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Der Sauerstoff wird also bei *Habrophlebia* in dem tracheolendurchsponnenen distalen Abschnitt der Kiemen aufgenommen, während die stärkste CO_2-Abscheidung an der Kiemenbasis erfolgt.

Bei *Habroleptoides* dagegen liegen die Dinge wesentlich anders. An der Phenolphthalein-Entfärbung (Abb. 4) nehmen die Tracheenkiemen überhaupt keinen Anteil. Die Entfärbung tritt am schnellsten und intensivsten in der Umgebung des Hinterendes ein und breitet sich von hier allmählich über das ganze Abdomen aus. Mit Silbernitrat tritt an keinem Abschnitt der Kiemen eine Schwärzung der Kutikula ein. Dagegen färben sich die Chitinporen, die hier die Kiemen ziemlich gleichmäßig bedecken (Abb. 5) schwarz und zugleich die Tracheenhauptstämme, die hier beide Äste der Kieme bis in die Spitze unverästelt durchziehen und an der ganzen Länge von der Basis der Kiemen bis zu den Spitzen der Gabeläste ein dichtes Netz fast radiär gestellter kurzer Tracheolen zur Oberfläche senden. Die Chitinporen liegen deutlich zwischen den Tracheolen und es sieht an den Totalpräparaten nicht so aus, als ob eine Verbindung zwischen beiden bestehen würde (Schnitte wurden nicht angefertigt).

Die Chitinporen, die von Schoenemund, Prey und Kühnelt bei verschiedenen Insekten beschrieben wurden, sind vorläufig rätselhafte Organe. Auch Kühnelt hat beobachtet, daß mit der Schwärzung der Poren eine Schwärzung der Tracheenstämme Hand in Hand geht, während die Kutikula ungeschwärzt bleibt. Eine funktionelle Deutung dieser Vorgänge ist vorläufig nicht möglich, doch kann eines sicher gesagt werden: Die Funktionsweise der Tracheenkiemen von *Habroleptoides* unterscheidet sich offensichtlich irgendwie sehr entscheidend von der bei *Habrophlebia!*

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EPHEMEROPTERA IN BRITAIN

T. T. MACAN

Forty-seven species have been recorded from Britain, and recent taxonomic studies are set out in the reference list.

The status of *Arthroplea congener* on the British list, being based on one specimen taken 40 years ago, is somewhat doubtful. *Ephemera lineata*, *Potamanthus luteus*, *Brachycercus harrisella*, *Baëtis atrebatinus*, and perhaps also *Rhithrogena haarupi*, are rare species inhabiting what in Britain pass for large rivers. Their range has possibly been reduced by man's use of rivers for a variety of purposes. *Heptagenia fuscogrisea* is common in the limestone lakes in Ireland but rare in the rest of the British Isles. It is the only

ecdyonurid I have ever found clinging to flat leaves. *Paraleptophlebia tumida* is known to me only from two chalk streams that are dry in summer. *Ameletus inopinatus*, a mountain and arctic species in Europe, is abundant in streams above 300—400 m though I have also found it in lakes at sea level in the north of Scotland.

Accounts of life histories have been published by Harker (1952), Macan (1957) and Gledhill (1959). Once a life history has been worked out, there is the problem of finding which internal or external factors cause the various events to happen when they do. Adults of *Rhithrogena semicolorata* were taken in an emergence cage up to late August in 1953, 1954, and 1956, three summers notable for persistently low temperature. In four other years emergence ended when the average air temperature, which is followed fairly closely, though with some lag, by water temperature, rose to 16—17°C and stayed there for at least a week (Macan 1960a). A destruction by lethally high temperature of nymphs that have not emerged seems likely. It is impossible to say what the actual lethal level is from the figures quoted; not only temperature reached but duration of exposure is important. As will be described presently, these small streams may be as warm in late May as at any time in the summer, but in this month they are colder at night than in July or August (Macan 1959). Whitney (1939) found a lethal temperature of 22.4—24.7°C but the value is likely to be lower during the critical period just before emergence (Pleskot 1953). Presumably the eggs can withstand a higher temperature than the nymphs, support for which idea comes from a comparison of the results of Harker (1952) and myself (Macan 1957). Harker found that emergence lasted well into July and was not over before the nymphs of the new generation appeared, whereas in my stream emergence was mainly in June or late May, the tiny nymphs never appeared before August, and the two yearclasses never overlapped. The later emergence and earlier hatching in Harker's stream is probably correlated with its lower temperature.

Heptagenia lateralis has a life history which is very like that of *Rhithrogena semicolorata* and shows the same difference in the two streams studied by Harker and myself. It differs from it in two respects, both of which restrict its range: it does not grow during the coldest part of the winter, whereas *Rhithrogena* increases in size at a steady rate regardless of temperature, and its upper lethal temperature is lower (Macan 1960b). In 1959, a summer with an unusually long duration of sunny weather, the maximum temperature at 18 stations in streams was measured at intervals. Where it was 18°C or less, *Heptagenia* was always numerous, and where it was 18°C or higher, *Heptagenia* was scarce or absent except at one station, which, however, was just above a particularly thickly populated cool zone. *Heptagenia* occurs also on the stony shores of Windermere, which gets several degrees warmer than 18°C. However, whereas the streams showed in May a maximum only a little below the highest temperature reached at any time in the summer, the lake warmed up slowly to a maximum in late summer and did not reach 18°C till towards the end of June. Nymphs would have emerged by this time and presumably the eggs are more resistant and can withstand the higher temperatures of late summer in the lake.

The life history of *Baëtis rhodani*, studied by both Pleskot (1958) and by myself (Macan 1957) illustrates a point of particular importance to a gathering of this kind — the value of doing the same thing in two different places. It also illustrates certain difficulties connected with work on streams, notably that it is not easy to find out the exact temperature conditions under which an animal develops, because the temperature is not the same at any two points and the animals move up or down the stream at different times of year.

I obtained some data about this movement by means of emergence traps. There were six stations altogether in the stream which I studied (Ford Wood Beck) and,

for the last seven years, emergence traps at two of them: Outgate near the source and station 1 near the mouth. Nymphs of *Baëtis rhodani* were always more abundant at st. 1 than at Outgate, though there were always fair numbers at the latter station. Emerging adults, on the other hand, were rare in Outgate; in 1955, a year of unusual abundance of all species, 20 were taken but in the other six years the total catch was 4. There have always been plenty in the trap at st. 1, from which it is evident that most nymphs move downstream before emergence.

The temperature at Outgate was measured by means of a thermograph over a period of years, and the resulting wealth of data makes one realize how difficult it is either to characterize the temperature in a few words or to make too close a comparison with streams in which readings were taken only occasionally. Pleskot describes the temperature of my stream as "maximum meist 16 bis 17°C", which is as fair a summary as anyone could make in five words. Table 1 shows in greater detail the figures on which this summary is based. St. 1 is 2—3°C warmer than Outgate (Macan 1958). Throughout most of 1959 the maximum lay between 19 and 20.5°C though in August it reached 22°C. A maximum of 18°C was recorded in Outgate that year, though not with the thermograph, which had been removed. Pleskot records "maximum über 20°C" in her stream. The interesting difference between the two is that, whereas in mine a quick summer generation of *B. rhodani* has started to emerge before the overwintering generation has finished, in hers there is a gap of a month and a half between the two during late summer. This is attributed to unfavourably high temperature. We are obviously reaching a stage when only laboratory experiments can establish exactly the critical temperatures which are beginning to become apparent from this field work, but I believe that these field results are an indispensable preliminary to indoor investigations.

Table 1

The figures show the number of hours during which the temperature was between the levels indicated.

	1952	1954	1955	1956
above 19°C..	3	0	0	0
18—19°C ...	12	0	1	0
17—18°C ...	40	0	82	0
16—17°C ...	165	7	342	0

Harker (1953) and Macan (1957) have written accounts of the Ephemeroptera of small stony streams. Six species, *Rhithrogena semicolorata*, *Ecdyonurus torrentis* or *venosus*, *Heptagenia lateralis*, *Baëtis rhodani*, *B. pumilus*, and *Ephemerella ignita* appear to be characteristic of such a biotope, not only in Britain but on the continent too, as the thorough surveys of Illies (1952) and Dittmar (1955) show. Both authors record a few species that do not occur in Britain. The list becomes longer as current slackens and as size increases. Recent changes in the fauna of Ford Wood Beck are probably correlated with the bringing of water to the village of Outgate and the consequent overloading of its one septic tank, which overflows into the stream. *Polycelis felina* (*cornuta*) has become much more numerous (table 2), and *Simulium* spp. and various net-spinning Trichoptera have also increased. *Ecdyonurus torrentis* disappeared from the emergence trap catches in 1959, and both *Baëtis rhodani* and *Rhithrogena semicolorata* have been sinking steadily since a peak in 1955; the latter, the most abundant species in 1953, was not taken in 1960. The wild fluctuations of *Baëtis pumilus* are inexplicable and no trend can be made out. *Ephemerella ignita* appears unaffected though collections in the

water indicate that it is more widespread than formerly. I suggest that the pollution did not affect the fauna through a toxin, because that should have caused an earlier and more abrupt decline and disappearance. Nearly all the houses were connected to the water supply by 1953 and the high numbers of so many species (Plecoptera were relatively more abundant than Ephemeroptera) in 1955 (table 2) suggests that these species were favoured by the pollution. Their subsequent decline must have been due to the activities of some other animal which could exploit the situation, presumably an increased food supply of organic matter, bacteria, fungi and ciliates, more efficiently. Such an animal is *Polycelis felina* (*cornuta*). Jennings (1957) describes how it traps animals in mucus nets and can capture quite large specimens. If the small flatworms have been enabled to survive in large numbers by food originating in the septic tank, the resulting adult population could well have produced the observed fall in the numbers of certain Ephemeroptera. I have made no direct observations, but the fact that the species that move over stones have suffered more severely than those such as *Baëtis pumilus* and the Plecoptera which live in the gravel, supports the hypothesis.

Table 2

Catches in Ford Wood Beck. The first five species were taken in an emergence trap near the mouth, *Habrophlebia fusca* at Outgate near the source. The totals for *Polycelis felina* are those obtained with a net at five stations in March.

	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961
Baëtis rhodani	—	—	153	66	140	178	77	30	15	36	7	—
B. pumilus	—	—	86	7	3	8	103	127	7	4	50	—
Rhithrogena semicolorata	—	—	37	109	65	112	31	30	19	4	0	—
Ecdyonurus torrentis	—	—	8	10	6	22	5	16	1	0	0	—
Ephemerella ignita.	—	—	6	10	34	76	19	7	2	9	22	—
Habrophlebia fusca	—	—	—	—	0	11	81	79	17	48	109	—
Polycelis felina ...	2	2	6	—	—	—	52	—	435	1052	291	633

The only species to have increased is *Habrophlebia fusca*, which has become abundant at Outgate. Previously I had supposed that its scarcity in the beck was due to a current just faster than its optimum but these findings suggest that food supply rather than current is the determining factor.

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