

FRESHWATER  
BIOLOGICAL ASSOCIATION



Scientific Publication No. 20

A Key to the  
NYMPHS  
of the British species of  
EPHEMEROPTERA

BY

T. T. MACAN, M.A., Ph.D.



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1961

# FRESHWATER BIOLOGICAL ASSOCIATION

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A KEY TO THE  
NYMPHS

OF THE BRITISH SPECIES OF

**Ephemeroptera**

with notes on their Ecology

by

T. T. MACAN, M.A., Ph.D.

*Freshwater Biological Association*

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## FOREWORD

The Association's original key to the Ephemeroptera (No. 7 in this series, by D. E. Kimmins, published in 1942) contained keys to the families and genera of the nymphs, but it was impossible at that time to make a key to species. Mr Kimmins's key to the adults was re-published in a revised form in 1954 as No. 15 of the series, but the nymphal keys were then omitted, because it was hoped that it would shortly be possible to compile a key to take them too down to the species.

This Dr Macan has now done. Descriptions and keys to the nymphs of forty-five of the forty-seven British species have been published during the last twenty years, most of them by Dr Macan himself. As the distinguishing features of the two missing ones have been described by continental workers, it is now possible to produce a key to all the species recorded in this country, except that in two cases no characters sufficiently clear-cut to be satisfactorily used in a key to distinguish the nymphs of a pair of closely related species have been found.

This key contains a new feature in the section on Life Histories, which it is hoped will contribute to an understanding of the ecological significance of the group. The practice, recently begun, of including distribution maps where possible has been continued here.

THE FERRY HOUSE  
February 1961.

H. C. GILSON  
*Director*

## INTRODUCTION

Eggs of the Ephemeroptera are laid in the water and from them emerges what is here called a *nymph*, though it is now fashionable in some zoological circles to use the term *larva*, and to a fisherman the word means only something at a later stage of development. The nymphs grow by shedding their skins, and there are a large number of such moults before full size is attained. Then a winged form emerges from the old skin and this undergoes a further moult, unique among insects, to produce the mature adult, which dies when it has mated and laid eggs.

The nymph of the Ephemeroptera could well be used to illustrate typical insect structure, and anyone who has dissected a cockroach will need no further introduction to the key. For those new to entomology a few words should suffice to make the key comprehensible. At the front end of the body is the head, which bears the slender tapering antennae, the large eyes and the mouthparts, which will be described later. The thorax bears three pairs of legs and is made of three segments of which the middle is large and the last not very obvious. The top of each is covered by a plate called the *notum*; the *pronotum* is the one immediately behind the head, and the *mesonotum* that of the middle thoracic segment. Fig. 13a (p. 24) shows a young larva, but most of the others are older and have reached the stage where the mesonotum bears a conspicuous pair of wing-buds. Behind the thorax come ten segments that form the abdomen, each consisting of an upper plate called a *tergum* and a lower one called a *sternum*. Springing from the side or from near the side of each one, except the last few, is an organ commonly known as a *gill*, though this is a misnomer in some species in that it has no direct respiratory function; it is indirectly concerned because by beating continuously it keeps a current of water flowing over the body surface, which is thought to be the seat of oxygen uptake. At the end of the abdomen are three tapering processes, which, properly known as the dorsal caudal appendage and the cerci, receive here the much shorter, if slightly inaccurate, name of *tails*.

The important parts of the leg (*e.g.* fig. 5, p. 10) are, starting from

the outer extremity for the sake of simplicity, the *claw*, the *tarsus*, the slightly longer *tibia* and the broader *femur*.

In most species the mouthparts hang down from the underside of the head, and consist of four main elements. The foremost is a flap capable of a little movement backwards and forwards and known as the *labrum* (fig. 23 shows half this plate). Next come a pair of jaw-like *mandibles*, which move inwards and outwards and which, in *Baëtis*, bear an unusual appendage known as a *protheca* (fig. 24). Behind them is another pair of chewing organs, the *maxillae*, and they are characterized by a three-jointed appendage known as the *palp* (fig. 17). Last comes the *labium* another plate which also bears a palp on either side (fig. 17 shows half a labium). Paired lobes project from the lower margin, and the inner pair are the *glossae*, the outer ones the *paraglossae*.

It is impossible to discover the true orientation of the appendages of a dead specimen and, accordingly, in the key all expressions such as "the top" or the "the lower margin" refer to the organ in the position in which it is illustrated.

The key should serve to identify all nymphs that are half full-size or larger, and quite a lot smaller than this. The smaller the nymph the more it tends to resemble closely related species.

#### COLLECTING AND PRESERVING

The most useful instrument is an ordinary pond-net, the error of which is discussed by Macan (1958d). It can even be used to scoop from the bottom and sieve samples of mud that may contain nymphs of *Ephemera*, but, when lightness is not a primary consideration, a proper dredge and sieve are obviously preferable. If it is desired to take nymphs home alive, containers holding a pint or more are recommended. There is something about many species, the angle at which the tails are held for example, which makes them easier to identify alive than dead. I have used 2½% formalin or a mixture of 500 ml of 70% alcohol, 10 ml of 40% formalin and 5 ml of glycerin for preserving specimens.

## KEY

- 1 Gills consisting of two branches each thickly fringed with filaments along both sides (fig. 1)— 2
- Gills not like this— 5

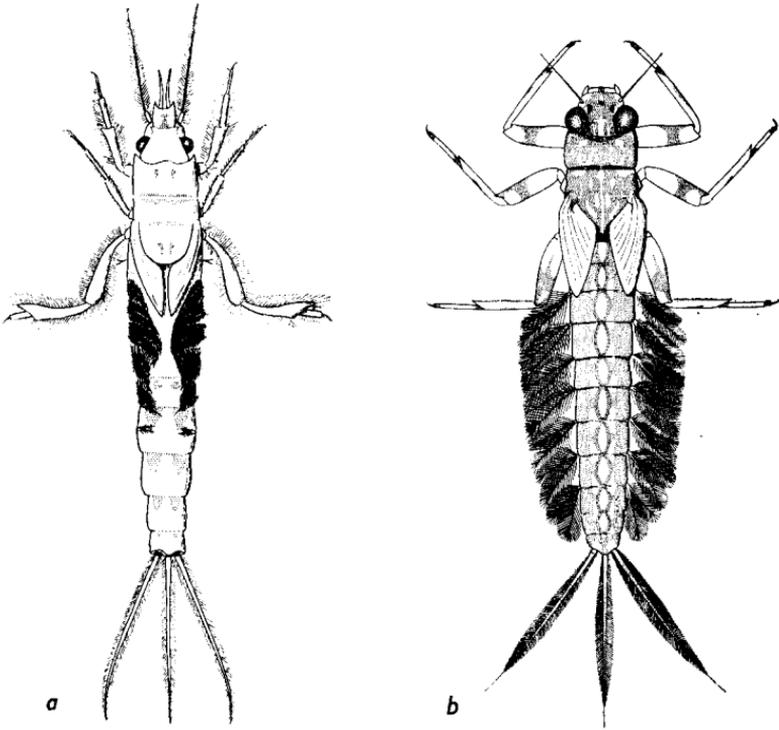


Fig. 1. a, *Ephemera danica*, 24 mm long, from life; b. *Potamanthus luteus*, 17 mm long.

- 2 Gills held over the back during life. Mandibles with a long curved process that projects well beyond the front margin of the head (fig. 1a). Full-grown nymphs up to 25 mm long—

EPHEMERIDAE 3  
(Macan 1958a)

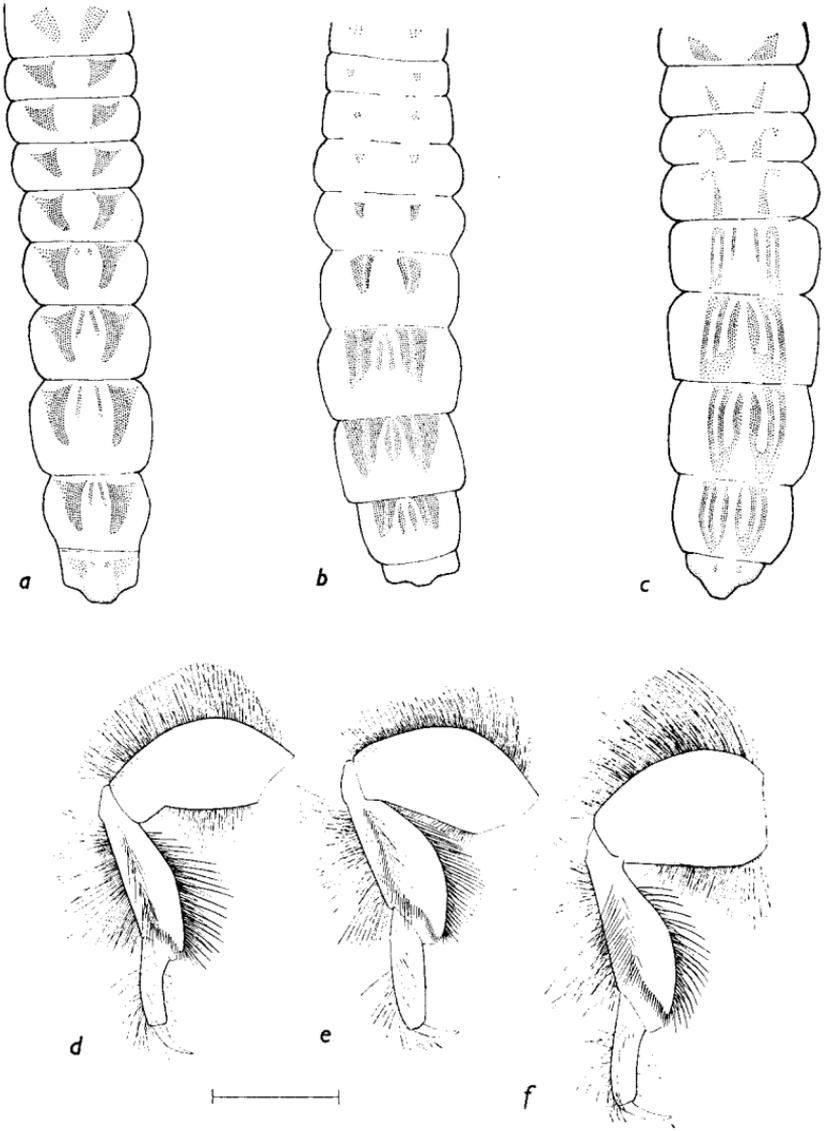


Fig. 2. *Ephemera*. Above, dorsal abdominal patterns of: a, *E. vulgata*, 16 mm long; b, *E. danica*, 15 mm; c, *E. lineata*, 15 mm. Below, fore-legs of: d, *E. vulgata*; e, *E. danica*; f, *E. lineata*. (Scale line 1 mm.)

- Gills extending out sideways from the body during life. No process of the mandibles projecting beyond the front margin of the head (fig. 1*b*). Full-grown nymph about 15 mm long—

POTAMANTHIDAE, **Potamanthus luteus** (L.)

R. Wye, 1958. R. Usk, in a side-pool floored with stones and sand, May 1955. R. Thames, Laleham and Weybridge, 1902 and 1878.

- 3 A distinct dark mark on either side of all the abdominal terga except the first and last, those on segments 7, 8 and 9 barely twice as big as those on other segments (fig 2*a*). Fore tibia relatively narrow, bounded on the inner side by two straight edges joined by a curve (fig. 2*d*). (Fore femur relatively narrow: fig. 2*d*)—

**Ephemera vulgata** L.

Fairly common and abundant\* in rivers with a muddy bottom.

Lake District: not recorded.

- The dark areas on abdominal terga 7, 8 and 9 large, those on segments 3 and 4 at least small, obscure and often absent (fig. 2*b*, c). Fore tibia broader and with the whole of the inner margin curved (fig. 2*e*, *f*)—

4

- 4 A large triangular mark on abdominal terga 7, 8 and 9; it may be divided into two and there is a narrow line inside it (fig. 2*b*). Femora relatively narrow (fig. 2*e*)—

**Ephemera danica** Müll.

Common and abundant in lakes and rivers, generally in a sandy or gravelly bottom.

Lake District: lakes and a few streams.

- Three dark lines on abdominal terga 7, 8 and 9 (fig. 2*c*). Femora broader (fig. 2*f*)—

**Ephemera lineata** Etn.

Rare. R. Wye and R. Thames.

\* The words 'common' ('rare') are used here to mean 'present in many (few) places', either generally or in the locality mentioned; 'abundant' ('scarce') mean 'present in large (small) numbers'.

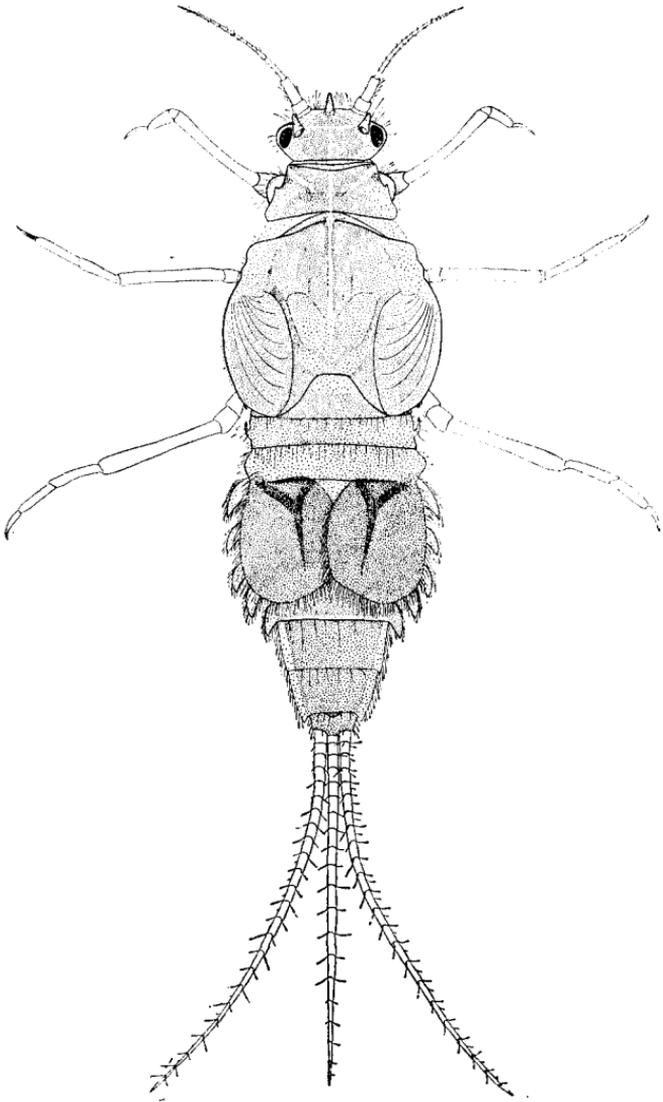


Fig. 3. *Brachycercus harrisella*. Length from head to tip of abdomen 8.5 mm, to ends of cerci 14 mm.

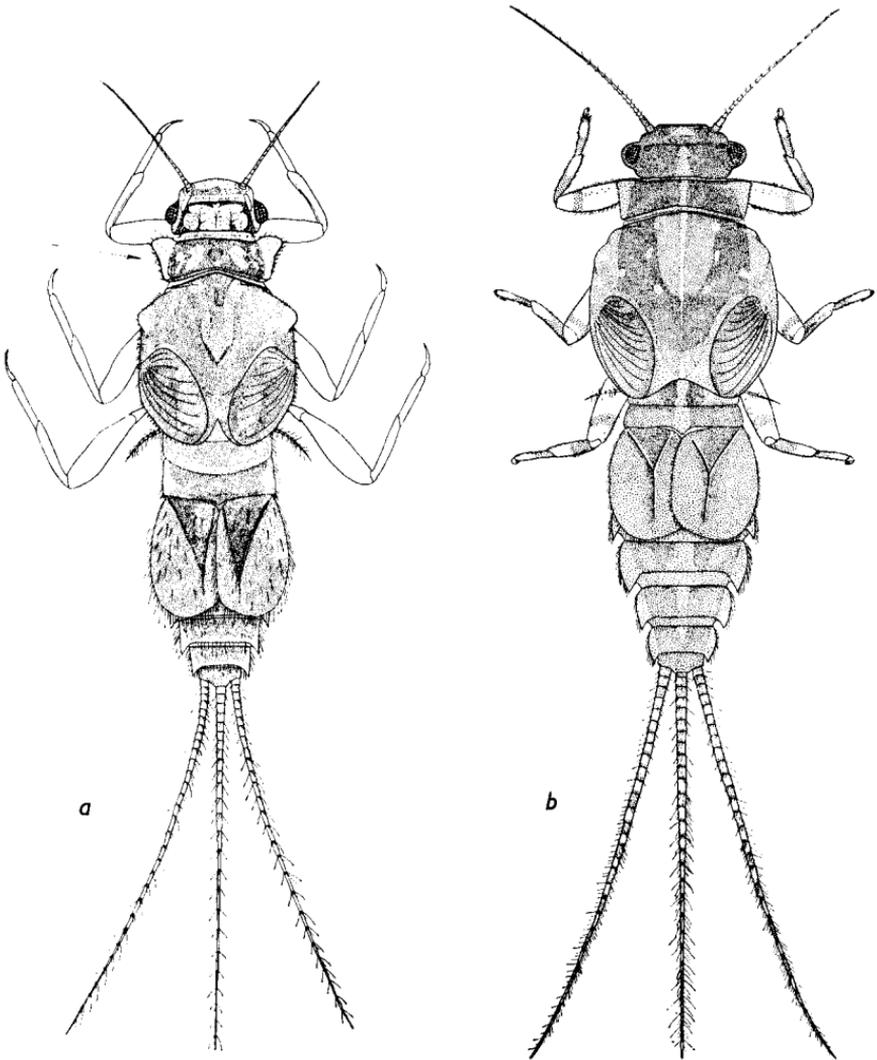


Fig. 4. *a*, *Caenis horaria*, 10 mm long including cerci; *b*, *C. robusta*, 15 mm long including cerci.

5 (1)\* Crawling nymphs living in the surface of the mud. First pair of gills reduced to tapering filaments; second pair forming a large flap which covers the rest (figs. 3-7). The body is usually covered with small particles of debris—

CAENIDAE 6

(Macan 1955)

\*Where a couplet is not reached directly from the preceding couplet, the number the couplet from which the direction came is indicated thus in parentheses.

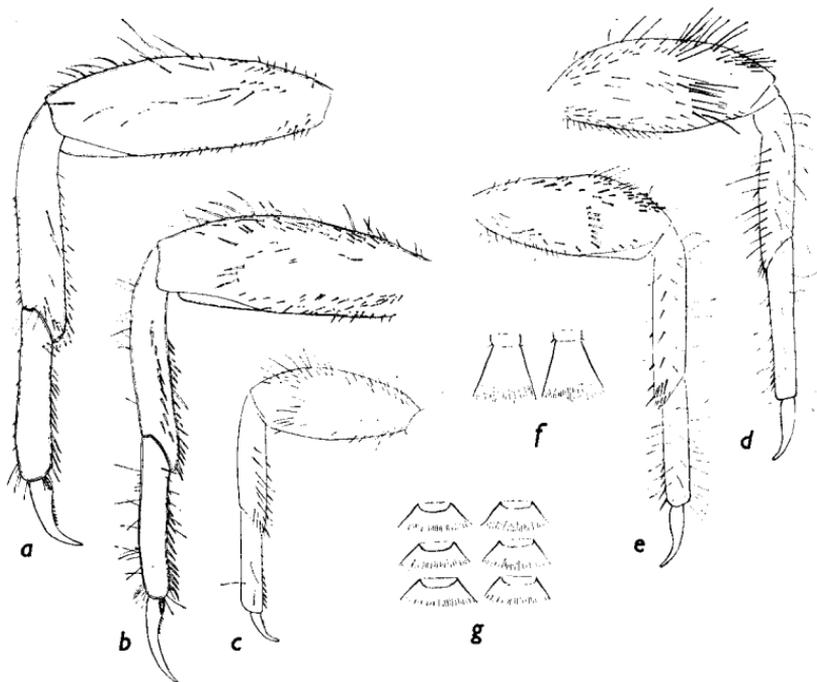


Fig. 5. *Caenis*. Front legs of: *a*, *C. robusta* (femur 1.1 mm long); *b*, *C. horaria*; *c*, *C. rivulorum* (femur 0.45 mm); *d*, *C. macrura*; *e*, *C. moesta* (femur 0.75 mm). Free-hand sketches of the cockade-like scales on the wing covers of: *f*, *C. moesta*; *g*, *C. horaria*. A scale of *C. moesta* is a little over 0.01 mm long.

— Crawling or swimming nymphs not living in the surface layers of the mud. More than two pairs of gills visible— **II**

- 6 Three protuberances on the head. Curved backwardly-directed processes on the sides of the abdominal segments 3-7 (fig. 3)—  
**Brachycercus harrisella** Curt.

R. Don, Aberdeenshire, July 1955, abundant in banks of silt.  
R. Clyde, Lanarkshire, Hyndford Bridge, July 1954, scarce in rock-pools floored with silt; the pools were isolated except in times of flood. R. Wye, Herefordshire, 1958. Old records from Berkshire, and London.

— Without either of these characteristics—

- 7 Sides of pronotum flaring outwards as they approach the anterior margin (fig. 4a  $\nearrow$ , b). More than one row of cockade-like scales in the band that runs along the underside of the gill-covers, parallel with the outer and gradually converging to meet the distal margin (fig. 5g). Fore femora relatively narrow (fig. 5a, b)— 8

- Sides of pronotum straight or slightly curved, and curving inwards to front and hind margins (figs. 6, 7). One row of cockade-like scales in the band that runs along the underside of the gill covers (fig. 5f). Fore femora relatively broad (fig. 5c, d, e)— 9

- 8 Side of pronotum beginning to flare outwards near the middle, and the fore margin curving down to meet it at the widest point (fig. 4a). No central light line on head, prothorax and mesonotum, nor dots on the last. Full-grown nymphs up to 6 mm long from front of head to tip of abdomen. A transverse row of spines towards the tip of the fore femora (fig. 5b). Two to four cockade-like scales in the band that runs along the underside of the gill covers (fig. 5g). Claws slender and slightly curved (fig. 5b)— **Caenis horaria** (L.)

In soft mud in still and flowing water.

Lake District: in lakes and tarns.

- Side of pronotum beginning to flare outwards only near the fore margin; the widest part of the pronotum at the level of the fore margin, which is straight (fig. 4b). A central light line running from the top of the head across the pronotum to the fore part of the mesonotum; light dots on the mesonotum (fig. 4b). Full-grown nymphs up to 9 mm long. No transverse row of spines on the femora (fig. 5a). Six to eight cockade-like scales. Claws more robust and abruptly bent (fig. 5a)—

**Caenis robusta** Etn.

Wheatfen Broad, and the nearby Scoulton Mere, Norfolk, 1951. Crampsmoor, Romsey, Hampshire, 1958. Pond near Reading, Berkshire, 1959. Canal, Shropshire, 1960.

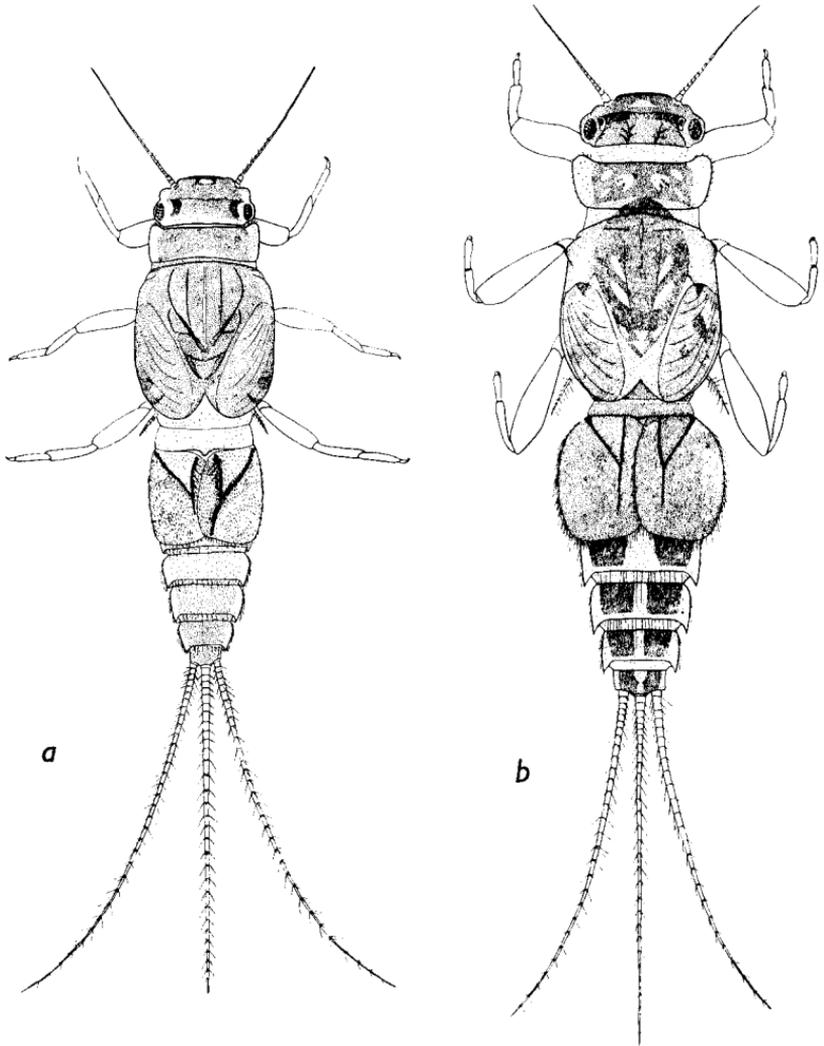


Fig. 6. *Caenis*. a, *C. rivulorum*, 5.5 mm long including cerci; b, *C. moesta*, 8.0 mm long including cerci.

- 9 (7) A small species (up to 4.5 mm long) with a characteristic pied appearance, the abdominal segments immediately before and behind the gill covers being light, and the rest of the upper surface rather dark (fig. 6*a*). About three-quarters of the way from the base of the fore femur, a transverse row of spines running from near the lower margin (the leg being in the position depicted in fig. 5) to just beyond the mid-line; 3-6 long, pointed spines in this row (fig. 5*c*)—

**Caenis rivulorum** Etn.

On a stony substratum in streams and rivers.

Lake District: becks and rivers.

- Larger species (up to 6.5 mm long) without a conspicuous pattern. 6-11 spines in the row that runs transversely across the distal part of the fore femora (fig. 5*d, e*) (if only 6 or 7 spines they are short and truncate)— **10**

- 10 Pronotum broader in front than behind (fig. 6*b*). Spines running transversely across the fore femora broad, close together, in a straight line, and 6-8 in number (fig. 5*e*); 16-24 spines along the margin of the hind tarsus—

**Caenis moesta** Bengtss.

Generally on a substratum of gravel or of large stones with finer material between them, in rivers, lakes and ponds.

Lake District: tarns and lakes.

- Pronotum generally parallel-sided (fig. 7), but sometimes a little broader in front than behind. Spines running transversely across the fore femora longer, finer, further apart, in a less regular line, and 8-11 in number (fig. 5*d*); 8-14 spines on the hind tarsi— **Caenis macrura** Steph.

On the same sort of substratum as *C. moesta* but so far found only in rivers.

Lake District: not recorded.

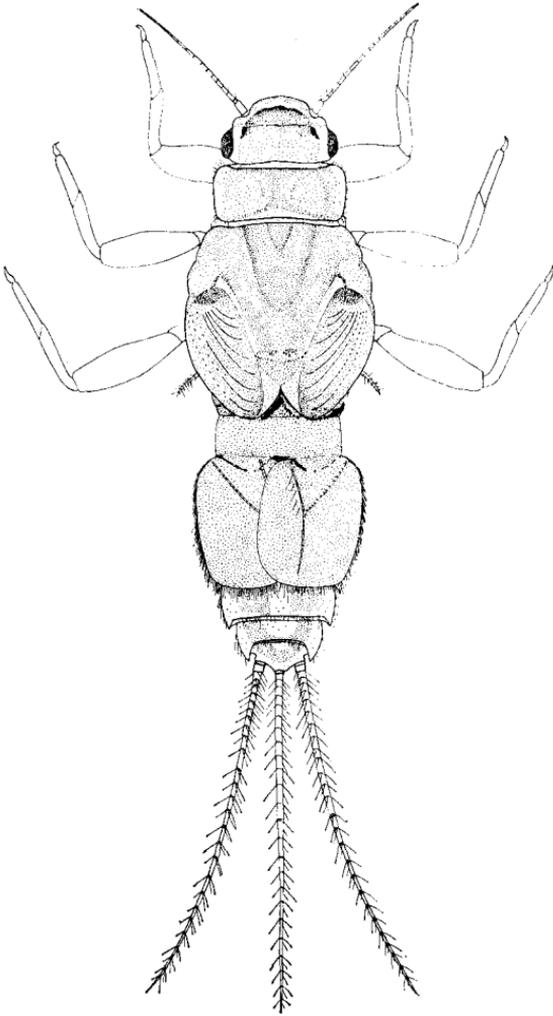


Fig. 7. *Caenis macrura*, 7 mm long including cerci.

- 11 (5) Crawling nymphs found in vegetation and on stones. Apparently 4 pairs of gills (the 5th pair is small and hidden beneath the 4th); gills on the back, so that if the nymph is looked at from above, the gills do not project beyond the sides of the body; each gill consisting of two parts, the upper a plate, the lower two divergent arms covered with imbricating lamellae. (Tails with short scattered bristles). (Fig. 8)—

EPHEMERELLIDAE 12  
(Kimmins & Frost 1943)

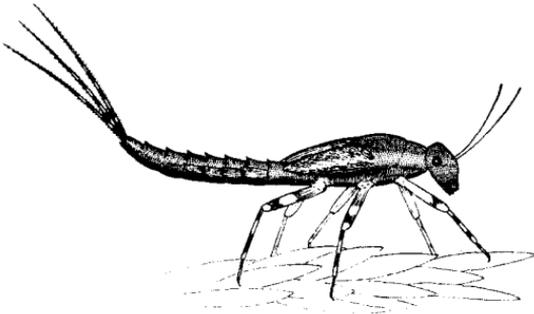


Fig. 8. *Ephemera ignita*, 9 mm long, from life.

- Nymphs that can swim or are adapted to cling to the surface of stones. Seven gills attached to the sides are a conspicuous feature of an outline of the nymph seen from above; gills of other form—

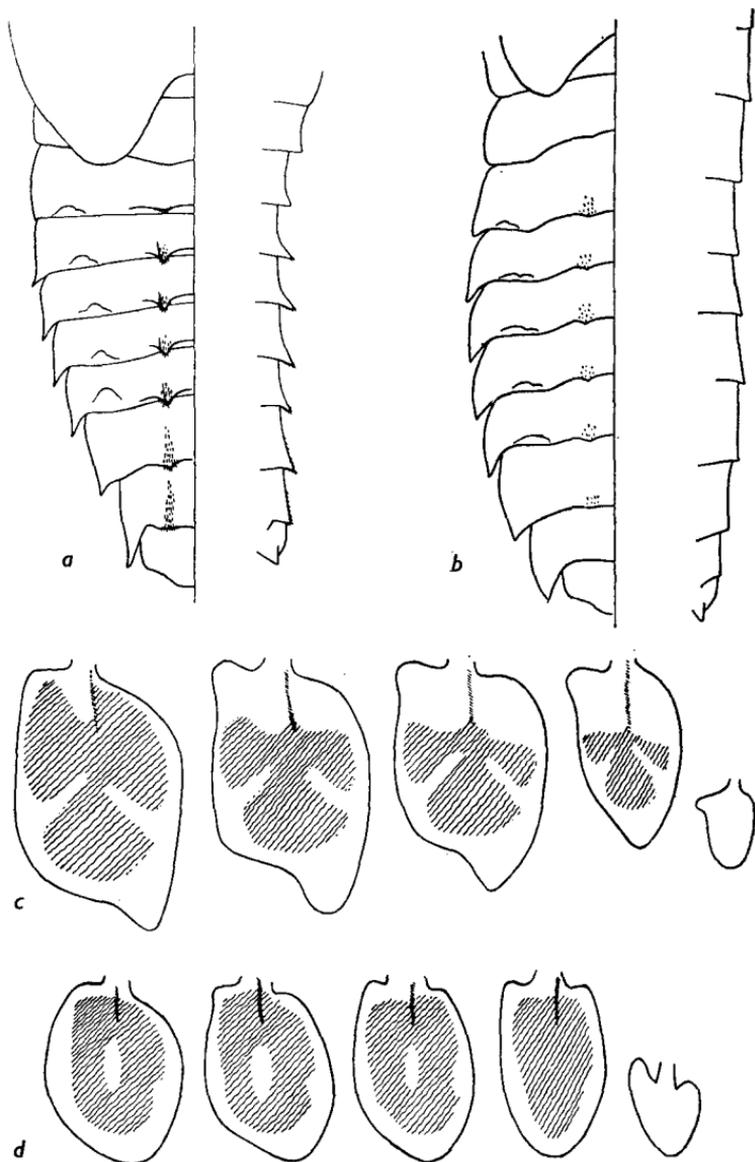


Fig. 9. *Ephemerella*. Above: dorsal view and lateral profile of the abdominal tergites of: a, *E. ignita*; b, *E. notata*.

Below: gill lamellae of abdominal segments 3 (left) to 7 of: c, *E. ignita*; d, *E. notata*.

(After Kimmins & Frost 1943.)

- 12 Tails with alternating light and dark bands. Posterior margins of abdominal terga with two distinct tubercles, one on either side of the mid-line (fig. 9a). The first three gills with the posterior margin produced on the inner side, and marked with a darker area shaped somewhat like a clover leaf (fig. 9c)—

**Ephemerella ignita** (Poda)

Abundant in rivers where the vegetation is thick, but extending to more torrential reaches, where it shelters among stones.

Lake District: in small stony streams, in rivers, and occasionally in lakes.

- Tails uniformly pigmented. Dorsal tubercles inconspicuous (fig. 9b). Gills of a somewhat uniform oval shape; the darker area the same shape as the gill (fig. 9d)—

**Ephemerella notata** Etn.

Moderately fast rivers.

Lake District: not recorded.

- 13 (11) Nymphs that cling to stones and boulders, over the surface of which they can move with great speed. Body, particularly the head and the innermost segments of the legs, flattened. Gills consisting of a plate and a bunch of filaments (except in *Arthroplea* which is distinguished immediately by its unique labial palp) (fig. 12)—

ECDYONURIDAE 14

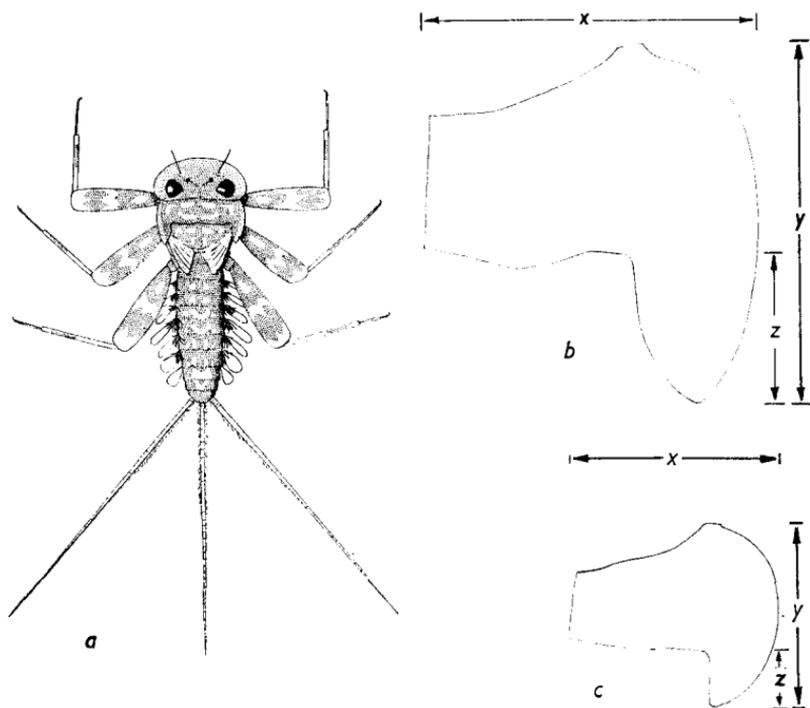


Fig. 10. *Ecdyonurus*. *a*, *E. venosus*, 11 mm long, from life; *b*, *c*, right half of the prothorax of: *b*, *E. venosus*; *c*, *E. dispar*. *x*, breadth; *y*, length; *z*, length of posterior prolongation.

— Nymphs that swim. Body long and more or less round in section. Gills never consisting of a plate and a bunch of filaments—

- 14 Basal segment of labial palp broad and nearly three times the length of the lacinia; the distal segment much thinner, nearly three times the length of the basal one, and bearing long fine hairs almost the whole way along its length—  
**Arthroplea congener** Bengtss.

One adult taken at Stanmore, Middlesex, in 1920.

- Basal segment of labial palp never much longer or shorter than the lacinia; distal segment, or middle segment plus small apical segment, never more than twice as long as the basal one, nor much thinner than it— **15**

- 15 Pronotum projecting backwards on either side of the mesonotum (fig. 10) (These projections are not present on very small nymphs.)— **ECDYONURUS 16**  
(Macan 1949a)

- Hind margin of pronotum without backward projections (fig. 11*b*)— **HEPTAGENIA or RHITHROGENA 19**  
(Macan 1958b)

- 16 All seven gills comprising a plate and a tuft of filaments—  
**Ecdyonurus insignis** (Etn.)

Rather large fast streams and rivers, possibly with a preference for calcareous waters.

Lake District: not recorded.

- Last gill without a bunch of filaments— **17**

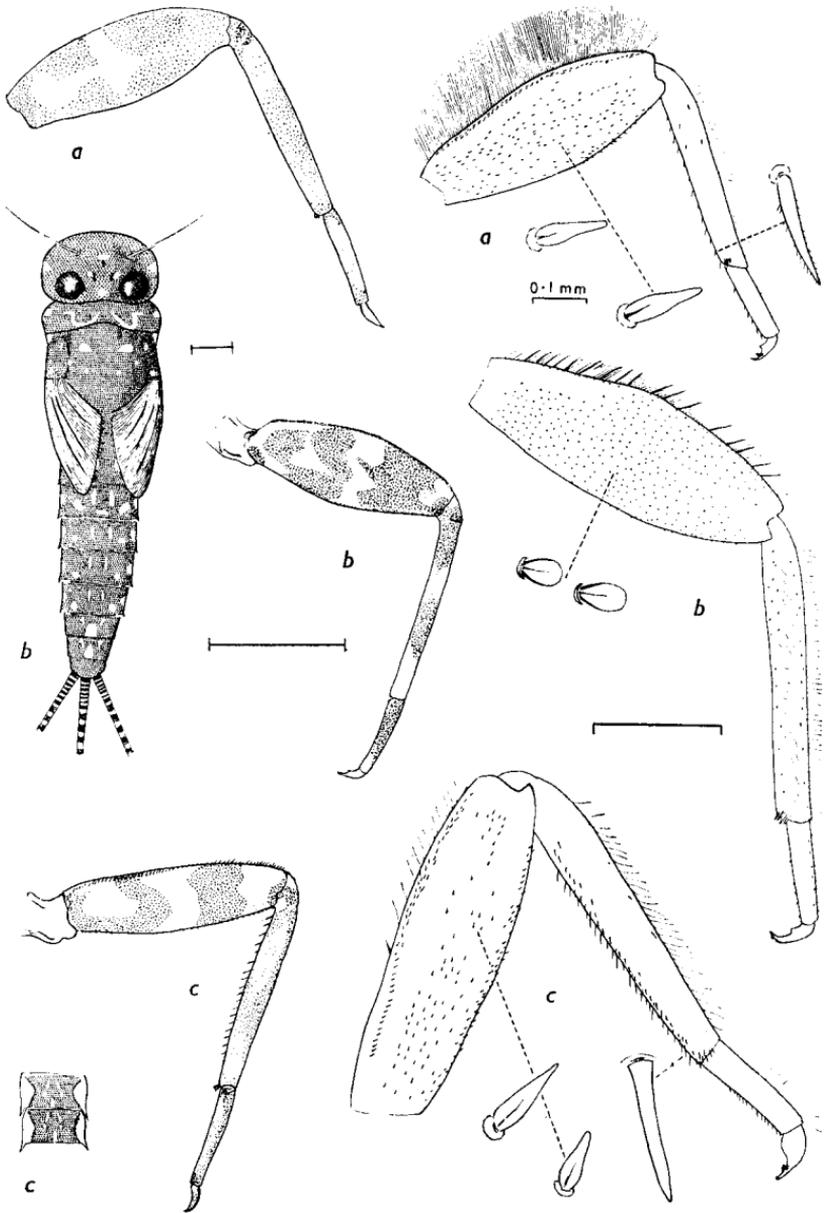


Fig. 11. *Heptagenia*. Body and leg markings, and details of middle legs of: a, *H. lateralis*; b, *H. sulphurea*; c, *H. fuscogrisea*. (Scale lines 1 mm; spines 0.1 mm)

- 17 Sides of prothorax rounded (fig. 10c). Half the breadth of the thorax generally exceeding the length (*i.e.*  $x$  is longer than  $y$  in fig. 10c). Projection of prothorax generally amounting to less than one-third of the total length (*i.e.* in fig. 10c,  $z$  is less than  $\frac{1}{3}y$ ). First gill at least three-quarters the length of the longest gill—  
**Ecdyonurus dispar** (Curt.)

Stony rivers and lake shores.

Lake District: common and abundant.

- Sides of prothorax straighter (fig. 10b). Half the breadth of the prothorax not exceeding the length ( $x$  in fig. 10b generally about the same as or less than  $y$ ) and  $z$  generally greater than  $\frac{1}{3}y$ . First gill less than three-quarters the length of the longest gill—  
**18**

- 18 Tarsi dark at base and apex. Claws of all legs usually with at least three teeth—  
**Ecdyonurus torrentis** Kimmins

Small stony streams.

Lake District: fairly common, though not often abundant, in becks.

- Tarsi dark at apex only. Rarely three teeth on the claws of all legs—  
**Ecdyonurus venosus** (Fabr.)

Stony rivers and streams.

Lake District: fairly common in the rivers and found also in some of the larger becks.

- 19 (15) First gill very large and meeting its fellow beneath the body. A dark dot in the centre of each femur—

**Rhithrogena semicolorata** (Curt.)  
or **R. haarupi** Esb.-Pet.

The nymphs of these two species are not distinguishable. *R. haarupi* is recorded only from a small number of large rivers, none in the Lake District.

*R. semicolorata*, stony streams and rivers.

Lake District: common and abundant in small becks and occurs also in rivers.

- First gill small and like the others in shape (fig. 12). Femora without a dark dot—  
**20**

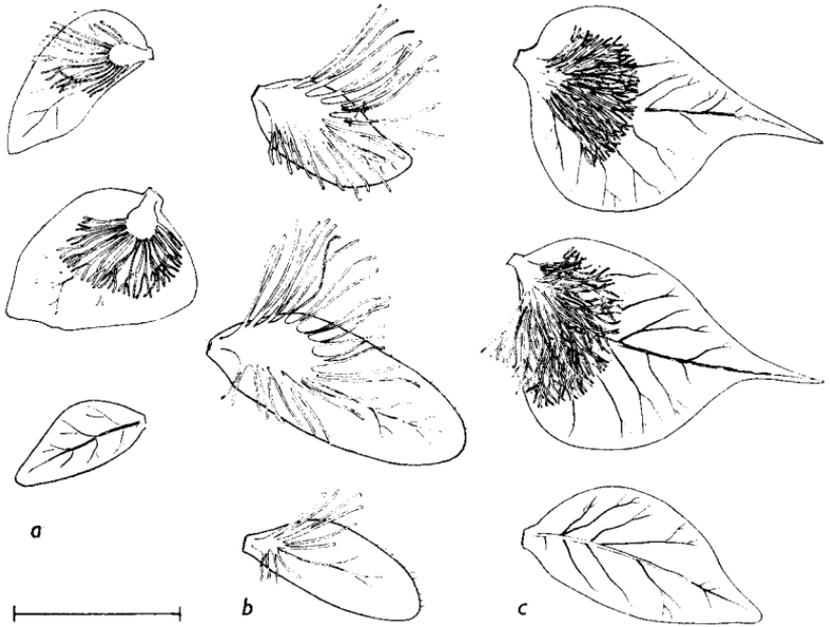


Fig. 12. *Heptagenia*. First (top), fourth and seventh gills of: *a*, *H. lateralis*; *b*, *H. sulphurea*; *c*, *H. fuscogrisea*.  
(Scale line 1 mm)

- 20 Filamentous part of the gill as large as the lamella—  
**Heptagenia longicauda** (Steph.)  
 Berkshire 1868, Middlesex 1904, Surrey 1933.
- Filamentous part of the gill smaller than the lamella— **21**
- 21 Rather little or no pattern on body and tails; a light cross-shaped area on the femora separating four dark areas which are often darker in the middle, so that four lines, each parallel with the margin, are apparent (fig. 11*a*). Upper margin of femur fringed with hairs which, if folded back, would extend more than half-way across the femur (fig. 11*a*). Gills narrowing gradually to a rather blunt point (the seventh without a tuft of filaments) (fig. 12*a*)— **Heptagenia lateralis** (Curt.)  
 Stony streams and lake shores.  
 Lake District: common and sometimes abundant in becks and on lake shores.
- Black-and-white nymphs with conspicuous pattern (fig. 11*b, c*); femora with transverse bars (fig. 11*b, c*). Hairs along upper margin of femur much shorter (fig. 11*b, c*). Gills either rounded or sharply pointed (fig. 12*b, c*)— **22**
- 22 Gills rather small and rounded at tip, the last with a tuft of filaments (fig. 12*b*). Femora with black transverse bands (fig. 11*b*); upper margin closely beset with short hairs and spines (fig. 11*b*)— **Heptagenia sulphurea** (Müll.)  
 In rivers in stony reaches, but extending further into slow stretches than any other eddyonurid; on stony lake shores. In Ireland it is abundant in the limestone lakes, whereas *H. lateralis* occurs in the non-calcareous lakes.  
 Lake District: common in some rivers.
- Gills large, produced into a point, the last without a tuft of filaments (fig. 12*c*). Femora with two reddish-brown bands (fig. 11*c*); upper margin with a few short hairs along the distal part (fig. 11*c*)— **Heptagenia fuscogrisea** (Retz.)  
 In Ireland it is common in the limestone lakes. In England it has been found recently in the Kennet and Avon canal near Reading.  
 Lake District: not recorded.

- 23 (13) Swimming laboured. Tails as long as or longer than the body, and with short sparse hairs on both sides. Gills as in fig. 13. (Nymphs usually dark reddish brown)—

## LEPTOPHLEBIIDAE 24

(Macan 1952)

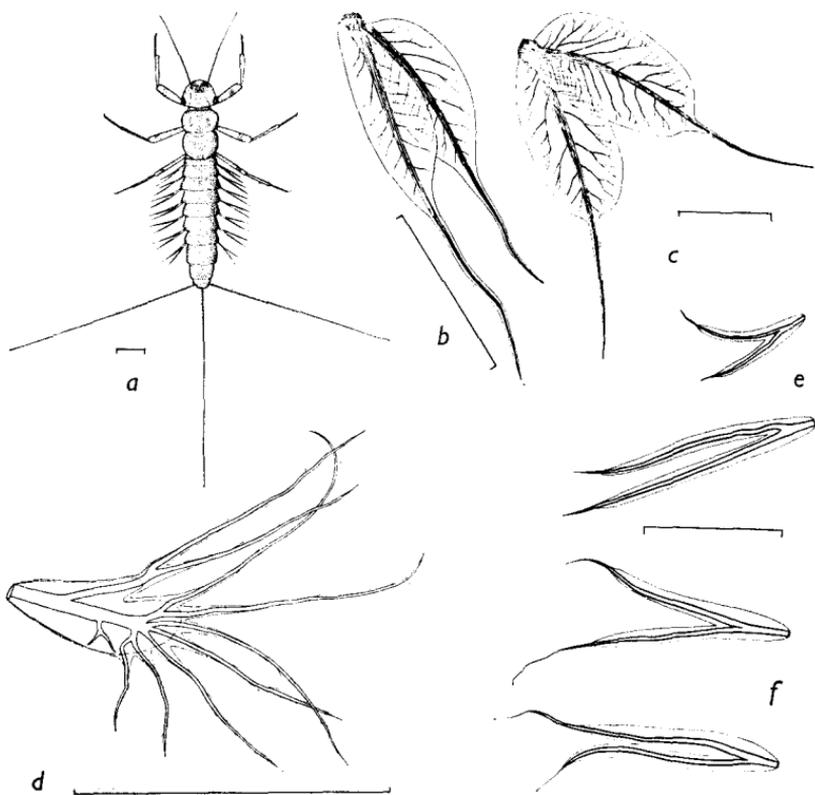


Fig. 13. Leptophlebiidae. *a*, *Paraleptophlebia submarginata*, 8 mm long, from life. *b-d*, fourth gills of: *b*, *Leptophlebia vespertina*; *c*, *L. marginata*; *d*, *Habrophlebia fusca*. *e, f*, first and second gills of: *e*, *Paraleptophlebia submarginata*; *f*, *P. tumida*. (Scale lines 1 mm)

- Swimming quick. Tails never as long as the body, with longer, more close-set, hairs on both sides of the middle one but only on the inside of the outer two. Gills shaped like the head of a tennis racket, a beech leaf, or a conventional heart; each gill consisting of a single plate or some, never more than 6, may consist of two plates—

- 24 Gills with several branches (fig. 13*d*)—  
**Habrophlebia fusca** (Curt.)

Often abundant in slow streams with vegetation or dead leaves, sometimes in rivers.

Lake District: Hog House Beck, Nor Moss Beck, Ford Wood Beck; generally rare and scarce.

- Gills with two branches (fig. 13*b, c, e, f*)— **25**

- 25 Gills (except the first) expanded at the base (fig. 13*b, c*)—  
**LEPTOPHLEBIA 26**

- Gills straight-sided (fig. 13*e, f*)— **PARALEPTOPHLEBIA 27**

- 26 Compound spines on the underside of the fore femora (fig. 15*a*).  
 Teeth extending about five-sixths of the way along the claw  
 (fig. 14*g*). Blade of gills tapering and merging gently into the  
 filament (fig. 13*b*)— **Leptophlebia vespertina** (L.)

Ponds, lakes and slowly flowing water, especially in districts poor in lime.

Lake District: common and abundant in tarns and lakes, and also found in slow parts of becks.

- Finely frayed spines, appearing simple except under high magnification, on the underside of the fore femora (fig. 15*b*).  
 Teeth extending about three-quarters of the way along the claw  
 (fig. 14*d*). Blade of gills strongly rounded, meeting the filament abruptly (fig. 13*c*) (only in full-grown specimens)—  
**Leptophlebia marginata** (L.)

Generally found with *L. vespertina*, but in smaller numbers; emerges earlier.

Lake District: in similar places to *L. vespertina*.

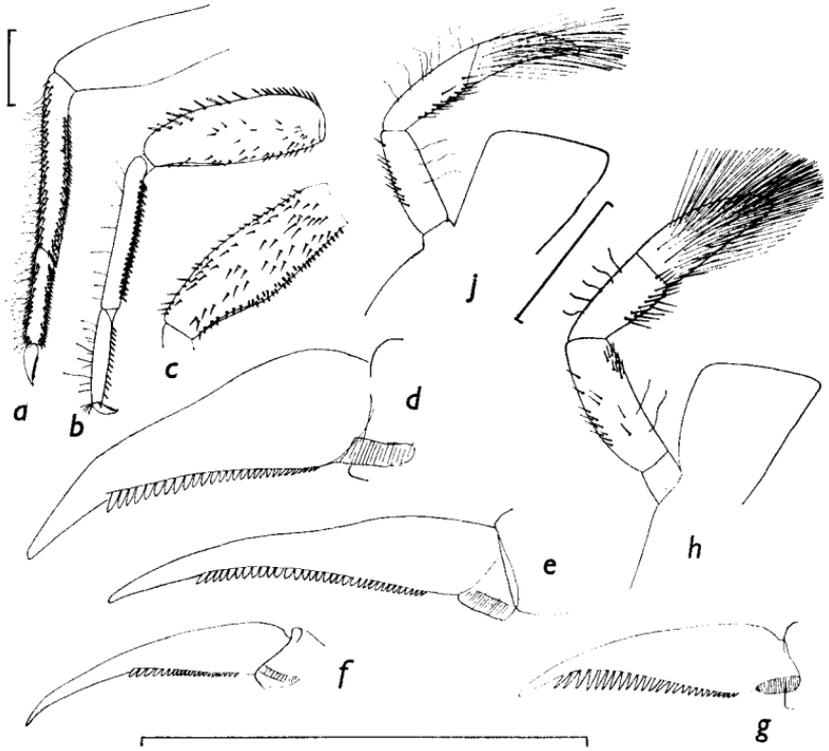


Fig. 14. Leptophlebiidae. *a*, hind leg of *Leptophlebia marginata* showing spines on tibia and tarsus; *b*, fore leg of *Habrophlebia fusca*; *c*, fore femur of *Leptophlebia vespertina*; *d-g*, hind claws of: *d*, *Leptophlebia marginata*; *e*, *Paraleptophlebia tumida*; *f*, *P. cincta*; *g*, *Leptophlebia vespertina*; *h, j*, maxillary palp and outline of maxilla of: *h*, *Paraleptophlebia submarginata*; *j*, *P. cincta*. (Scale lines 0.5 mm)

- 27 (25) First gill distinctly smaller than all the rest (fig. 13*e*). Spines on underside of hind femora parallel-sided and blunt at the tip, many of them short (fig. 15*d*). Maxillary palps large, the last segment densely covered with long fine hairs (fig. 14*h*)—  
**Paraleptophlebia submarginata** (Steph.)

In slowly flowing water.

Lake District: rare and scarce in becks, except in a few where the current is quite slow.

- First gill only slightly, if at all, smaller than the others (fig. 13f). Spines on underside of hind femora tapering (fig. 15c, e). Maxillary palps smaller, the last segment less densely covered with long fine hairs (fig. 14j)— 28

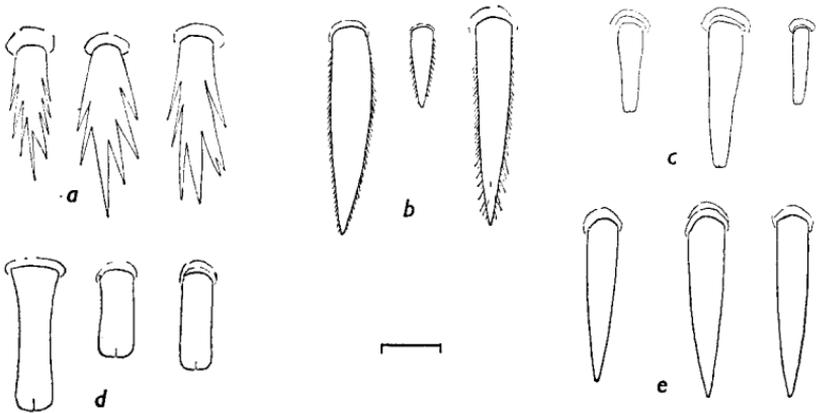


Fig. 15. Leptophlebiidae. *a, b*, spines from the underside of the fore femur of: *a*, *Leptophlebia vespertina*; *b*, *L. marginata*. *c-e*, spines from the underside of the hind femur of: *c*, *Paraleptophlebia cincta*; *d*, *P. submarginata*; *e*, *P. tumida*. (Scale line 0.01 mm)

- 28 Spines on underside of hind femora pointed, rather few of them short (fig. 15e). Teeth extending nearly three-quarters of the way along the claw (fig. 14e)—

***Paraleptophlebia tumida* Bengtss.**

In heavily weeded streams that cease to flow in summer; recorded only from streams in Hampshire, Wiltshire and Cambridgeshire.

- Spines on underside of hind femora tapering but blunt at the tip, some short (fig. 15c). Teeth not extending far beyond the middle of the claw (fig. 14f)—

***Paraleptophlebia cincta* (Retz.)**

In rivers, rather rare and scarce.

Lake District: not recorded.

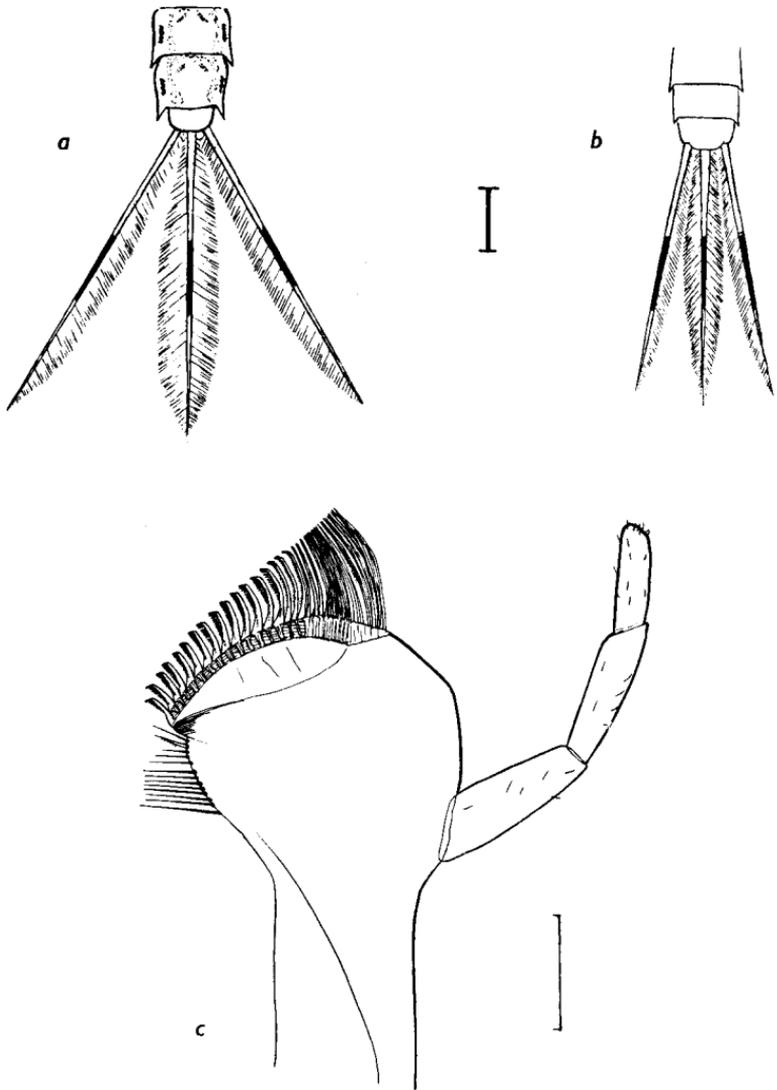


Fig. 16. Siphonuridae. *a*, hind end of *Siphonurus lacustris* from life; *b*, hind end of *Ameletus inopinatus* from life; *c*, maxilla of *A. inopinatus*.

(Scale lines: *a*, *b*, 1 mm; *c*, 0.2 mm)

- 29 (23) Hind corners of the last few abdominal segments drawn out into spines (fig. 16). (Tails with a black band but no dark rings [fig. 16])—

SIPHILONURIDAE 30

(Macan 1951)

- Hind corners of last few abdominal segments not drawn out into spines—

BAËTIDAE 33

The spines are clearly marked in *Siphlonurus*, and there should be no difficulty in distinguishing this genus, but less clear in *Ameletus*, which can at first be mistaken for a *Baëtis*. Its three tails of equal length (fig. 16*b*) distinguish it at once from this genus, and there are also differences in the mouthparts; for example the maxillae bear comb-bridles (fig. 16*c*) which are found also in the Ecdyonuridae but not in the Baëtidae. *Siphlonurus* is superficially like *Cloëon*; additional points of difference are the banding of the tails in the latter (fig. 21*b, c*) and the shape of the mouth parts (*e.g. cf.* figs. 17 and 18).

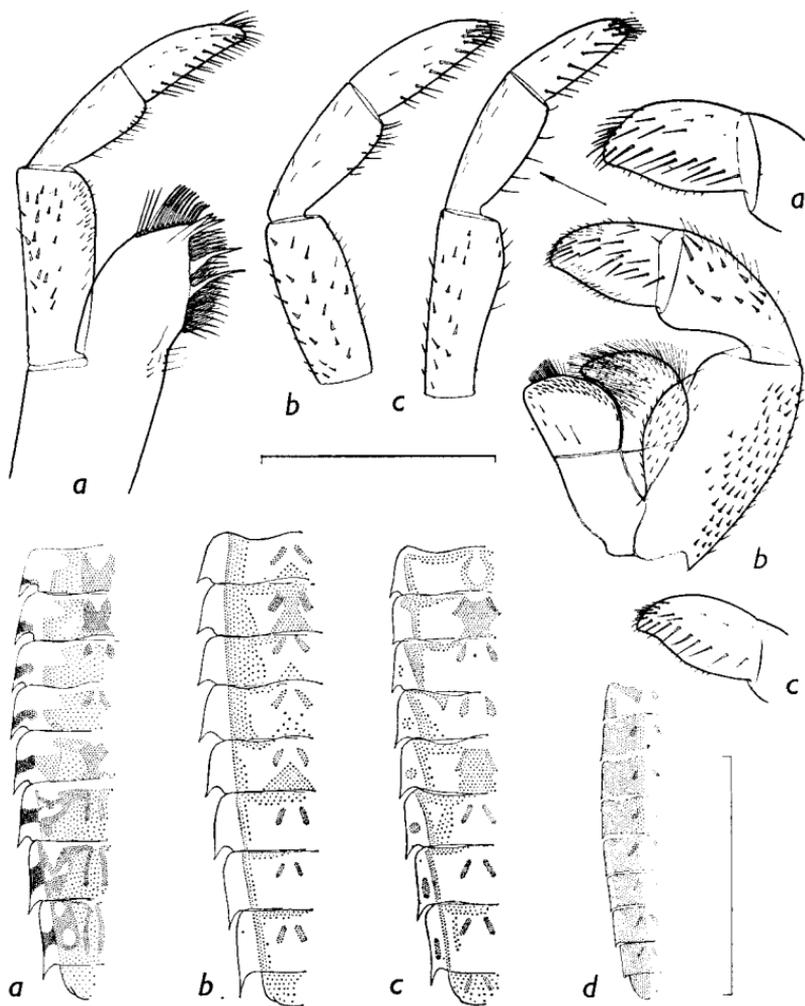


Fig. 17. Siphonuridae. Left, maxilla and maxillary palps; right, labium and labial palps; below, markings on the abdominal tergites. *a*, *Siphonurus linneanus*; *b*, *S. armatus*; *c*, *S. lacustris*; *d*, *Ameletus inopinatus*.

(Scale lines — above 0.5 mm; below 5 mm)

- 30 All gills simple. Tails held close together in life (fig. 16*b*). Up to 11 mm long—  
**Ameletus inopinatus** Etn.

Generally a stream species confined to high altitudes, but recorded in some numbers from several lochs in the extreme north-west of Scotland.

Lake District: common and often abundant in becks above 1000 ft.

- Some gills with two lamellae. Tails held further apart in life (fig. 16*a*). Up to 18 mm long— 31

- 31 First six gills with two lamellae. A dark band running transversely from the central pigmented area right to the margin of each abdominal segment (fig. 17*a*)—

**Siphonurus linneanus** (Etn).

- First two gills with two lamellae. The flat margins of the abdominal segments either unmarked or with dots, but not with bands (fig. 17*b, c*)— 32

- 32 Inner margin of middle segment of maxillary palp with 4 to 7 bristles in a single row (17*c*′). The large bristles on the last segment of the labial palp lie in a regular line between the base and a group of similar bristles towards the apex (fig. 17*c*). An isolated round or oval dark mark on the flat margin of abdominal segments 8 and 9 at least, and usually on 2-9 (fig. 17*c*)—

**Siphonurus lacustris** Etn.

- Inner margin of middle segment of maxillary palp with 8 to 12 bristles in two rows (fig. 17*b*). Bristles on last segment of labial palp not in a regular row (fig. 17*b*). Flat margins of abdominal segments uniformly pale except numbers 8 and 9 which may have an elongate dark mark (fig. 17*b*)—

**Siphonurus armatus** Etn.

All species of *Siphonurus* have an inexplicably sporadic distribution. *S. lacustris*, the only one recorded from the Lake District, occurs in tarns at high altitudes, in slow reaches of becks, particularly high up, and of rivers, and in lakes. Elsewhere it is not common. The other two are possibly typical of calcareous conditions and occur in slow-flowing and still water. *S. linneanus*, though widespread, is rarely encountered, but seems undoubtedly to be commoner in Ireland than in any other country.

33 (29) All three tails of more or less the same length; marked with dark rings (fig. 19a) (which are easily distinguishable on specimens, though less so on drawings, from the rings due to the segmentation of the tails), and often a black band as well (figs. 19b, 21). If all the gills are simple, they are pointed at the tip (fig. 20d, e). Penultimate segment of labial palp not produced inwards at the distal corner (fig. 18a-e)—

CLOËON, PROCLOËON or CENTROPTILUM 34  
(Macan 1949b)

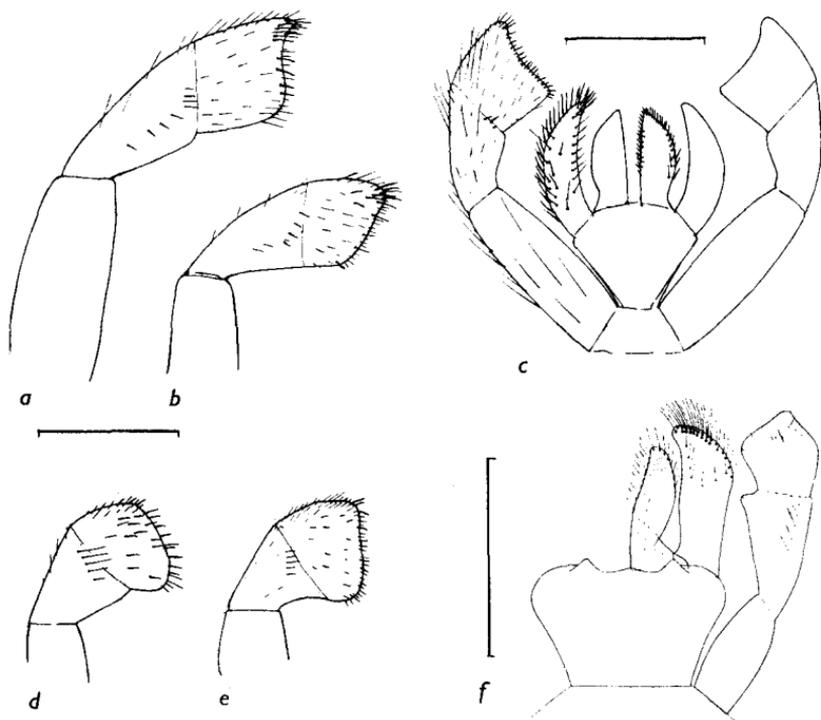


Fig. 18. Labium and labial palps of: a, *Cloëon dipterum*; b, *C. simile*; c, *Centroptilum luteolum*; d, *C. pennulatum*; e, *Procloëon pseudorufulum*; f, *Baëtis pumilus*.  
(Scale lines 0.25 mm)

— Middle tails shorter than the outer ones; tails with a black band, (figs. 25f, 26b) or without (figs. 25b, 26a) but never with dark rings. All gills simple and rounded at the tip (fig. 24g-j). Penultimate segment of labial palp produced inwards to form a lobe at the distal corner (fig. 18f)—

BAËTIS 38  
(Macan 1950, 1957a)

- 34 About seven distinct dark rings on the tails, but no dark band. All the gills single and shaped like a beech leaf (fig. 20*d*). Tip of labial palp with the end face somewhat hollow and the inner corner sharply angled (fig. 18*c*). A few small spines on the sides of abdominal segments 8 and 9 near the distal corners. (A small sandy-coloured species, usually with a clearly defined variegated pattern on the upper surface of the abdomen). Length 6-8 mm (fig. 19*a*)— **Centroptilum luteolum** (Müll.)

In rivers and streams, where the current is not fast, particularly on sandy patches and in weeds, and on fairly exposed lake shores.

Lake District: in a few becks, more common in rivers, and fairly abundant in some lakes.

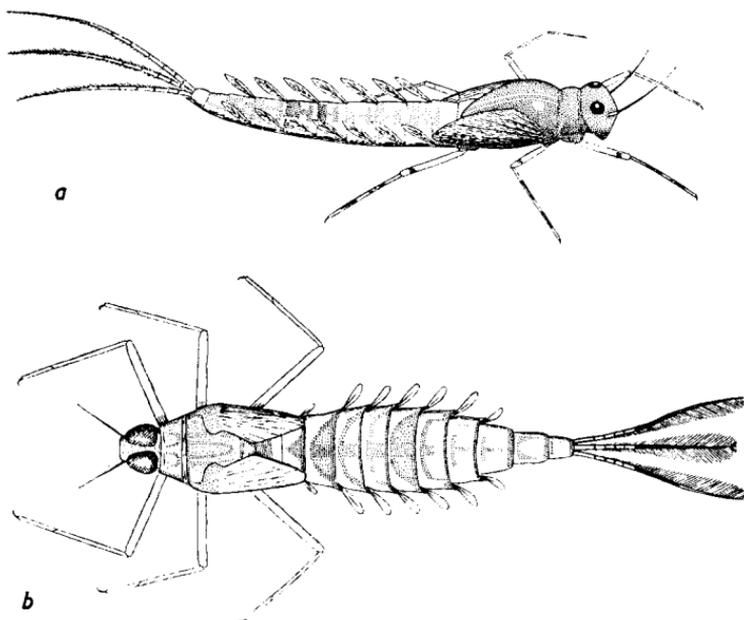


Fig. 19. *Centroptilum*. *a*, *C. luteolum*, 7 mm long, from life; *b*, *C. pennulatum*, 9 mm long, from life.

- Dark rings and a dark band on the tails. Gills of other shape, consisting of one or two plates (fig. 20). Tip of labial palp with the end face nearly flat or convex, and the inner corner rounded (fig. 18*a, b, d, e*). Sides of abdominal segments 8 and 9 with spines all the way along. Full-grown specimens larger— 35

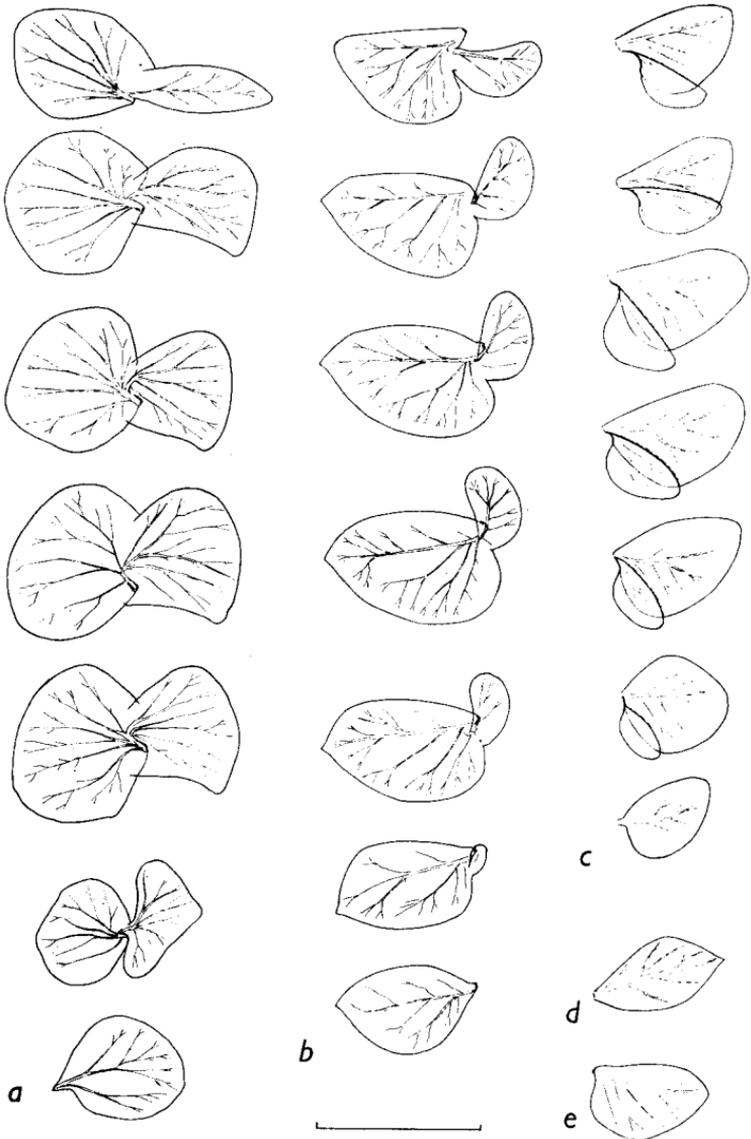


Fig. 20. Gills of: *a*, *Cloëon dipterum*; *b*, *C. simile*; *c*, *Centroptilum pennulatum*; *d*, third gill of *C. luteolum*; *e*, third gill of *Procloëon pseudorufulum*. (Scale line 1 mm)

- 35 About five dark rings on the tails between the dark band and the body. Sandy-coloured with a variegated pattern in which the contrast between dark and light is strong (fig. 19b). Four to six spines along the sides of abdominal segment 8, and 5-8 on segment 9; generally none on segment 7 and the more proximal ones. (First six gills double, with one plate much larger than the other, round at the tip, shaped rather like a royal-tennis racket (fig. 20c). Tails held close together in life). Length 8-10 mm (fig. 19b)— **Centroptilum pennulatum** Etn. In similar places to *C. luteolum*, but rarer and scarcer, and not recorded from still water.

Lake District: Hog House Beck, a slow stream floored with sand.

- More than five dark rings on the tails between the dark band and the body. Sandy-coloured, usually without strong contrast between light and dark areas of the pattern on the upper surface. Spines along the sides of abdominal segments 5-9 and sometimes on 4 as well—

36

- 36 All gills single (fig. 20e). In life the tails are held rather close together; hairs fringing them usually thick and extending to the tip; dark band on tails rather narrow and situated well beyond the middle; about 9 rings between it and the body. Four to seven spines along the side of abdominal segment 8 and 6-8 on segment 9. Terminal segment of labial palp bulging inwards (fig. 18e). Usually darker and with a more contrasting pattern, though the contrast is not as strong as in *Centroptilum* (fig. 21a)—

**Procloëon pseudorufulum** Kimmins

(Kimmins 1957)

In the same sort of places as *Centroptilum pennulatum*.

Laké District: R. Brathay, Hog House Beck.

- First six gills double (fig. 20a, b). In life the tails, seen from above, are held well apart (fig. 21c); in side view they are curved downwards in a characteristic way (fig. 21b); the hairs fringing the tails are not very obvious and do not extend to the tip, which gives the end a lash-like appearance (fig. 21c); dark band on tails broad, a little beyond the middle, about 12 dark rings between it and the body. 8-14 and 12-17 spines on abdominal segments 8 and 9 respectively. Terminal segment of labial palp not bulging inwards (fig. 18a, b). Usually light-coloured without a strongly contrasting pattern—

37

- 37 Gills round, the second lamellae relatively large (fig. 20a). Outer corner of last segment of labial palp produced into a point (fig. 18a). No hairs in the apical angle of the maxilla. Maxillary palp with three segments— **Cloëon dipterum** (L.)

Abundant in small rich ponds but also in lakes and the slowest parts of rivers.

Lake District: common in tarns but rarely abundant; occasionally in lakes.

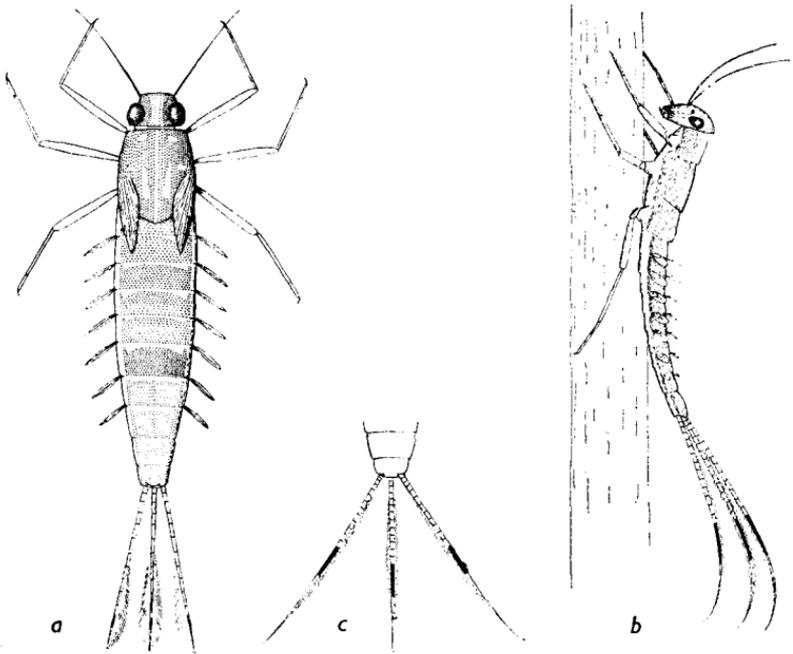


Fig. 21. *a*, *Procloën pseudorufulum*, 8 mm long, from life; *b*, *Cloëon dipterum*, 6 mm long (half grown), from life; *c*, hind end of *C. dipterum* in dorsal view, from life.

- Gills pointed, the second lamellae relatively small (fig. 20b). Outer corner of last segment of labial palp not produced into a point (fig. 18b). 5-7 hairs in the apical angle of the maxilla. Maxillary palp with two segments— **Cloëon simile** Etn.

Often with *C. dipterum*, but also in weed-beds in 2-3 metres of water in lakes and tarns.

Lake District: more abundant than *C. dipterum* in lakes and tarns.

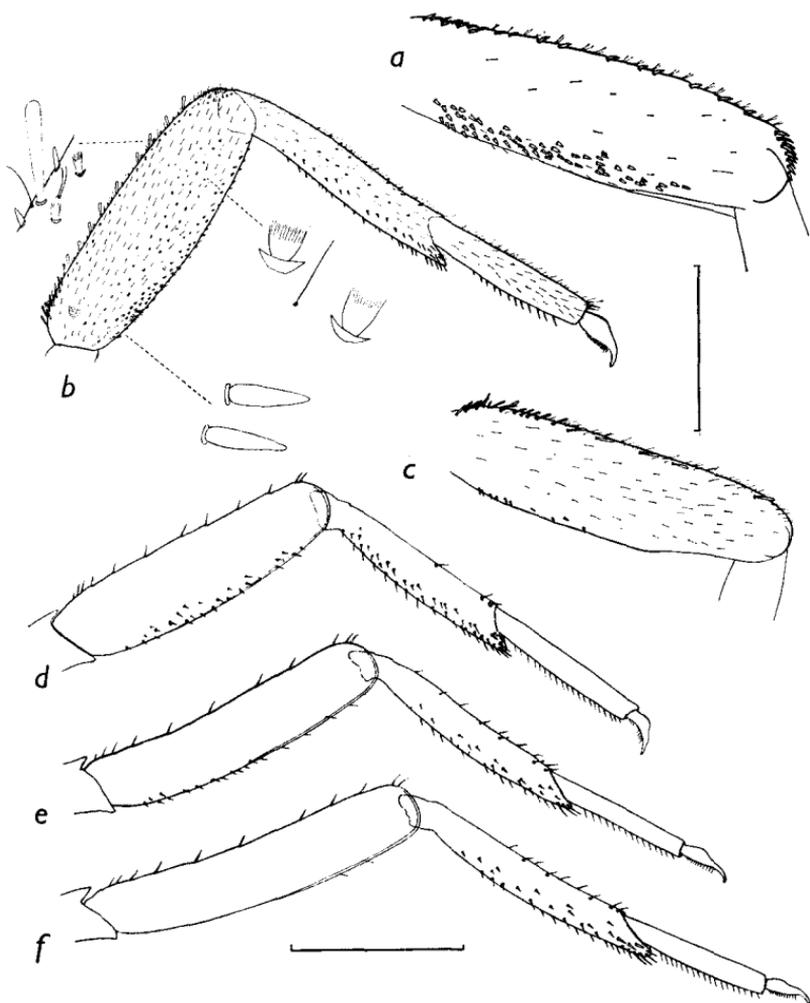


Fig. 22. *Baëtis*. a, c, femora of a, *B. atrebatinus*; c, *B. scambus*; b, leg of *B. buceratus* (the individual spines are drawn freehand not all to the same scale); d, e, f, fore, middle and hind legs respectively of *B. pumilus*.

(Scale lines 0.5 mm)

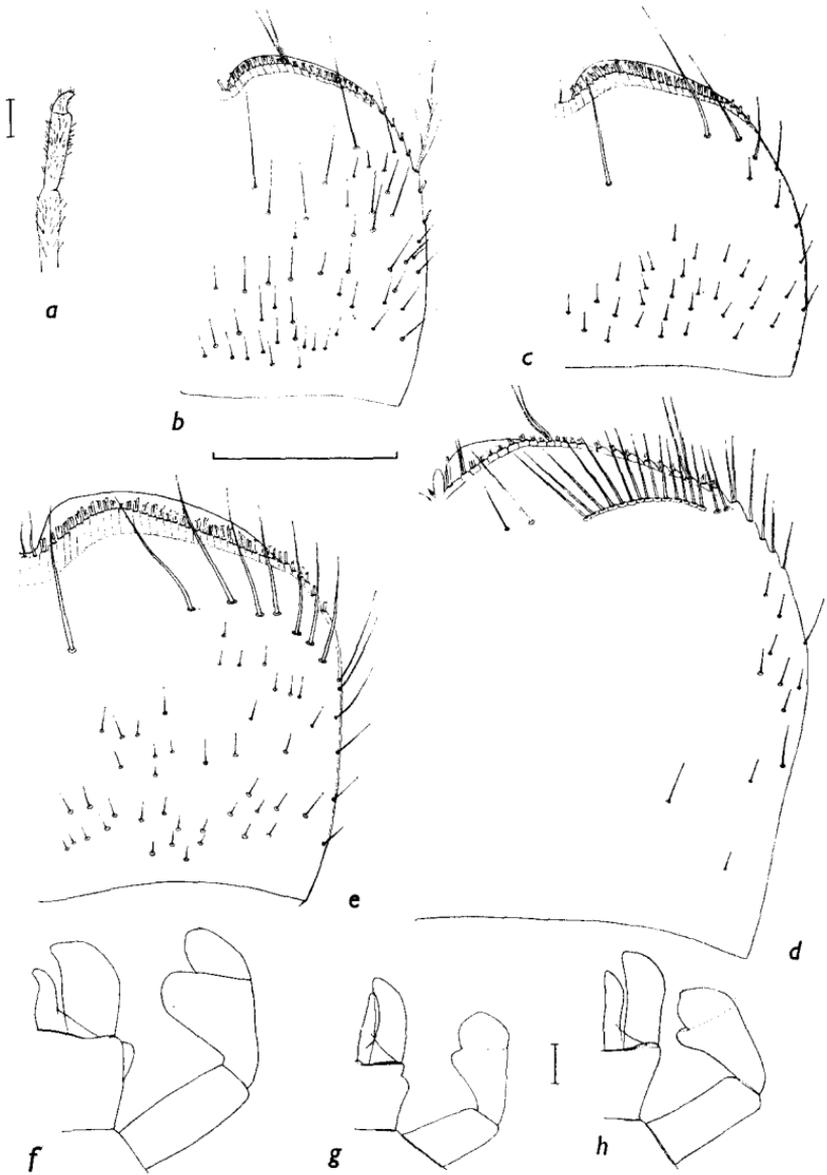


Fig. 23. *Baëtis*. a, maxillary palp of *B. atrebatinus*; b-e, labrum of b, *B. pumilus*; c, *B. scambus*; d, *B. atrebatinus*; e, *B. rhodani*; f-h, labium of f, *B. atrebatinus*; g, *B. rhodani*; h, *B. tenax*.

(Scale lines 0.1 mm)

38 (33) Spines along the top of the femora short and pointed; the number in a group at the distal end about the same as the number along the shaft (fig. 22*a*). Labrum with a close-set row of 15-20 long bristles just behind the anterior margin (fig. 23*d*); labium with a small glossa, a broad paraglossa and a wide penultimate joint to the palp (fig. 23*f*). About 20 teeth on the claws. Maxillary palp with a rounded projection at the tip of the penultimate segment, and the end segment somewhat hooked (fig. 23*a*). (A narrow brownish-red species which may have two or four dots near the centre of each abdominal tergum. Outermost tooth of mandibles set back (fig. 24*b* ♂). First gill smaller than all the rest)— **Baëtis atrebatinus** Etn.

Stony and weedy parts of calcareous streams and rivers; widely distributed in Ireland but rare and scarce in England.

Lake District: not recorded.

— Spines along the top of the femora, if pointed, longer, and always more numerous along the shaft than in the apical group. If there is a distinct line of long bristles behind anterior margin of the labrum, they are well spaced and no more than 10 in number (fig. 23*b*, *c*, *e*); labium of other shape. 10-16 teeth on the claws. Maxillary palp with a regularly rounded tip— 39

39 Spines along the top of the femora relatively long, tapering and pointed (fig. 22*d*, *e*, *f*); similar spines along the top of the tibiae. Mandible with outermost tooth pointed and set back (fig. 24*a*, *c*). Gills rather elongate with strongly denticulate margins (fig. 24*g*, *l*), the first smaller than all the rest. The body tapers only slightly from the thorax to the tip of the abdomen (fig. 26*a*) and, apart from light markings which may or may not be present along the middle line (fig. 25), is uniformly pigmented, and dark except in the early stages and at the beginning of each instar— 40

— Spines along the top of the femora, if pointed, more parallel-sided; no long spines along the top of the tibiae. Mandible with outer tooth broad, truncate and not set back (fig. 24*d*, *e*). Gills less elongate (fig. 24*h*, *j*), with less strongly denticulate margins (fig. 24*k*) and the first and last of about the same size. The body tapering more (fig. 26*b*) and, if uniformly pigmented, generally light— 41

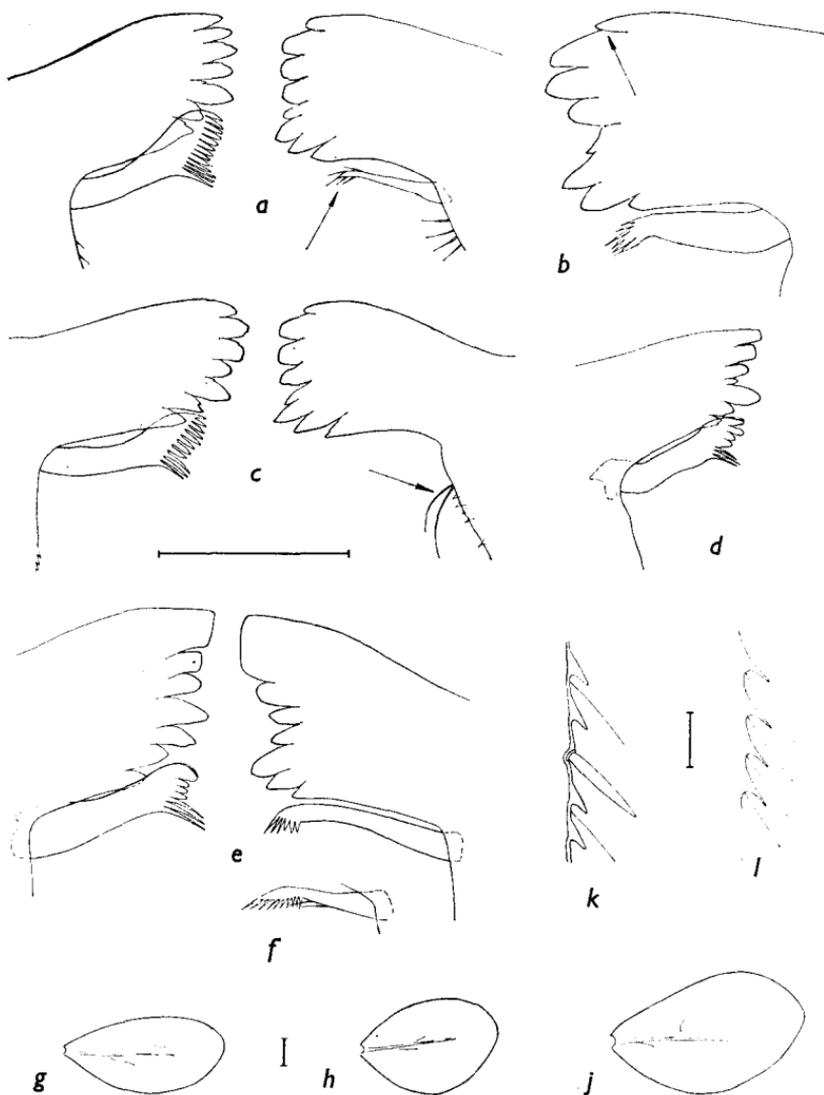


Fig. 24. *Baëtis*. a-e, canine area of the mandible of: a, *B. niger*; b, *B. atrebatinus*; c, *B. pumilus*; d, *B. scambus*; e, *B. rhodani*; f, right prosthema of *B. tenax*; g-j, third gill of: g, *B. pumilus*; h, *B. buceratus*; j, *B. vernus*; k, l, portion of gill margin of: k, *B. rhodani*; l, *B. pumilus*.

(Scale lines — k, l, 0.01 mm; others, 0.1 mm)

- 40 Tails with a distinct black band near the middle (fig. 25*f*).  
 Prostheca (small appendage) of right mandible as in other  
 species (fig. 24*a*)— **Baëtis niger** (L.)

Rivers and streams with vegetation.

Lake District: in weedy rivers and streams.

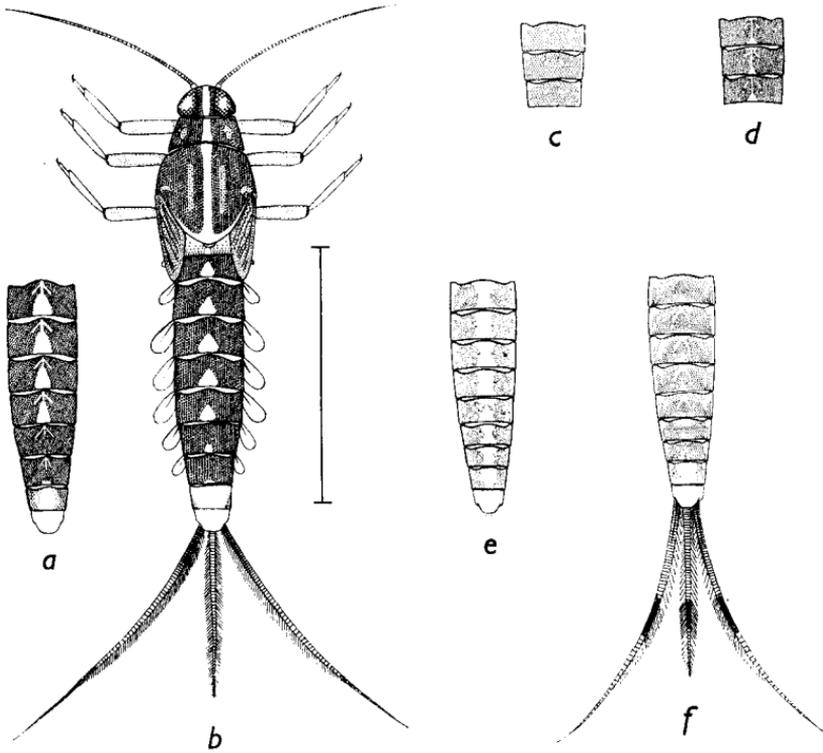


Fig. 25. *Baëtis*. Some specimens to show the patterns on the back of: *a, b*, *B. pumilus*; *c-f*, *B. niger*. *a, b, c* from R. Avon, Hants; *d* from Cunsey Beck, Lancs; *e* from R. Winster, Westmorland; *f* from Ober Water, Hants. (Scale line 5 mm)

- Tails sometimes a little darker near the middle than elsewhere, but never showing a distinct black band. Prostheca of the right mandible represented by two hairs (fig. 24*c*)—

**Baëtis pumilus** (Burm.)

With *Baëtis rhodani*, this is the species typical of small stony streams, but it extends to rivers.

Lake District: common and often abundant.

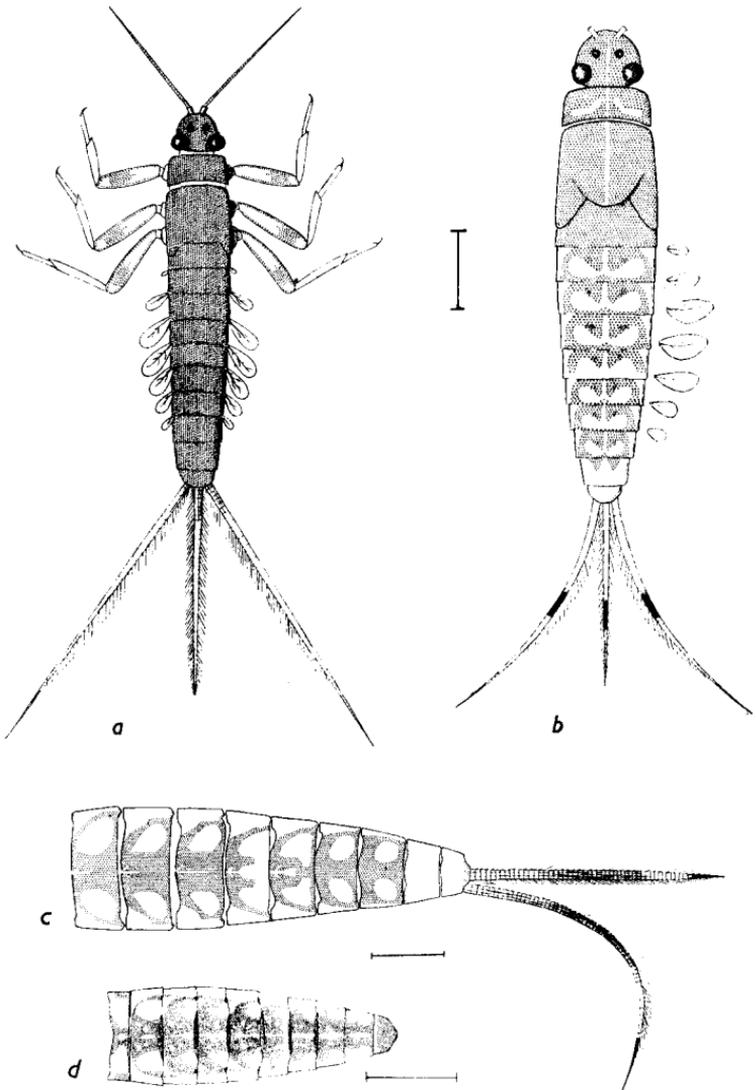


Fig. 26. *Baëtis*. a, *B. pumilus*; b, *B. scambus*; c, *B. rhodani*; d, *B. buceratus*.  
(Scale lines 1 mm)

- 41 (39) Tails with a distinct black band in the middle. Long clavate spines along the upper margin of the femora; between them a small number of very small spines; no or very few small spines in the middle part of the femora (fig. 22c). Two rows of bristles on outer margin of paraglossae. Light oval marks on abdominal terga with long axis sloping from near the posterior margin centrally to near the anterior margin laterally (fig. 26b)—

**Baëtis scambus** Etn.  
or **B. bioculatus** (L.)

Both species are typical of fairly fast rivers, *B. bioculatus* possibly being typical of more calcareous waters.

Lake District: only *B. scambus* recorded.

- Tails without a distinct black band in the middle. Long clavate or pointed spines along the upper margin of the femora; between them small spines, some pointed, some frayed at the end, more numerous than they are; small frayed spines in a band right along the middle of the femora (fig. 22b). Three rows of bristles on outer margin of paraglossae. Light oval markings on abdominal terga, when visible, sloping the other way (fig. 26c)—

42

- 42 Small pointed spines in addition to scale-like objects on the terga, on the edges of the gills (fig. 24k) and on the bases of the antennae—

**Baëtis rhodani** (Pict.)

Common and abundant in small streams and extending into rivers.

Lake District: one of the commonest and most abundant species.

- No spines on these places—

43

- 43 Four light dots on the abdominal terga (fig. 26*d*). Gills not much longer than broad (fig. 24*h*). Semilunar marks on the abdominal terga generally separated by a distance greater than their diameter (fig. 27*b*). Paraglossae about 3 times as long as broad (fig. 27*b*)—  
**Baëtis buceratus** Etn.

Abundant in the R. Usk in 1956, in the R. Wye in 1958, and the R. Exe in 1959. Earlier records from R. Barle, Somerset, R. Kennet near Reading, Berkshire, and Ringwood, Hampshire.

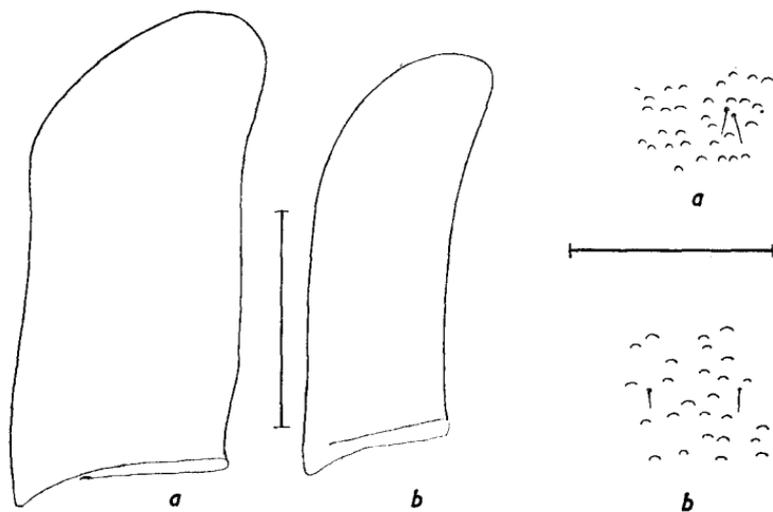


Fig. 27. *Baëtis*. Paraglossa and sculpturing of the abdominal terga of: a, *B. vernus*; b, *B. buceratus*. (Scale lines 0.1 mm)

- Without four dots on the terga. Gills distinctly longer than broad (fig. 24*j*). Semilunar marks on the abdominal terga generally separated by a distance less than their diameter (fig. 27*a*). Paraglossae not more than  $2\frac{1}{2}$  times as long as broad (fig. 27*a*)—  
**Baëtis vernus** Curt.  
 or **B. tenax** Etn.

I am doubtful whether these two species are distinct. They are often abundant in weedy rivers, though found in stony reaches as well. *B. tenax* occurs in stony streams in mountains.

Lake District: *B. tenax* recorded.

## LIFE HISTORIES

Figures 28 and 29 attempt to give maximum information about life histories in the shortest and simplest way. They are drawn freehand after an inspection of the data and are not accurate plots of the measurements. Another point to be emphasized is that they are slightly speculative in parts, notably where they show the duration of the egg stage, as will be seen later. It has seemed better to draw complete diagrams in accord with the available data and indicate in the text which parts are based on probability not hard fact, rather than incomplete ones spattered with queries.

The top horizontal line (a) represents the period when adults were on the wing. I trapped emerging adults in a cage; the other authors observed them in the field. The periods shown are those in which adults were moderately abundant — the important thing to know for practical purposes; the enthusiastic collector who set out to observe the very first and the very last adult would easily lengthen the lines. The dotted areas are the periods when nymphs occur. The left-hand bounding line indicates the size of the largest nymphs, which is quite easy to observe. The central thick line represents the size of the greatest number, in other words the mode of a figure showing numbers in each size-group. The mean size of many species signifies little because of the difficulty of assessing the relative importance of the two factors causing it to change: growth and the number added to the population from eggs unhatched at the time of a previous sampling (Macan 1958c). There is some indication (Macan 1957b) that, although eggs of *Baëtis rhodani* and *B. pumilus* are hatching throughout the winter, the rate is higher in the autumn and again at the beginning of the year, and accordingly two thick lines are shown. Two similar peaks are detectable also in the summer generation of *Baëtis pumilus* (fig. 29c). The right-hand bounding line represents the size of the smallest members of the population.

The horizontal line (e) at the foot of each diagram indicates the presence of eggs. The first eggs must coincide with the first adults, but when the last egg hatches is much less easy to determine. It will be noted that in some species, such as *Rhithrogena semicolorata* (fig. 28g) or both *Baëtis* (figs. 29c, d), tiny nymphs persist in the collections for a long time. It is possible that these are specimens

that have lived for several months without growing, but I have considered it more likely that they have only recently hatched, and that some eggs therefore persist for a long time. Illies (1959) has shown that the eggs of *Baëtis rhodani* hatch over a long period, but until studies of the eggs of other species have been made this part of their life history diagrams must remain speculative.

The measurements of length are not shown, first because full-grown nymphs of the summer generation may be much smaller than those of the winter generation, and secondly because size varies from place to place. The numerous instars are not identifiable, and therefore I have used three categories: "tiny nymphs" (t), "half-grown nymphs" (h) and "full-grown nymphs" (f). Pleskot (1958) has introduced a more complex classification in which "larvae" are all instars without any trace of wing-pads, and "nymphs" are the older instars in which the wing-pads have appeared. Larvae of the first three or four instars, which are often somewhat different from older ones and often impossible to identify to species, are distinguished as "larvulae". Nymphs are "young" "half-grown" or "full-grown" according to the length of the wing-pads. These darken just before metamorphosis, which makes possible the recognition of "ripe nymphs" and the determination of the flight period from collections of the aquatic stages alone. A literal translation of the German terms would add unnecessarily to the existing confusion about the meaning of "larva" and "nymph", but, apart from this, Pleskot's more refined categories are clearly preferable to the ones I have used.

None of the life-histories known are identical, and moreover, when data are available for one species from two different places, the course of events is frequently not the same (figs. 28*f* and *g*, 28*h* and 29*a*). It is not, therefore, desirable in the present stage of knowledge to embark on a scheme of classification. In any case, grouping may mislead by focussing attention on similarities and diverting it from differences, and is probably best attempted only when life histories have been described and in addition the factors governing the various events in them have been investigated. The figures are, however, arranged to bring similar life histories together, although in the text the species are taken in the same order as in the key.

Pleskot's (1958) statement that *Ephemera danica* completes a generation in one year has a better claim to recognition than the many which allege that development takes two years, because it is the only one supported by figures. Peart (1916, 1919) appears to be alone among British authors in believing in a one-year cycle.

*Caenis horaria* nymphs appear towards the end of July and emerge 11 or 12 months later, having grown in the autumn and again after a winter pause that lasts till the end of March (Moon 1939). There was, however, no reliable key to this genus when Moon was doing this work, and *C. moesta*, now known to be abundant in Windermere, had not been recognized. It is therefore impossible to be certain that Moon's data refer only to *C. horaria*.

*Ephemerella ignita* (fig. 29f) spends some 10 months in the egg, and grows rapidly after hatching in the middle of the summer (Macan 1957b). Although Pleskot's (1958) findings in an Austrian stream are identical, in other parts of England the flight period of this species is longer (Sawyer 1953), though whether this is due to a longer hatching period or to two generations is unknown.

*Rhithrogena semicolorata* and *Heptagenia lateralis* are the exact opposite of *Ephemerella ignita* in that for them it is the summer that is the unfavourable season to be tided over in the egg, presumably a stage more tolerant of high temperature than others, to judge from the later emergence and earlier hatch (figs. 28f, g) in the stream studied by Harker (1952), who found a lower maximum temperature than I did. *Rhithrogena semicolorata*, at least in some streams, grows steadily all through the winter apparently little influenced by temperature (fig. 28g) whereas *Heptagenia lateralis* (fig. 28c) does not grow at the coldest time of year. Moreover the upper lethal temperature of *H. lateralis* is lower, in consequence of which it is the less widespread of the two species (Macan 1960a, b).

In Ford Wood Beck, the stream studied by myself, *Ecdyonurus torrentis* had a life history similar to that of the last two except that growth of nymphs and emergence of adults went on throughout the summer (fig. 28h) and there was no suggestion of a check by unfavourably high temperature. Tiny nymphs disappeared in May, the month in which adults were first taken, and did not appear again until August, and there was no evidence of a cycle of three generations in two years as found by Harker (fig. 29a). *E. venosus* (fig. 29b) has a slow-growing winter and a quick-growing summer generation (Rawlinson 1939).

*Paraleptophlebia submarginata* (fig. 28b) has a life history like that of *Heptagenia lateralis* (Macan 1957b). Fig. 28a, based on the measurements made by Moon and observations of my own, shows that *Leptophlebia marginata* and *L. vespertina* are also similar, except that there is no delayed hatching of the eggs and accordingly a smaller size range in the later stages. The two species are very

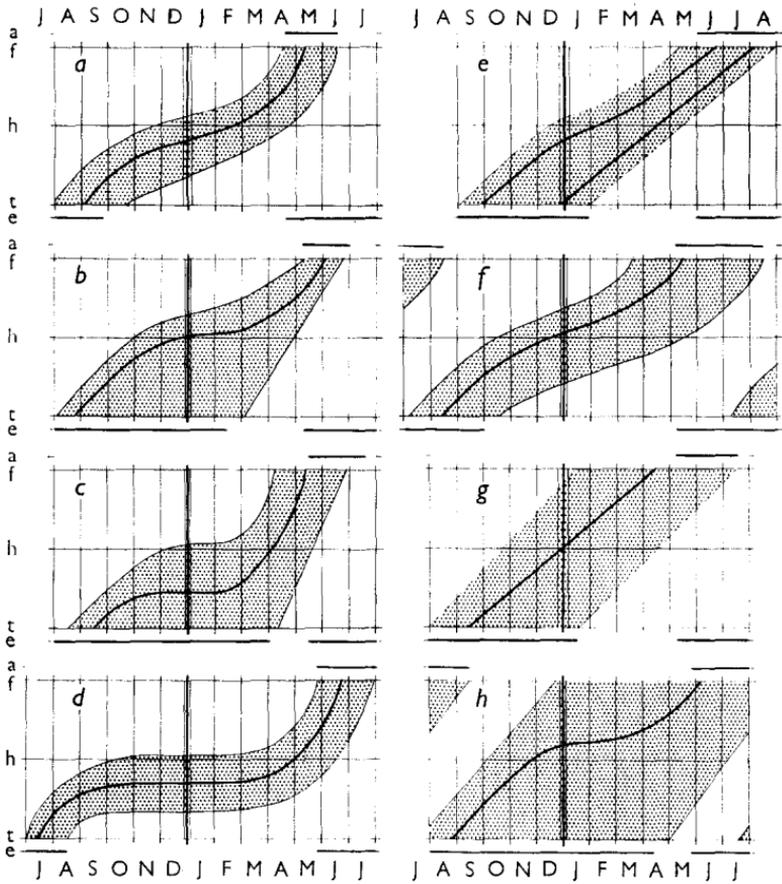


Fig. 28. Life histories of:

- |   |   |
|---|---|
| <i>a</i> , <i>Leptophlebia</i> spp.             | <i>e</i> , <i>Ameletus inopinatus</i>                 |
| <i>b</i> , <i>Paraleptophlebia submarginata</i> | <i>f</i> , <i>Rhithrogena semicolorata</i>            |
| <i>c</i> , <i>Heptagenia lateralis</i>          | (Harker's data)                                       |
| <i>d</i> , <i>Cloëon dipterum</i>               | <i>g</i> , <i>R. semicolorata</i> (Macan's data)      |
|   | <i>h</i> , <i>Ecdyonurus torrentis</i> (Macan's data) |

a, adults; f, full-grown nymphs; h, half-grown nymphs;  
t, tiny nymphs; e, eggs.

often found together and cannot be distinguished in the early stages, but *L. marginata* grows larger and emerges earlier. *Habrophlebia fusca* has become much more abundant in Ford Wood Beck since

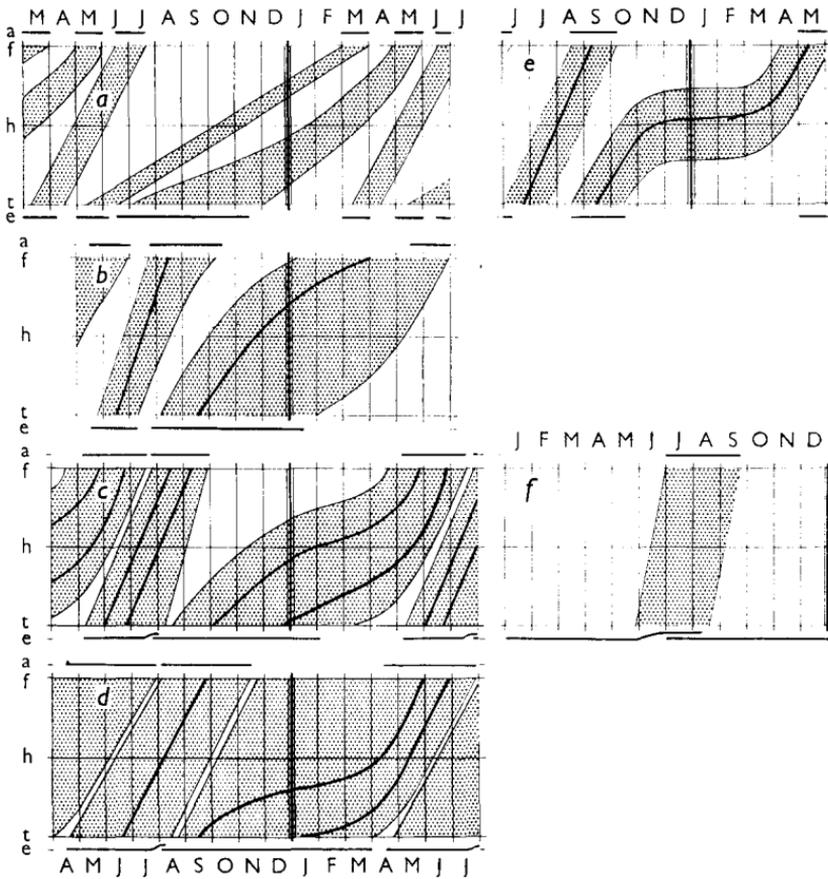


Fig. 29. Life histories of:

- |  |                              |
|--|------------------------------|
| a, <i>Ecdyonurus torrentis</i> (Harker's data) | d. <i>Baëtis rhodani</i>     |
| b. <i>E. venosus</i> (Rawlinson's data)        | e. <i>Cloëon simile</i>      |
| c. <i>Baëtis pumilus</i>                       | f. <i>Ephemerella ignita</i> |
- a, adults; f, full-grown nymphs; h, half-grown nymphs;  
t, tiny nymphs; e, eggs.

regular sampling of nymphs came to an end. In 1960 very small nymphs, which could have overwintered, but which I believe were more likely just to have hatched, were taken in March, and adults appeared in an emergence trap from 8 June to 4 August.

*Ameletus inopinatus* (fig. 28e) grows throughout both winter and

summer, and has a long emergence period. There are two peaks in the histograms showing numbers in each size-group, and they appear to be due to two bursts of hatching, one in the autumn and the other at the beginning of the year. The later adults, presumably derived from the eggs that hatch later, are smaller than the earlier ones (Gledhill 1959).

Figures 28*d* and 29*e* are based on unpublished information from a moorland fishpond. *Cloëon dipterum* overwinters as a small nymph, and there is a long period of no growth. In 1960 emergence of this generation took place in the months of June and July, and it gave rise to another overwintering one (fig. 28*d*). In 1957, on the other hand, there is distinct evidence of a quick summer generation starting in July and finishing early in September. *C. simile* is of about the same size as *C. dipterum* in winter, but starts to grow sooner in spring and is on the wing in May and June. The offspring from this generation are growing up while *C. dipterum* is emerging, and fly in August, September and October (fig. 29*e*).

*Baëtis rhodani* and *B. pumilus* (figs. 29*c, d*) have two generations per year, one growing slowly through the winter, the other growing rapidly in summer, and there are, as already noted, two peaks of hatching (Macan 1957*b*). Both generations of *B. rhodani* have a longer emergence period than those of *B. pumilus*, and another difference is that the first nymphs of the winter generation of *B. rhodani* appear to grow fast and attain full size in November. It is possible, however, that growth is really more like that of *B. pumilus*, and that the full-sized nymphs found in late December are members of the previous generation which have failed to emerge. In the two figures I have separated the generations, though actually there is some overlap. Pleskot (1958), however, finds in *B. rhodani* a gap between them in the second half of July and the whole of August, during which time only small nymphs are found, and she attributes this to a temperature too high for all but the smallest stages. In Austria nymphs of *B. vernus* are found only from April to September, and adults start to emerge in May, in which month and June they are 7-8 mm long. In July and August they are 4.5-5.5 mm, from which Pleskot deduces two generations, one of large specimens from the eggs that have lain dormant all winter, and one of small specimens arising immediately from it. *B. bioculatus* adults occur in the four months from June to September, and nymphs are almost confined to these months. The size of the adults varies in such a way that Pleskot postulates several quick summer generations.

## DISTRIBUTION

Since this appears to be the first time that the distribution of the British species has been summarized (Harris (1952) gives maps for 15 species only), all the papers consulted have been included in the list of references. In compiling the following maps the policy has been to include only the records of persons recognized as authorities on the group, of those who show evidence of having consulted such authorities, and of those observing a species that could not easily be identified wrongly. The maps are based also on a considerable number of the author's unpublished records. Most of the information from Ireland is due to Harris (1952) who has indicated exact localities and has not made use of the usual vice-county method. In translating the one into the other we have encountered the difficulty that each of Harris's dots covers about 30 square miles which sometimes makes it difficult to discover which vice-county the record refers to. Species referred to in the text as 'widely distributed in Ireland', but not so shown on the maps, are species of which Harris makes mention but gives no map. A further problem arises from the frequent use of rivers as county boundaries. We have blacked in only one of the two possible vice-counties for a record from such a river, making an arbitrary selection if there is no indication of which bank the collector was on. For example, all the records of the survey of the Tees by Butcher, Longwell & Pentelow (1937) have been referred to Durham.

It has been necessary to ignore all records of *Caenis macrura* before Kimmins distinguished *C. moesta*, and all records of *Ecdyonurus*, except Rawlinson (1939), before Kimmins (1942) revised the genus.

## DISTRIBUTION MAPS

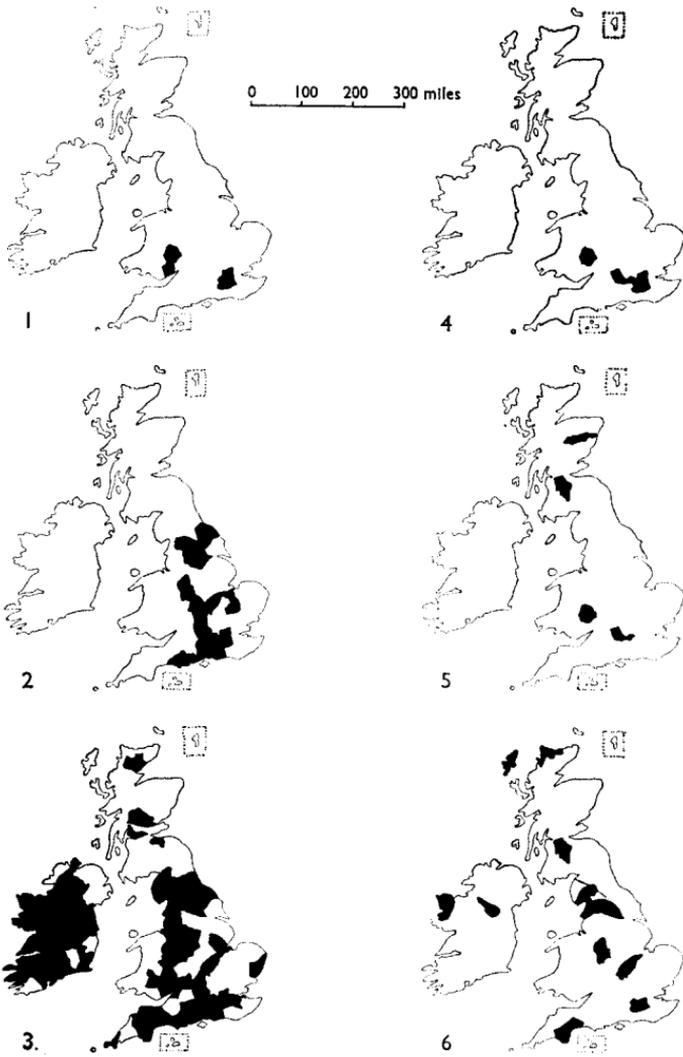


Fig. 30. Distributions of:

1. *Potamanthus luteus*
2. *Ephemera vulgata*
3. *E. danica*

4. *E. lineata*
5. *Brachycercus harrisella*
6. *Caenis horaria*

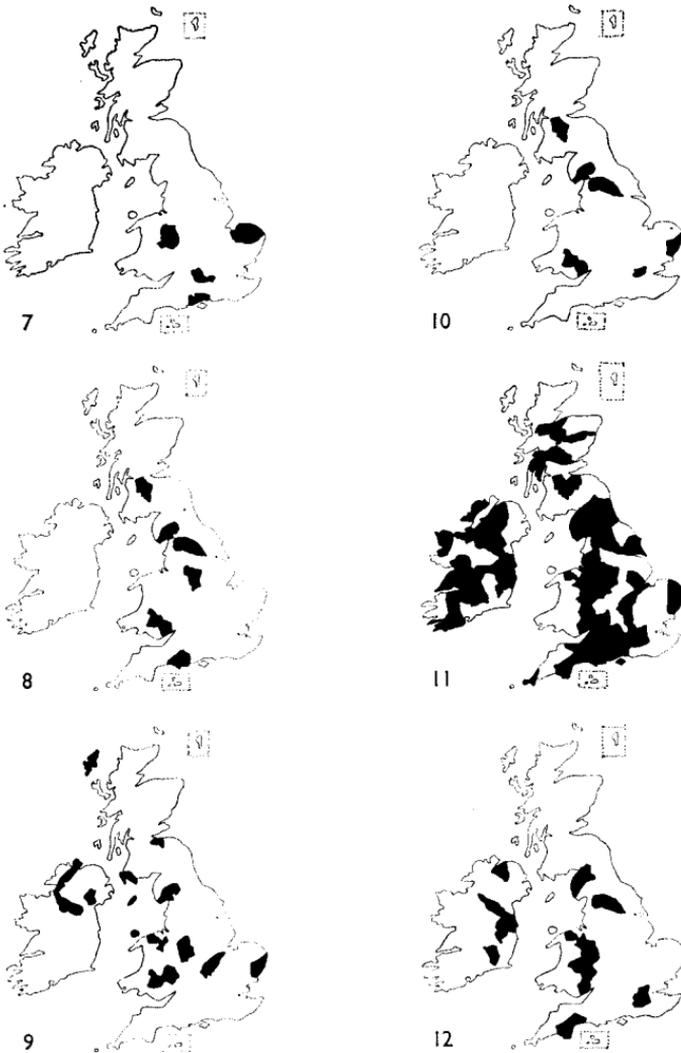


Fig. 31. Distributions of:

7. *Caenis robusta*  
 8. *C. rivulorum*  
 9. *C. moesta*

10. *C. macrura*  
 11. *Ephemerella ignita*  
 12. *E. notata*

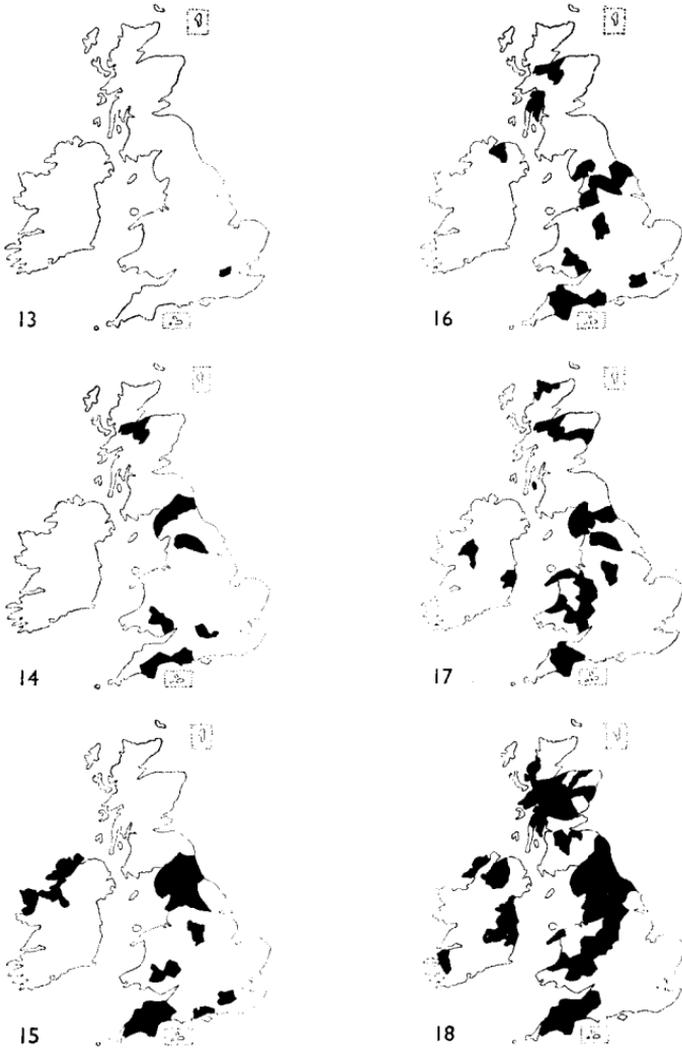


Fig. 32. Distributions of:

13. *Arthroplea congener*  
 14. *Ecdyonurus insignis*  
 15. *E. dispar*

16. *E. torrentis*  
 17. *E. venosus*  
 18. *Rhithrogena semicolorata*



Fig. 33. Distributions of:

19. *Rhithrogena haarupi*  
 20. *Heptagenia longicauda*  
 21. *H. lateralis*

22. *H. sulphurea*  
 23. *H. fuscogrisea*  
 24. *Habrophlebia fusca*

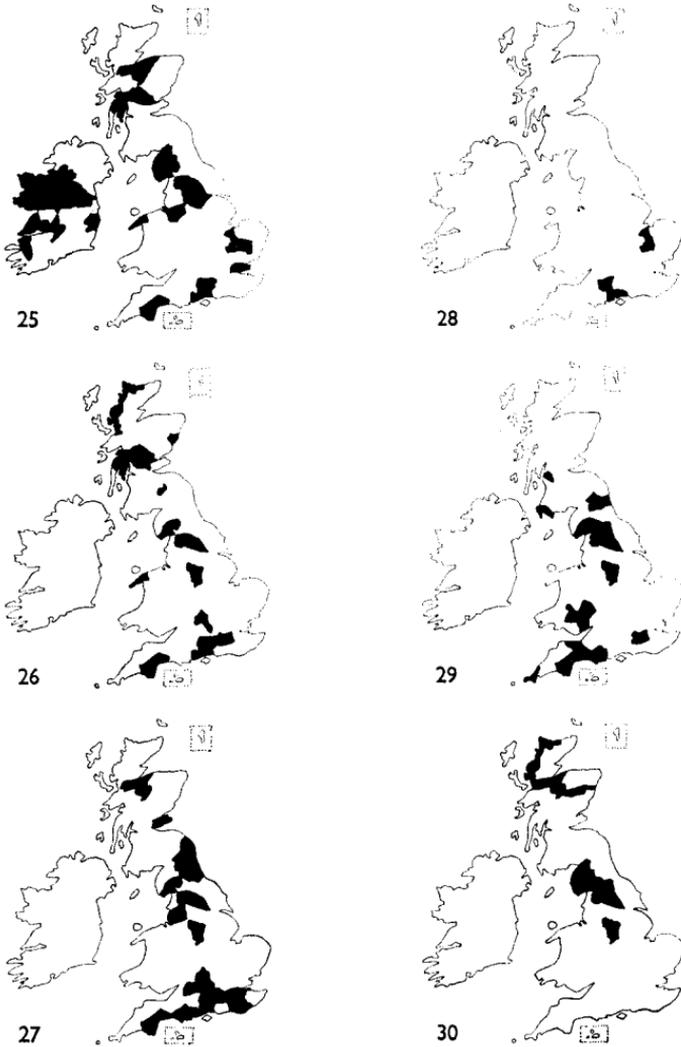


Fig. 34. Distributions of:

25. *Leptophlebia vespertina*

26. *L. marginata*

27. *Paraleptophlebia submarginata*

28. *P. tumida*

29. *P. cincta*

30. *Ameletus inopinatus*



Fig. 35. Distributions of:

31. *Siphonurus linneanus*

32. *S. lacustris*

33. *S. armatus*

34. *Centroptilum luteolum*

35. *C. pennulatum*

36. *Procloëon pseudorufulum*

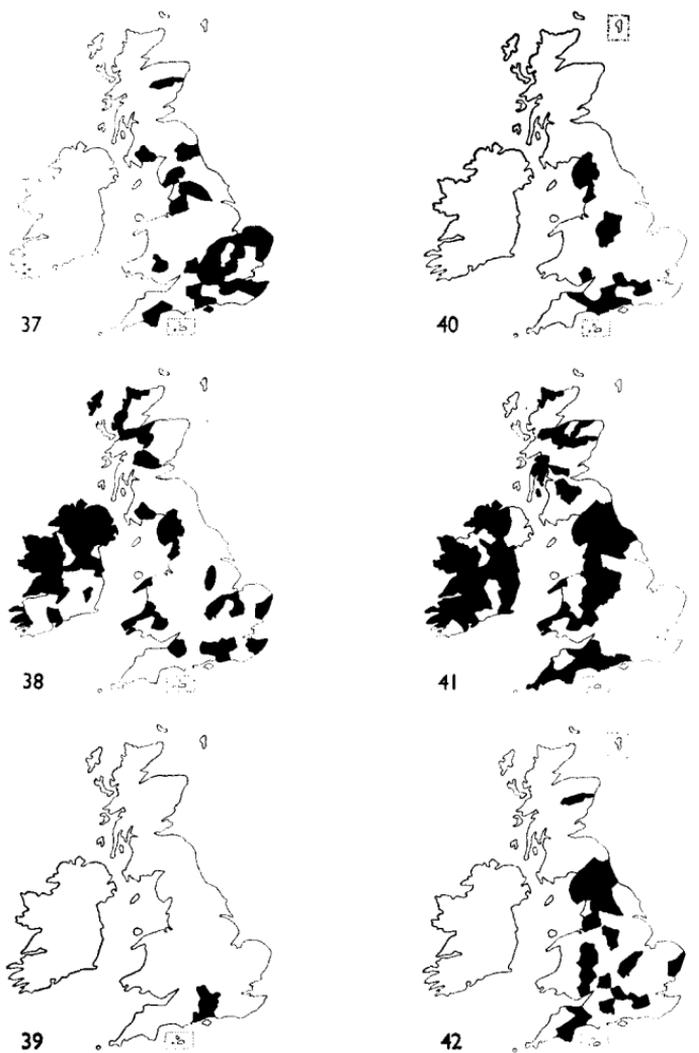


Fig. 36. Distributions of:

37. *Cloëon dipterum*  
 38. *C. simile*  
 39. *Baëtis atrebatinus*

40. *B. niger*  
 41. *B. pumilus*  
 42. *B. scambus*



43



46



44



47



45

Fig. 37. Distributions of:

43. *Baëtis bioculatus*44. *B. rhodani*45. *B. buceratus*46. *B. vernus*47. *B. tenax*

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