth of black and dark green lichens (*Verrucaria aethiobola*, *V. aquatilis* and *Staurothele fissa*). Throughout the streams there is a conspicuous scarcity of aquatic vascular plants. In the gorge some parts of the banks are composed of bare rock, and in other parts there is a sparse vegetation of grass, gorse or heather. Several nutrient-rich wet flushes drain into the stream in this reach.

Although the stream loses about the same amount of altitude in the gorge as it does in the upland valley, the current is much swifter owing both to the series of small falls, and to the greater volume of water since several tributaries have joined the stream by this stage. The gorge is slightly shorter than the upland reach.

In their lower reaches the valleys widen out, and have flat floors made up of crudely sorted, stony material which lies several metres thick on top of the solid rock. In this part of the valley the stream bed consists mainly of loose stones, varying in size from 100 mm. across down to fine gravel, which shift in times of spate. Many of the stones are rather thin and flat, because of the slate-like nature of much of the parent rock material. The stream meanders and is cutting down into the valley floor. The width of the stream varies between one and three metres. Like the bed of the stream the banks consist of loose, stony material in this reach. The banks are topped by a thin soil supporting grass which is kept short by sheep. In most places the banks are only 150–200 mm. high, though undercutting by the stream has formed banks 0·7 m.–1·0 m. high at a few points. Except at times of spate the water is usually about 100 mm. deep.

Some valleys (Minton Batch, Callow Hollow, Ashes Hollow and Gog Batch) have their streams in the lower part of this last reach overshadowed by alder, ash, hazel, hawthorn and wych elm. These trees contribute a large amount of leaf debris to the stream bed each autumn. The tree-shaded stream channels flow through improved pastureland. The banks in this part consist of mud and loose soil mixed with rocky or stony material. They are as much as 2 m. high in places, owing to more recent down-cutting. The bed of the stream is still stony and the water is only about 100–150 mm. deep in non-spate conditions.

Few plants grown on the shifting bed of this lowest reach, which is about 1·5 km. long with a fall of only 30 m. The streams ultimately flow out into the Church Stretton valley at about 200 m. altitude.

The collecting stations in Ashes Hollow

A brief preliminary survey in the later summer of 1960 revealed no obvious differences between the faunas of the various streams investigated. For a variety of reasons (including accessibility and the need for conservation) the stream in Ashes Hollow was chosen for more detailed study of the invertebrate animals at set points along its course. Four different stations were selected on this stream, and numbered downwards from the source:

Station 1: (Plate II1) 446 m. (1,450 ft. O.D.); SO 428939; a rocky spring at the head of the north branch of the northern tributary, with water fanning out over a silty and mossy flush area (*Pellia epiphylla*, *Philonotis fontana*, *Brachythecium rivulare*, *Cratoneuron commutatum*, *Bryum pseudotriquetrum*, *Acrocladium cuspidatum*, etc.).

Station 2: (Plate II2) 355 m. (1,150 ft. O.D.); SO 429936; in the open upper reaches of the northern tributary a short distance downstream from the confluence of its two headmost branches, narrow and overhung by vegetation; bed of large stones with sparse moss cover (*Eurhynchium*) and much seasonal plant detritus.

Station 3: (Plate II3) 246 m. (800 ft. O.D.); SO 433929; in the rocky gorge reach, including a fall about 1 m. high, a few metres above the fall, and the pool below it; there was moss (*Eurhynchium riparioides*, *Hygroamblystegium fluviatile*) at the sides of the fall and liverwort (*Pellia epiphylla*, *Conocephalum conicum*) on the solid rock banks of the pool; bed of large stones.

Station 4: (Plate II4) 200 m. (650 ft. O.D.); SO 441925; in the tree-shaded and high-banked part of the lower reaches, among improved pastureland about 200 m. downstream from Ashes cottage which is the highest habitation in the valley; bed of stones (mostly small) and finer material suitable for burrowers, unstable and unvegetated but with much leaf litter from overhanging trees.

These four stations were on physically contrasting parts of the stream, and should have brought out any marked variations in the composition of the fauna along it.

Maximum and minimum temperature readings of the water at Stations 2, 3 and 4 were taken between spring and autumn of 1962 by means of boxwood-mounted Sixes thermometers, which were protected from stones by half-cylinders of cellulose acetate sheet and attached within the base-frame of the emergence traps (see below). Regular readings were not taken at Station 1 because it was impossible to submerge the attached thermometer properly.

The periodic maxima and minima recorded at the three stations are shown in Table 1. They suggest wide diurnal fluctuations, though the low summer minimum values may reflect single unusually cold nights. Intermittent readings at Station 1 revealed the constantly rather low temperature (not rising above 12° C. here and probably never freezing) characteristic of springs.

Water samples for analysis of major ions were taken at the four stations on 30 October 1962, when a week's rain had followed a long dry spell. The ionic concentrations recorded are compared in Table 2 with values for certain other streams and for (Lake District) rain water. The figures (apart from NO_3^-N) are fairly high for a non-calcareous mountain stream. An interesting feature is the progressive dilution (possibly by surface runoff) of almost all ions from the spring through Stations 2 and 3, and the slight rise in most at Station 4 where the stream has entered the zone of farming and human habitation.

Table 1. *Maximum and minimum temperatures (°C) recorded at three stations in Ashes Hollow stream in 1962*

		Stations		
		2	3	4
31 March–14 April	Max. Min.	12.0 2.5	10.5 2.0	10.5 1.5
14 April–18 May	Max. Min.	15.5 4.0	16.0 4.0	17.5 3.5
18 May–12 June	Max. Min.	20.0 5.5	21.0 5.5	(22.5)* (12.5)*
12 June–10 August	Max. Min.	20.0 9.5	20.5 8.0	(22.0)† (9.0)†
10 August–20 September	Max. Min.	17.0 7.5	— —	— —
20 September–12 November	Max. Min.	17.5 4.5	— —	— —

* 6–12 June only at Station 4.
† 4 July–10 August only at Station 4.

Table 2. *Ionic concentrations (milligrams/litre) in Ashes Hollow stream compared with values for certain other streams and for Lake District rain*

	Ca^{++}	Mg^{++}	Na^{+}	K^{+}	HCO_3^-	Cl^-	$SO_4^=$	NO_3^-N
ASHES HOLLOW								
Station 1	18.8	3.02	6.4	0.40	50.0	8.8	17.7	0.06
Station 2	10.4	2.62	5.9	0.50	26.6	7.3	16.8	0.06
Station 3	8.2	2.62	5.7	0.30	21.6	7.0	14.7	0.03
Station 4	8.9	3.00	6.0	0.30	24.2	7.2	15.6	0.05
TARN BECK, MALHAM (1) ..	80.0	3.00	3.70	0.70	236.0	4.49	18.3	0.28
FORD WOOD BECK (mouth) (2)	11.56	1.52	4.39	0.89	19.1	8.09	10.7	0.78
WALLA BROOK (source) (2) ..	1.14	0.77	5.70	0.51	4.9	8.17	2.4	0.07
LAKE DISTRICT RAIN (3) ..	0.30	0.19	1.90	0.19	nil	3.26	3.2	<0.02

TARN BECK flows directly from springs in Carboniferous Limestone; FORD WOOD BECK is intermediate and WALLA BROOK is a typical soft water stream, both in the Lake District; Reference (1) Lund (1961); (2) Unpublished data from F.B.A.; (3) Gorham (1957).

METHODS

Collecting aquatic stages of invertebrates

Collections were made at the four stations throughout 1961, at first at monthly intervals and later every other month; in 1962 samples were taken only in March and July, at times of year when the composition of the fauna was expected to differ most. The months of collecting are given with the results in Table 3.

Collecting was based on a method described by Macan (1958), with one five-minute sample at each occasion. Macan points out that this method yields comparative rather than absolute values. A 20 mesh-per-inch net of 28·5 cm. diameter attached to a metal frame on the end of a pole was used (standard F.B.A. pond net). As the collector worked upstream, stones were lifted into the net without being taken out of the water. Animals clinging to the stones were brushed off by hand. Most of the material and animals loosened from beneath the stone that was lifted were washed into the net, though some may have escaped in eddies. The net was held immediately downstream from the stone, with its metal ring firmly against the stream bed. Animals small enough to pass through the holes of the mesh were necessarily ignored. Bottom material below the superficial layer was not sampled by this method, and certain animals now known to be present (e.g. *Ephemera danica*) were inevitably missed.

The contents of the net were washed into a pie dish of clean water. The rest of the sample was then poured into a half-gallon polythene jar in which it was taken to the laboratory for sorting. In this volume of water most of the animals reached the laboratory alive, which made sorting from the debris easier.

The collecting method described above was not designed to catch fish, but the Bullhead (*Cottus gobio*) was common in the stream and frequently caught at stations 3 and 4; young trout (*Salmo trutta*) were sometimes seen, and the river lamprey (*Lampetra fluviatilis*) was found on one occasion in Minton Batch.

It was found that collections from two stations could be made and sorted in a day by one person, and usually two consecutive days were used to collect samples from the four stations.

The animals were sorted as far as possible by eye, and then preserved for later critical identification. Sorting from the debris was carried out in large pie dishes or on large white enamel trays. Animals were brushed from the stones and leaves with a small paint brush. A wide-mouthed pipette was used to transfer the animals to their appropriate dishes.

Any animals which could be identified to species on the spot, e.g. the freshwater limpet *Ancylus fluviatilis* and the flatworm *Crenobia alpina*, were counted and returned to the stream.

The identification of the animals was the most time-absorbing part of the work. Where keys were available the animals were identified to species. In other cases the advice of experts on the various groups was sought. In some orders and families of insects insufficient research has as yet been carried out to enable identification to species. In such cases, for example the caddis, identification of the young stage was made to whatever degree possible.

The only method of finding out what species are present in these critical groups is to obtain the emerging adults, by one or other of two methods. The first is to rear the young in the laboratory and note which adults develop from which larval and pupal skins. The second is to place in the stream traps which are designed to catch the adults as they emerge from the pupal or nymphal stages. The first of these methods is theoretically ideal, because it does connect particular adults with particular young. However, it is extremely difficult to simulate stream conditions satisfactorily in the laboratory and thus rearing of the young is not easy. The emergence trap method ensures obtaining adults, but does not reveal from which larva any given adult came. This latter method was used.

Emergence traps for winged adults

The design of the trap used was an adaptation of that described and illustrated by Mundie (1956). This adaptation is shown in Fig. 3. The "chimney" at the top of the trap encloses a strong polythene jar, replacing the bare glass jar of Dr. Mundie's trap and making it more vandal-proof.

Ideally the traps should have been visited every day during the main emergence season. As this was not possible, killing and preserving fluid was placed in the jar where it was retained by the inverted funnel. The top of the jar was a removable lid, to enable the jars to be filled and the insects to be collected.

The underside of the funnel was roughened with sandpaper, and calcite chippings were glued on to make the upward climb easier for the insects. The jar rested on a flange in the framework at the base of the chimney.

In Mundie's emergence trap the unenclosed glass jar makes it possible for plenty of light to penetrate and attract the emerging insects upwards. Enclosing the jar excluded a great deal of light. In order to minimize this loss white polythene was used for the jar, and the calcite was chosen in preference to a darker material.

The whole jar fitted closely inside the chimney and could not be removed by levering with fingernails or a penknife. The only way to remove the jar illicitly was by tipping the whole trap or by smashing one of the perspex sides of the trap and pushing the jar from underneath; the writer used a rubber suction cap pressed onto the lid for normal removal.

The traps were placed in the stream with two perspex sides facing upstream and the gauze side facing downstream, which allowed any water eddying up into the

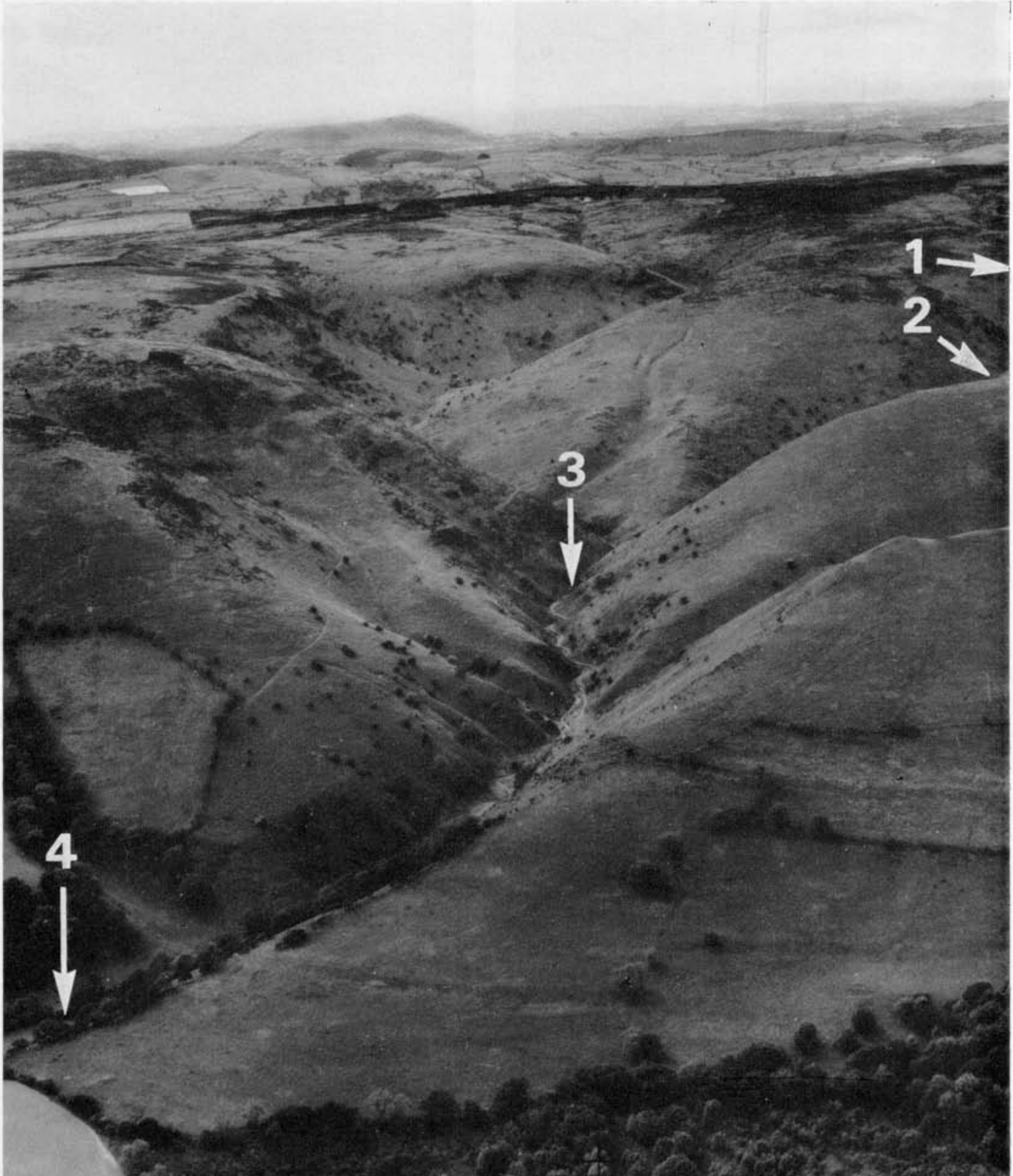

PLATE I.

Ashes Hollow and part of Long Mynd plateau, looking WNW (up valley); numbered arrows mark collecting stations.

Aerial photo by J. K. St. Joseph. Crown copyright reserved.

PLATE II.

The collecting stations: Station 1 (the spring), looking downstream from above source; Station 2, looking upstream; Station 3, looking upstream; Station 4, looking upstream.

Photos by P. J. Herlihy and C. A. Sinker.

trap to escape easily from the downstream side. The two perspex sides let enough light into the main part of the pyramid. The emergence trap must have its base submerged, so that emerging insects do not escape.

The traps were anchored in the stream by wires attached at one end to the corners of the iron framework and at the other end to angle iron, wooden pegs, or pitons driven into the substratum.

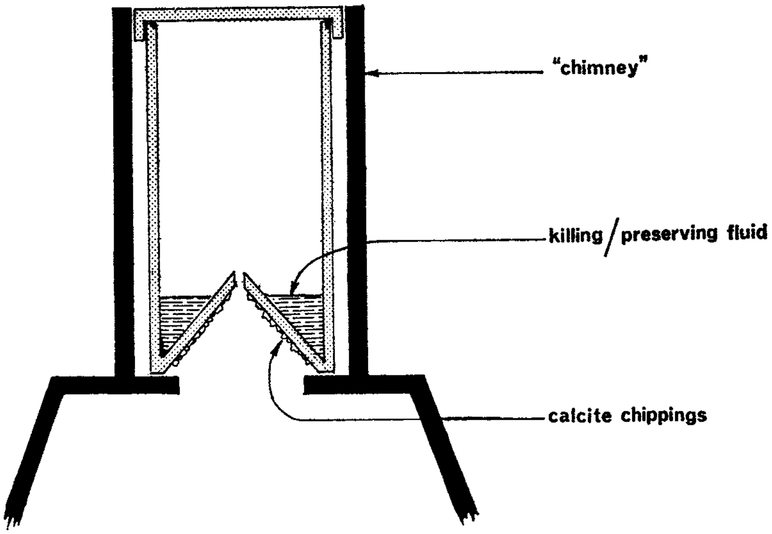

FIG. 3.
Modified top of Mundie-type emergence trap (see text).

Traps were installed in the stream at each of the four sampling stations on the 31st March 1962, and the two survivors (see below) were removed on 12th November the same year after the main period of emergence was over. The primary purpose in using these traps was not to obtain quantitative data (for which they were unsuited) but to catch and identify adults of those Trichoptera species whose larvae are not identifiable. This limited objective was attained in spite of repeated damage to two of the traps. Because the identification data is incorporated in the tables, the bare results in terms of total numbers are mentioned below as part of a summary of the fate of each trap.

The traps at stations 1 and 2 were not discovered by vandals and caught respectively totals of 83 and 49 Trichoptera between May and November, with peak numbers in September. The trap at station 3 was found severely damaged on 21 August, removed and not returned (total catch 78). The trap at station 4 was repeatedly found damaged, removed for repair and replaced, being brought in finally on 4 September and not returned to the stream (total catch 32).

Discussion of results

A survey of the animals of most biotopes results in a list so long that it is difficult to present an account comprehensible to any except those familiar with the community. In an attempt to obviate this difficulty common animals (some of them common in other streams but not this one) have been separated in Table 3 from the rarer ones which are listed in Table 4. In Table 3 the species have been arranged to bring those abundant at station 1, the spring, to the top of the table, those most abundant at station 2, the next station down, below them, and so on.

The fauna of the spring

This is the most distinct. The occurrence here and nowhere else of *Crenobia alpina* is as expected and nothing need be added to what has already been written about the

Table 4. *The less common species*

Species	Group	Records
Pisidium *sp.*	ML	Apr **2**(3). Aug **1**(1). Dec. **1**(1). Jul **2**(1)
Sphaerium *sp.*	ML	Jan **4**(1)
Oligohcaeta	AO	Feb **4**(1). Aug **1**(2). Dec **1**(4), **2**(3), **4**(3). Mar **2**(4)
Gordiacea	NG	Jul **4**(1)
Velia caprai Tamanini	IH	Jun **2**(5)
Latelmis volkmari (Panzer)	IC	Apr **3**(2)
Oreodytes rivalis (Gyll)	IC	Aug **4**(1). Jul **3**(12)
Limnius tuberculatus Müll.	IC	Apr **3**(1). Jul **3**(7)
(Anthrenus fuscus Olivier	IC	Jul **1**(1))
Helophorus affinis (Marsham)	IC	Aug **3**(1)
Helophorus arvernicus Mulsant	IC	Jul **4**(3)
Anacaena globulus (Paykull)	IC	Mar **1**(1)
(Caenopsis waltoni (Boheman)	IC	Jul **1**(1))
Gyrinid larvae	IC	Jan **4**(1). Apr **4**(2)
Hydroporine larvae	IC	Jul **3**(2)
Perla bipunctata (Pictet)	IP	Dec **4**(1). Jul **4**(1)
Brachyptera risi (Morton)	IP	Jan. **3**(1). Apr **3**(1). Mar **2**(1), **3**(2), **4**(1)
Leuctra nigra (Olivier)	IP	Apr **4**(1)
Leuctra fusca (Linn.)	IP	Dec **4**(3)
Leuctra moselyi Morton	IP	Jul **4**(1)
Ecdyonurus dispar (Curt.)	IE	Aug **3**(2), **4**(11)
Pericoma *sp.*	ID	Apr **1**(1). Dec **3**(1). Mar **1**(1). Jul **1**(5)
Pedicia rivosa (Linn.)	ID	Jan **1**(2). Apr **1**(3), **2**(1). Aug **1**(2) Jul **1**(1)
Dicranota *sp.*	ID	Apr **3**(1). Jun **1**(1). Aug **2**(3). Dec **4**(1). Mar **1**(1). Jul **1**(10), **2**(3)
Sperchon clupeifer Piers.	AH	Aug **4**(20). Jul **3**(3), **4**(3)
Sperchon brevirostris Koen.	AH	Aug **3**(1), **4**(3). Jul **4**(1)
Sperchon glandulosus Koen.	AH	Aug **4**(1). Dec **1**(2). Mar **4**(1). Jul **3**(3), **4**(1)
Sperchonopsis verrucosa Protz.	AH	Aug **3**(2), **2**(1). Jul **2**(5)
Atractides nodipalis Thor.	AH	Aug **4**(8). Oct **4**(1). Jul **3**(3), **4**(4)
Atractides tener Thor.	AH	Dec **3**(1)
Hygrobates nigromaculatus Leb.	AH	Aug **4**(1)
Hygrobates fluviatilis Ström	AH	Aug **4**(4). Jul **3**(10), **4**(3)
Paniscus torrenticolus Piers.	AH	Aug **3**(1), **4**(2). Jul **3**(1)
Lebertia porosa Thor.	AH	Aug **3**(2). Jul **3**(3)
Lebertia glabra Thor.	AH	Mar **4**(1)
Lebertia fimbriata Thor.	AH	Jul **4**(2)
Aturus scaber Kram.	AH	Jul **4**(1)
Torrenticola madritensis Viets	AH	Jul **4**(3)
Torrenticola anomala Koch	AH	Jul **3**(3), **4**(1)

Abbreviations in the Group *column as in* Table III, *plus the following:* ML: *Mollusca, Lamellibranchiata.* AO: *Annelida, Oligochaeta.* NG: *Nematomorpha, Gordiacea.* IH: *Insecta, Hemiptera.* AH: *Arachnida, Hydracarina.*
Records *show month, station (bold type) and number taken (brackets) at each collection.*
Small numbers of unidentified larvae were found belonging to the following families of Diptera: Ceratopogonidae, Dixidae, Psychodidae, Tipulidae, Tabanidae, Culicidae, Empididae, Thaumaloidae.

species. On the other hand the restriction of *Polycelis felina* to the same zone is unusual. The two species occur together when the slope is not steep but *P. felina* generally extends further downstream. However, it was not abundant and may have been missed.

Hynes (1961) found *Plectrocnemia geniculata* at all his stations, with greatest percentage occurrence at the topmost. His lowest was at an altitude of 235 metres and the highest temperature he recorded was 14·5° C. Gledhill (1960) took it at 600 m. and Mackereth (1960) and Maitland (1966) record it mainly in the upper reaches. It is probably a cold-water species though this remains to be proved experimentally. Brinkhurst (1957) also records *P. geniculata*. Edington (1965) writes that, if streams have small side tributaries, the polycentropids are represented by *P. conspersa* or *P. geniculata* and not by *Polycentropus flavomaculatus*, which occurs in the main stream.

Nemoura erratica is recorded as common by Brown, Cragg and Crisp (1964) and occurring up to 750 m. In the Lake District Hynes (1941) found it abundantly only in one small stony stream that dried up. Mackereth (1957) found only four specimens in three years. Maitland did not record it, and Hynes (1961) found it only at the highest station of the Afon Hirnant. There is no reason to suppose that this is a cold-water species and its erratic distribution suggests that it maybe one which, tolerant of most unfavourable conditions except competition, establishes itself here and there where it happens to find an empty or not too heavily contested niche.

Little is known about Helodid larvae.

Macan and Mackereth (1957) confirm earlier observations that *Gammarus* moves upstream readily, and postulate that the number that are pushed out from a secure hiding place and carried downstream again depends on the density of population. In this way they explain a uniform distribution throughout the length of the stream. This explanation involves the assumption that the population was always so large that many specimens were being pushed out and washed away at all levels of the stream. If the population did not reach this size, the phenomenon should lead to a diminution in numbers from the top downwards, exactly as seen in Table 3, but it must be stressed that this explanation rests on a fairly large basis of untested theory.

Elmis aenea (*Helmis maugei* or *mougetii*) was one of the common species at the topmost station from Afon Hirnant and occurred at all the others. Maitland (1966) records a uniform distribution from the top downwards. Nobody has explained the observed distribution of this beetle. *Agapetus fuscipes* is mentioned by Nielson (1950) as a species that survives in springs because the winter temperature remains higher than elsewhere. This hypothesis requires further examination in Britain where the species is very widespread and abundant. It clusters on the surface of stones and must presumably be favoured by a stable substratum.

There is much less difference between the communities of the three lower stations than there is between that of the first and that of the others, and many species appear to be uniformly distributed in the rest of the stream. At the moment there is no explanation of the distribution of those that are not. Comparison with other surveys is facilitated if the groups are taken one by one, as so many of them have been confined to one group.

Ephemeroptera

Mayflies are scarce at the topmost station, which is in accord with the findings of other workers; Maitland's fig. 4 E (1966) illustrates this clearly. It is not known why Ephemeroptera are scarcer near the top of a stream.

The species recorded here, excluding Caenidae for the moment, are:

Baetis rhodani	*Ecdyonurus venosus*	*Heptagenia lateralis*
B. pumilus	*E. torrentis*	*Rhithrogena semicolorata*
B. scambus	*E. dispar*	*Ephemerella ignita*

Ecdyonurus dispar is generally found in larger bodies of water than the stream under discussion (Macan, 1957a, 1961). The distribution of *B. scambus* is similar though Macan (1957a), Hynes (1961), Staddon (1961) and Crisp and Nelson (1966) record a few specimens in small streams. Elliott (1967) records large numbers, which, since his stream had extensive stretches of gravel, confirms the suggestion about the habitat of this species made earlier. The remaining seven species are those which Macan (1957a, p. 331), reviewing all the available data, regards as the typical species of small stony streams, except that he includes *Paraleptophlebia submarginata* and writes "*Ecdyonurus torrentis* OR *venosus*". *P. submarginata* has not been recorded in abundance and tends to occur in the regions of slowest flow (Maitland, 1966). The current of the stream under discussion may be too rapid for it. The relationship between *E. torrentis* and *E. venosus* requires elucidating: Maitland (1966) records that *E. torrentis* is the common species at the highest station and extends to where *E. insignis*, a river species, comes in. *E. venosus* does not extend to the highest station but at the rest is generally more abundant than either of the other two. Staddon (1961) and Crisp and Nelson (1966) find both species in small numbers by Hynes (1961) does not record *E. torrentis*.

Work by Hynes (1961), Staddon (1961), Crisp and Nelson (1965) and Maitland (1966) confirm the earlier statement by Macan and it can be stated that the species recorded here are those typical of small stony stream at moderate altitude. Were it higher, *Ameletus inopinatus* and *Baetis tenax* might be expected (Gledhill, 1960, Staddon, 1961, Crisp and Nelson, 1965). If there were slow reaches *Siphlonurus lacustris* would probably occur (Crisp and Nelson, 1965, Maitland, 1966) together with *Paraleptophlebia* as already noted.

Baetis pumilus is recorded by all the authors mentioned but only Macan (1957a) and Staddon (1961) record more than small numbers. The large catches are generally near the sources of streams but in Ford Wood Beck it was most abundant at the lowest station. Professor Pleskot of Vienna states that this species lives in the gravel, a statement that is corroborated by the sudden increase in numbers under stones in spring (Macan, 1957b) when, presumably, the fully developed nymphs are getting ready to emerge. A further study of the substratum may lead to an understanding of the irregular occurrence of this species.

Heptagenia lateralis is another species whose occurrence is sporadic. Macan (1963) explained its abundance in some streams and absence in others in terms of temperature, observing that it did not occur in streams whose summer maximum exceeded 18° C. The highest figure recorded in the present investigation was well above this (Table 1), but on the other hand minimum temperatures were unusually low. Species intolerant of high temperatures can often survive in lethally warm water provided exposure is brief. These results do not, therefore, conflict with those of Macan (1963). Harker (1953) records that *H. lateralis* was more adversely affected by floods than *Ecdyonurus venosus* and *Rhithrogena semicolorata*, but this is another observation that does not explain the distribution recorded here. *Caenis rivulorum* is found typically in small stony streams, but *C. horaria* usually inhabits mud.

Plecoptera

The stonefly species recorded in the present survey are listed below. The numbers in parenthesis show how many of nine other authors recorded each species. Eight are referred to; the ninth is the survey of the River Duddon (which separates Cumberland and Lancashire) and its tributaries, which Dr. G. W. Minshall very kindly made available in the typescript stage.

Carnivores	Herbivores
Dinocras cephalotes (3)	*Amphinemura sulcicollis* (9)
Isoperla grammatica (9)	*Protonemura meyeri* (9)
Perla bipunctata (5)	*Nemoura cambrica* (6)
	N. erratica (0)
	Chloroperla torrentium (9)
	C. tripunctata (5)
	Leuctra hippopus (8)
	L. fusca (8)
	L. inermis (9)
	L. nigra (7)
	L. moselyi (0)
	Brachyptera risi (7)

The present stream is unusual in that *Dinocras cephalotes* is abundant. Maitland (1966) records it as quite common in stretches of the upper and middle reaches. Brown, Cragg and Crisp (1964) record it among large stones and stable boulders, and Elliott (1967) took a few. Hynes (1941), in his original taxonomic survey, records that it "is always much commoner in places where the substratum is stable and moss-covered" whereas nymphs of *Perla bipunctata* (then known as *P. carlukiana*) "were much commoner on unstable parts of the substratum". Brown, Cragg and Crisp (1964) confirm its occurrence in the stable regions, but unfortunately it is not possible to make out from the other records whether this is always true. Possibly related to the abundance of this species in the stream under consideration is the scarcity of *P. bipunctata* and the absence of *Perlodes microcephala* recorded by all the other authors except Gledhill (1960). Mackereth (1957) found most of her specimens of this species in a tributary which dries up, whereas *Perla bipunctata*, common lower down, was not taken there. *Perlodes* completes its life cycle in one year and is likely to have emerged before the stream dries up whereas *P. bipunctata* takes more than one year to complete development.

Diura bicaudata is another carnivore generally found at higher altitudes (Brinkhurst 1957, Brown, Cragg and Crisp, 1964; Hynes, 1961; and Gledhill, 1960). Its inability to co-exist with *Perlodes microcephala* has been referred to already, and the present records suggest that it is unable to compete with other carnivores as well.

In contrast, the list of herbivores indicates that this is a typical stonefly fauna. Three not taken by most of the other workers, *Chloroperla torrentium*, *Leuctra nigra* and *Brachyptera risi* are all species that are generally scarce. The same is true of the species not recorded here but taken by other authors. *Protonemura montana*

(Brinkhurst, 1957, Brown, Cragg and Crisp, 1964, Hynes, 1961 and Gledhill, 1960) is a species of high altitudes. The same authors also record *Protonemura praecox* through Hynes (1961) and Mackereth (1957) record it at lower altitudes.

Trichoptera

Comments on the caddis-flies must be less concise as not all specimens can be identified to species. The list is:

Plectrocnemia geniculata	*Rhyacophila munda*
Agapetus fuscipes	*R. obliterata*
Philopotamus montanus	*Glossoma boltoni*
Wormaldia occipitalis	*Odontocerum albicorne*
Hydropsche fulvipes	*Stenophylax latipennis*
H. instabilis	*Chaetopteryx villosa*
Diplectrona felix	*Apatidea muliebris*
Chaumatopsyche lepida	*Hydroptila forcipata*
Rhyacophila dorsalis	*Brachycentrus subnubilus*

According to Nielson (1950) *Apatidea muliebris* is confined to springs because the temperature elsewhere is generally warmer than it can tolerate, and what is known of its occurrence elsewhere confirms this. In the present survey only adults were recognized. *Wormaldia occipitalis* and *Diplectrona felix* were both found by Mackereth (1960) to be far more common in the upper parts of the stream than lower down. Nielson (1950) suggests that *Wormaldia occipitalis. Agapetus fuscipes* and *Odontocerum albicorne* are southern species that cannot tolerate the temperature to which water falls in winter in countries such as Denmark or Britain. In springs and the streams just below them, however, they may find refuges where, though the temperature is low in summer, it remains higher than that of other waters all winter. No exploration of the temperature tolerance of these species has been carried out and in Britain *Agapetus fuscipes* is so widespread that its tolerance of most ecological factors must be great. Edington (1965) notes that *Diplectrona felix* tends to occur in sidestreams whereas *Hydropsyche fulvipes* or *instabilis* replaces it in the main streams. A similar relationship exists between *Plectrocnemia conspersa* or *geniculata* and *Polycentropus flavomaculatus*. Edington does not offer to explain it. All the hydropsychids mentioned above occur in this stream, but of the polycentropids, *Polycentropus* is a notable absentee, found in abundance by Maitland (1966), Brinkhurst (1957), in small numbers by Scott (1958) and Hynes (1961) and not at all by Gledhill (1960) and Mackereth (1960). Another absentee from the present stream which is abundant or fairly abundant in the others is *Sericostoma personatum* (Brinkhurst, 1957, Mackereth, 1960, Hynes, 1961, Maitland, 1966).

When more larvae can be identified this stream may be found to harbour some typical spring species. Otherwise it has a fauna characteristic of small stony streams. The carnivorous free-living *Rhyacophila* was well represented by three of the four British species. The net-spinning families Hydropsychidae, Philopotamidae and Polycentropidae contribute a large number of species and individuals to the community. The first two are confined to running water but some species of polycentropids occur in lakes and ponds.

Coleoptera

Of the beetles *Elmis aenea*, *Latelmis volkmari* and *Limnius tuberculatus* are all Elmidae (or Helminthidae) that are common in streams (Hynes, 1961, Maitland, 1966). *Oreodytes* is a genus of Dytiscidae that is frequently taken in running water and appears to have adapted its way of life to the conditions there. *Helpohorus* and *Anacaena* are hydrophilids with no obvious adaptation to life in a current. *Helophorus* flies from place to place more than most aquatic insects and this may account for its occurrence in small numbers both here and in the streams studied by Hynes and Maitland. The other two beetles recorded had probably fallen in.

Other groups

The Chironomidae contain a large assemblage of flies and midges which are at present extremely difficult to identify as larvae (Bryce, 1960). Very little is known concerning their ecology though they are often an important group in stream communities. Many genera are detrital and algal feeders and reach highest densities where detritus collects in slow reaches and between stones. The relatively high count of larvae at station 3 came chiefly from the moss patches where detritus was trapped and shelter from the current provided.

Platyhelminthes and Crustacea have been discussed already. The only snail was *Ancylus*, a characteristic member of the community. Its distribution is similar to that shown by Maitland. Hynes, however, lists it among the species found in "very small numbers". An outstanding feature of the Afon Hirnant is the absence of *Gammarus* which, with the scarcity of *Ancylus*, may reflect a deficiency in some substance. *Ancylus* is unable to live on an unstable bottom but this would not account for its scarcity in the Afon Hirnant.

Life histories

By measuring the lengths of nymphs of the same species caught at each collecting date, and studying the sequence of size-ranges and means so produced, it is possible to draw inferences about the pattern of that animal's life history. Diagrams have been drawn (Fig. 4) for four insect species occurring in reasonable numbers, representing several different types of life history: data for stations 2, 3 and 4 (which are geographically very close) have been combined to increase the sample size. It should be remembered that young nymphs of 1 mm. or less in length were not collected.

The life histories of *Amphinemura sulcicollis* (Fig. 4a) and *Rhithrogena semicolorata* (Fig. 4b) show a simple, one-year pattern of growth of nymphs throughout the late autumn, winter and spring, emergence of adults in late spring/early summer, presumable egg stage in the summer, and hatching of young nymphs in late summer/autumn.

The short and rapid growth period of *Ephemerella ignita* (Fig. 4c) indicates a very long egg stage in the life history, lasting from late summer one year until late spring the following year.

The diagram for *Dinocras cephalotes* does not show a clear-cut pattern. There is a definite emergence period in late June/early July. The continual large size-range of the nymphs is because they take more than one year to develop from egg to adult. This period is normally 3 years (Hynes, 1958).

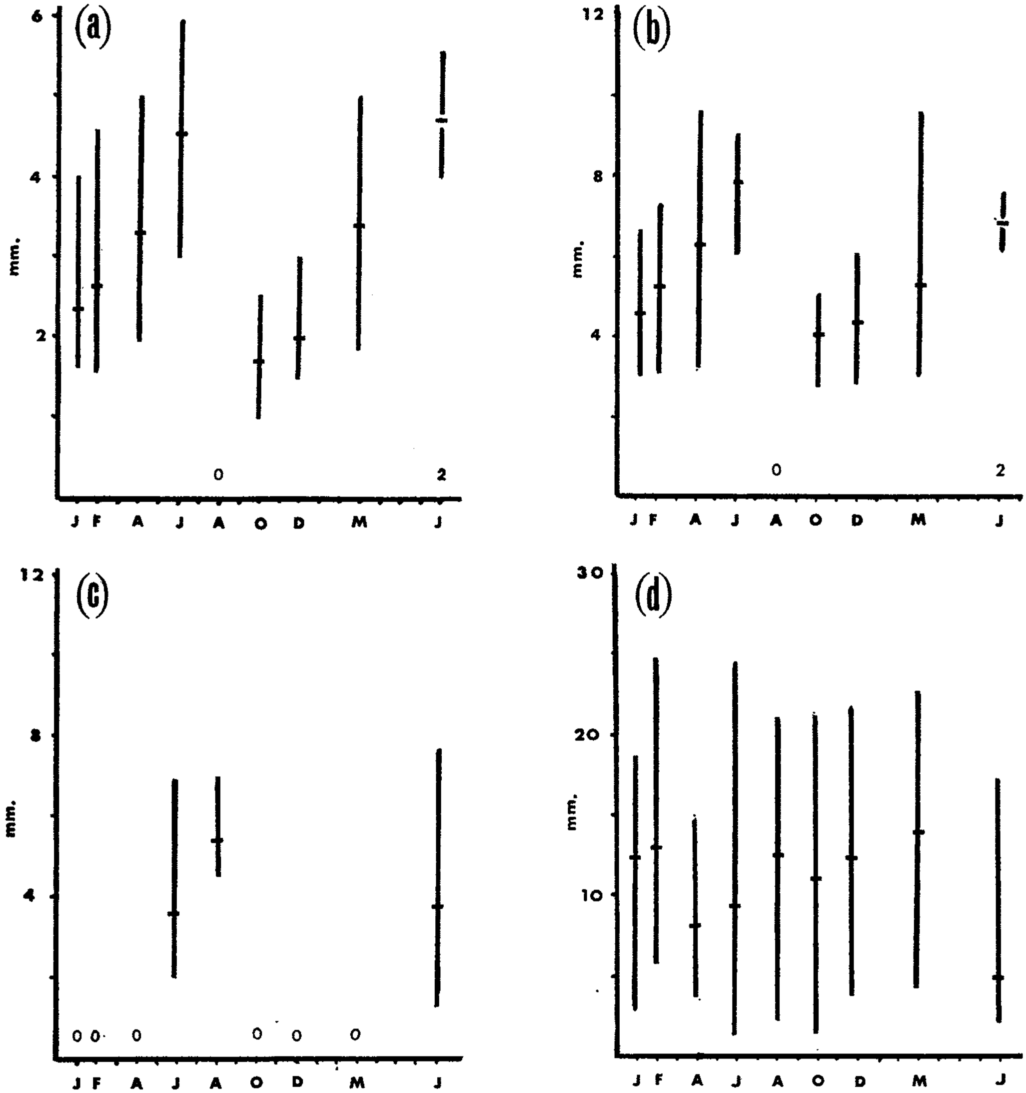

FIG. 4.
Seasonal variations in body length of some aquatic insect larvae. Based on measurements of all individuals of a species caught at any station on a given date in the routine collecting programme; the range (vertical line) and mean (crossbar) of each combined sample are shown. Small or nil samples are shown by a number over the collecting date. (a) *Amphinemura sulcicollis*; (b) *Rhithrogena semicolorata*; (c) *Ephemerella ignita*; (d) *Dinocras cephalotes*.

CONCLUSION

The stream rises at about 500 m. above sea level and flows over hard Pre-Cambrian rock. The drainage area is covered with mountain heath and rough grassland on which sheep graze. Except at the source, where the temperature did not exceed 12° C., temperature rose to 20° C. or above in summer which is probably near equilibrium with air temperature. By night the water was unusually cool, and compared with other streams, the average temperature must have been low. The water was soft but all the common ions were present in moderate amounts compared with the concentration in other streams of the same type.

At the topmost station the fauna was restricted, the species found being confined to such places, or commoner in them than lower down in other streams. At the remaining three stations the fauna was similar, and the composition of the community resembled that recorded elsewhere in biotopes of the same kind. Unusual features were the relative abundance of *Dinocras cephalotes* and the scarcity of other large carnivorous stoneflies, and the abundance of *Polycelis felina* at the topmost station and nowhere else. No feature peculiar to the stream that might explain these differences was observed, and there was no obvious explanation of the slight difference that did exist between the communities of the three stations below the source.

The stream is relatively rich in species and all the animals typical of running water were obtained easily. Simuliidae, the larvae that show the greatest morphological adaptation to life in running water, increased in abundance with distance from the source, which, since they feed on particles carried down by the current, is to be expected. Net-spinning Trichoptera (Hydropsychidae and Philopotamidae), which also rely on the current to bring food, were more evenly distributed. Three species of elminthid, the small beetles with plastron respiration, an adaptation that facilitates life in a current, were taken. *Ancylus*, the limpet adapted to cling to a hard surface, and the three mayfly genera in the family Ecdyonuridae, whose flat spreadeagled form enables them both to cling to and move rapidly across bare stones and rocks, were all abundant. Of these, it will be remembered, *Ecdyonurus* and *Heptagenia*, which can move their gills, occur also on stony substrata in lakes. *Rhithrogena*, whose gills are modified to form a sucker, cannot, and it is confined to running water. It provides a good example of a species so restricted by physiological requirements. The other example is *Crenobia* (*Planaria*) *alpina* confined in Britain to the neighbourhood of springs because nowhere else is cold enough. High in the Alps it occurs in lakes as well.

One of the most numerous animals, at least in the upper reaches, is *Gammarus pulex*, a widespread species that is frequently abundant in swift water. Its success appears to be due to modifications of behaviour rather than to modifications of structure.

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