STUDIES OF NEW ZEALAND MAYFLY NYMPHS

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Plates XVI–XXIII.

Contents.

General.

Introductory.

Ephemeroptera or mayflies are insects which spend almost the whole of their life-cycle as aquatic nymphs, the winged stages lasting only a few days at most; they constitute a prominent item in the food of freshwater fish, notably trout, and such economic importance as they possess lies largely in this direction.

Little work has been done on this order in New Zealand, particularly on the nymphs.

Hudson (1) has published a short account of a number of mayflies. Hutton (2) gives a few brief notes on some of our species and includes a very complete generic key to the adults. In 1898 Lillie (3) described two species in rather more detail. The only mayfly nymph which has been at all adequately described is that of the rare *Oniscigaster wakefieldi* by Eaton (4) over forty years ago, who also wrote masterly accounts of a number of imagines and sub-imagines (4 and 5), though the only specimens available to him were either dried or in alcohol. Of recent years, Tillyard (6) has described two new species, but only in certain of the winged stages.

It is evident that there are big gaps in our knowledge of New Zealand

mayflies, and, as a preliminary, it is necessary to supply descriptions of the undescribed stages of Ephemeroptera already named and keys for the identification of the various families and genera.

Consequently, I have embodied in this paper a key to the families and genera of New Zealand mayfly nymphs and short descriptions of the genera, showing their nymphal characters.

The accompanying key groups the Ephemeroptera into the three families recognised by Tillyard (7).

The generic key to nymphs has been drawn up so as to correlate their distinguishing features with those of the adults.

For this reason and because New Zealand mayfly nymphs possess structural features of their own, it has unfortunately been impossible to use the nymphal classification of either Needham (8 and 9) or Lestage (10).

It is usual to classify Ephemerid nymphs as *diggers*, *swimmers* and *crawlers*, and the three families in this country may fairly be considered in this aspect, though, among the SIPHLONURIDAE, *Coloburiscus humeralis* is a poor swimmer, and the term "crawling" is perhaps barely adequate to cover the diverse movements of all the LEPTOPHLEBIIDAE.

The structure of mayfly nymphs is described, so far as it affects New Zealand species, and their origin, affinities and distributions are discussed. Mention is made of their enemies and of the condition affecting their environment.

This paper is only concerned with the nymph proper, that is to say, the completely developed aquatic stage. The earlier or "larvule" stage, immediately after the emergence from the egg, when the insect is microscopic and devoid of many of the features which it possesses as a true nymph, is outside the scope of this work.

Papers dealing with all stages of the New Zealand Mayflies appear elsewhere (26 and 27).

Notes on Terminology.

In the following descriptions I have used certain terms that may not be in accord with those applied to similar parts of mayfly nymphs by writers in other countries.

To avoid any possible misunderstanding, the terms, together with the sense in which they are used, are as follows :—

PROSTHECA applied to the small finger-like process on the mandible, proximal to the inner canine. This term is used by Lestage and Imms. The prostheca is the *endopodite* of Eaton and the *lacinia* of American writers.

SUPERLINGUAE applied to the lateral lobes of the hypopharynx. Imms uses this term. American writers use the expression *lateral lobes*, Lestage *pièces laterales*, and Eaton calls them *paraglossae*.

GLOSSAE and PARAGLOSSAE applied to the internal and external paired lobes, which occur on the labium and are appended anteriorly to the mentum.

These terms are used by Imms and also by American writers on mayfly nymphs. Lestage, however, calls them *lobes internes* and *lobes externes*, and Eaton refers to them as the lobes of the *labium*.

LEGS. The terms *anterior* and *posterior*, *dorsal* and *ventral* are used in the same sense as they are used anatomically, irrespective of the actual position of the portion of the limb visible.

Thus the femur, tibia and tarsus of the limb of a mayfly nymph may be held with the *anterior* surfaces turned over so that they appear *dorsal*—as is very frequently the case—and may be figured so; nevertheless these surfaces

will be described as *anterior surfaces*; the real *dorsal* surface will be described as such in the text, but in the case instanced will appear in the specimen—and probably the illustrations—as turned over so that it faces *posteriorly*.

Origin.

According to Tillyard (7), we owe our mayflies to a fauna which came from Antarctica in the Cretaceous Period. At this time there was a land mass over a considerable part of what is now the southern Pacific Ocean. "... While Western Australia was separated off, Eastern Australia extended over the Tasman Sea to include Tasmania, New Zealand, New Caledonia and even the Fiji Islands, and there was also a broad extension southwards, giving, at any rate for a time, a connection with Antarctica. This connection affected Eastern Australia and New Zealand about equally and supplied both with a number of types of cold climate and aquatic insects which form a very distinct element at the present day and are chiefly confined to New Zealand, Tasmania and the mountains of Eastern Australia. The chief representatives of this fauna are the whole of the mayflies except the BAETIDAE. . . ." (Tillyard).

The BAETIDAE, which are found in Australia but not, so far, in New Zealand, probably did not reach the former country until after New Zealand became separated from it.

The genera, which are found in this country, are mostly represented in Australia too, but never by the same species. Where the genera are unrepresented, there are genera of similar type.

Thus, in the family EPHEMERIDAE, there is, according to Tillyard (7), a nymph resembling *Ichthybotus* in New South Wales. The same authority states that our two genera of the family LEPTOPHLEBIIDAE, viz. *Atalophlebia* and *Deleatidium*, are represented in Australia.

Finally, among the SIPHLONURIDAE there are species of *Coloburiscus* in Victoria and New South Wales, and in the latter State there are mayflies very closely akin to *Ameletus*. *Oniscigaster* is not found, but in Tasmania and New South Wales there are species of a genus, *Tasmanophlebia*, Tillyard, which would appear to partake of some of the characters of both *Oniscigaster* and *Ameletus*.

So far as my information goes, no nymphs of a similar type to *Ameletopsis* * have been found in Australia. Did this remarkable mayfly spread to New Zealand with the other species, or is it possible that it originated from other sources? As yet, only the fringe of Ephemerology has been touched in this part of the world; further exploration may clarify the origin and position of this genus.

Distribution.

The fact that New Zealand is over 1200 miles from the nearest land mass has resulted in the evolution of a fauna different from that of the rest of the world.

Ephemeroptera are insects so incapable of surviving, for any appreciable period of time, when removed from their habitat, that it is impossible for individuals of species from outside to migrate here; nor, indeed, could any

* After this paper was written, I received a letter from Dr. Tillyard, dated Nov. 25th, 1930, stating that he had found a single nymphal specimen of an *Ameletopsis* sp. in the Cotter River, Australia. This nymph was almost exactly like that of *A. perscitus*, except that the cerci had no external fringe-hairs, but only internal ones.

exotic species be accidentally introduced here in the winged stages—*e.g.* by lodgment on the structure of a ship at Sydney—as they do not live long enough.*

All New Zealand species, therefore, are indigenous, and, as far as is known at present, are confined in their distribution to this country.

The narrowness of a land which, though extending through thirteen degrees of latitude, has no place more than seventy miles from the sea, has made the climate a remarkably equable one, and the temperature of the streams and rivers is not subject to marked seasonal changes.

Because of the hilly nature of the terrain in most parts of both Islands, the prevailing type of stream is rapid—and therefore well-oxygenated—and has a rough bed, usually of rock, boulders or shingle.

The annual rainfall is abundant, only falling short of twenty inches in a small area in the South Island and exceeding two hundred inches in parts of the West Coast. In the North Island, it is more uniform, as the annual rainfall ranges from forty to seventy inches in approximately eighty-seven per cent. of its area (22).

The consequence of so plentiful a precipitation on this hilly country is that there are innumerable streams and rivers and a large number of lakes; in fact, few countries can boast so large a mileage of fresh-waters in proportion to their area.

All these factors combine to produce an environment which is a singularly favourable habitat for Ephemeroptera, and naturally those species predominate which are most suited to the prevalent conditions, *i.e.* rapid mountain streams. There is, consequently, a large proportion of species of LEPTOPHLEBIIDAE and SIPHLONURIDAE and very few EPHEMERIDAE.

Little is known of the distribution of Ephemerid species in this country, except in the more settled areas.

Both the warm, sparsely-inhabited districts in the north of North Auckland and the wild hilly country of the Cold Lakes region in the south-west of the South Island are unknown territory, as far as mayflies are concerned, and there are probably many new species waiting to be discovered in such parts.

Nothing is known of the altitudinal range of the different species and a research into their zonation in the Southern Alps, for instance, on similar lines to the work carried out in the Rockies by Dodds and Hisaw (15), would be of immense interest and of no little value.

Such scanty information as we possess, at present, may be summarised as follows :—

The EPHEMERIDAE occur in the slower-flowing waters. Of the species of this family, *Ichthybotus hudsoni* is found in sandy patches of streams in the Wellington and Hawkes Bay districts and *I. bicolor* among rubble in the Nelson district.

Species of the SIPHLONURIDAE are found mainly in cold, well-aerated waters. *Coloburiscus* occurs in rapid waters in the Wellington, Hawkes Bay, Taupo, Nelson, Canterbury, Otago and Southland districts. *Oniscigaster* spp. live in well-bushed, cool, moderately-rapid streams among rock pools, boulders and shingle in the Wellington, Hawkes Bay, Nelson and Canterbury districts. *Ameletopsis* has been found in slow and moderately-flowing parts of streams in the Wellington and Hawkes Bay districts of the North Island.

* This explains the absence of mayflies from all true "oceanic" islands, and the presence of any species of Ephemeroptera might almost be taken as proof that an island is not actually of the "oceanic" type.

Ameletus spp. are found in pools and in moderately-flowing rivers in the North Auckland, Taupo, Hawkes Bay, Wellington, Nelson and Canterbury districts.

Species of both genera of LEPTOPHLEBIIDAE are very abundant, according to Tillyard, all over New Zealand. In North Auckland I found the nymph of an *Atalophlebia* species, which I have not found further south. *Atalophlebia* appears to be the dominant genus in this district, whereas further south, *i.e.* throughout the greater part of the North Island, *Deleatidium* spp. would seem to predominate.

Unless otherwise stated, the data of distribution are from personal experience, either by visits to different places or from examination of trout stomachs sent from various parts of the country.

The accompanying map (Pl. XXIII) shows the position of the various districts.

As shown elsewhere (25), the mayfly is a most useful "indicator-organism," and a knowledge of the different species is, accordingly, a useful guide to anglers.

Enemies.

The chief enemy of mayflies in New Zealand is Man. His influence is entirely an indirect one, but is nevertheless very deadly.

By felling the bush near the water-courses he has altered the conditions in the streams, so that the beds dry up during the summer and nymphs and egg-masses become dessicated and die. Maimed insects are also occasionally found after freshets (due to the great increase in the rapidity of "run-off" from cleared land), in which they have been pounded by stones or other current-borne debris. A further result of felling has been the removal of shelter for the winged stages, and where transformation from the nymph takes place out of the water and the sub-imaginal stage is of long duration, *i.e.* among the SIPHLONURIDAE, this increased exposure has left the insects an easy prey to birds.

Among birds, the chief predators are the Pied Fantail (*Rhipidura flabellifera*), the Groundlark (*Austranthus novaeseelandiae*) and the Chaffinch (*Fringilla caelebs*), the first two being natives, the last being introduced by man.

An even more deadly predator is the introduced trout (both brown and rainbow varieties). As I have shown elsewhere (23), mayflies form nine per cent. numerically of the food of trout in the Wellington district. Tillyard (24) found that various Siphlonurids had been practically exterminated by the trout in various parts of the country.

The stomach of an Atlantic Salmon, sent to me from the Waiau river, Southland, contained between two and three hundred nymphs of *Coloburiscus humeralis*, showing that another introduced fish was levying toll on the mayfly.

Native fish, especially the bully (*Gobiomorphus gobioides*) were found (23) to eat mayfly nymphs, as do the nymphs of some stone-flies, the larvae of aquatic, carnivorous beetles and of the "creeper" (*Archichauliodes dubitatus*). I have found small mayfly nymphs helplessly ensnared in the traps of web-spinning caddis larvae.

Species of LEPTOPHLEBIIDAE are particularly susceptible to attack by Nematodes, and a large percentage of the individuals of this family are parasitised.

EXTERNAL ANATOMY.

New Zealand mayfly nymphs vary considerably in appearance according to genus. Their general shape is campodeiform. The longitudinal axis of

the head is usually in line with that of the body, which in that case is more or less flattened dorso-ventrally, the eyes being placed dorsally; but, in all species of the family SIPHLONURIDAE except *Ameletopsis*, the axes of the head and body are at right angles, and the body is not flattened dorso-ventrally, the eyes then being placed laterally.

The Head.

The head may be comparatively small as in *Ichthybotus*, or large as in *Ameletopsis*. In other species it is intermediate in sizes between these two, in comparison with the body.

The dorsal region of the head is formed of three pieces—a medio-anterior portion, the clypeo-frons, which bears the antennae and the median ocellus, and two symmetrical posterior parts, which comprise the epicranium; each of these two parts bears a compound eye and one of the lateral ocelli. These three parts are separated from each other by the Y-shaped epicranial suture (shown in the head of *Ichthybotus hudsoni*, Pl. XX, fig. 4).

The compound eyes, which are of the eucone type, are placed dorsally (Pl. XX, fig. 4, Pl. XXI, fig. 1, Pl. XIX, fig. 1), except in most of the SIPHLONURIDAE (not *Ameletopsis*), where they are laterally placed; they are composed of a large number of ommatidia. The eyes seem to occupy a considerable part of the head, especially in such genera as *Ameletus* and *Oniscigaster*, where the head is small and its axis is placed at right angles to that of the body. In the males of a number of genera (*Atalophlebia*, *Deleatidium* and *Ameletopsis*), the eyes are larger than those of the female. In these three genera, the male has turban eyes, *i.e.* each eye is composed of an upper and inner portion and a lower and outer one: the upper portions have appreciably larger facets than the lower ones and are, moreover, usually of a lighter colour; the colour of the lower parts is similar to that of the eyes of the female of the species.

In addition to the compound eyes, there are three small ocelli (Pl. XX, fig. 4, Pl. XXI, fig. 1, Pl. XIX, fig. 1), two being placed laterally—each about midway between the eye and the antennal pit—and the third placed medianly and slightly posterior to a line joining the antennal pits.

The antennae are filiform and multiarticulate, being about as long as the head and thorax combined, considerably shorter in *Ameletus* and *Oniscigaster*.

The Mouth-parts.

These are very highly developed and show marked differences in the various genera.

(1) *The Labrum* is a median unpaired appendage, placed antero-medianly of the clypeus, with which it articulates. It is connected to the clypeo-frons by pairs of muscular attachments—a median pair, which is abductory in function, and a pair of lateral attachments, which connect at the latero-posterior angles and are adductory in function. The labrum appears to be used mainly as a scraper, but it also pushes food into the mouth from above or in front. The anterior edge is always armed with hairs or spines, except in that of *Ameletopsis perscitus* (Pl. XIX, fig. 2). This edge may be straight as in *Coloburiscus humeralis* (Pl. XVI, fig. 17), or convex as in *Ameletopsis perscitus* (Pl. XVI, fig. 20), or concave as in *Atalophlebia versicolor* (Pl. XVI, fig. 22); it may have a deep notch as in *Deleatidium* spp. (Pl. XVI, figs. 14 and 15), or a number of teeth as in *Atalophlebia cruentata* (Pl. XVI, fig. 21), or a slight bay as

in *Ichthybotus hudsoni* (Pl. XVI, fig. 18). The proportion of breadth to length also varies to some degree. Both surfaces of the labrum are covered with hairs or spines, particularly on the anterior half (except in *Ameletopsis perscitus*, which is hairless).

In the LEPTOPHLEBIIDAE there is an inconspicuous tongue-shaped patch of small hairs, placed medio-posteriorly—though slightly to one side—on the ventral surface.

(2) *The Mandibles* are paired appendages which move laterally. Usually, each is armed distally with two sets of teeth—the canines and the molars; the latter set are placed differently in each mandible, being placed dorso-anteriorly on the inner margin of the right mandible and ventrally on the inner part of the anterior margin of the left mandible, but when the mandibles are closed, the molars fit into each other dorso-ventrally. They are used for grinding; each consists of a number of parallel ridges—about ten—which rub together and triturate the food. These ridges are usually serrated and armed with short, stiff bristles. The canines are used for tearing; they consist of an outer and an inner canine, each of which is subdivided into smaller teeth—usually three; interior to the canines is a minute, jointless, mobile, finger-like process, the prostheca, and attached to its base is a small bunch of hairs of about its own length. The exterior edge of the mandible always bears a fringe of hairs.

This type of mandible is the normal one and occurs in all the LEPTOPHLEBIIDAE (Pl. XVIII, fig. 6), and in *Coloburiscus* and *Oniscigaster* (Pl. XVII, fig. 6) among the SIPHLONURIDAE. In *Ameletus* (Pl. XXII, fig. 6) the canines have coalesced; in *Ameletopsis* (Pl. XIX, fig. 3) the molar surface has almost disappeared and the canines have developed very strongly and become a formidable weapon; the only other mayfly with canines at all like this is Eaton's unidentified nymph from Chili.

In the EPHEMERIDAE (Pl. XX, fig. 6) the salient feature is the development of part of each mandible into an enormous fossorial tusk, pointed at the end and armed extensively with short, stout spines and a fringe of long hairs. This tusk, which is used for digging burrows, has been called a canine by some writers, but it is not one, for the real canines, somewhat modified in form, are there too, as are the molars.

(3) *The Maxillae* are also paired appendages, working laterally. They consist normally of a basal part—the cardo, a stipes, which merges distally into a fused galea-lacinia, and a palp, the palpifer of which may or may not be fused with the basal segment.

In the EPHEMERIDAE (Pl. XX, fig. 7) the palp is three-segmented and large, and the galea-lacinia is greatly reduced.

Among the SIPHLONURIDAE, *Coloburiscus* (Pl. XXI, fig. 3) has a very large two-segmented palp, heavily fringed with hairs, and a short galea-lacinia [Murphy (12) suggests—with reference to an American species with a similar palp and rapid-water habitat—that this fringe acts as a diatom strainer], *Oniscigaster* (Pl. XVII, fig. 7) has a three-segmented palp with a galea-lacinia of about equal length; in *Ameletus* (Pl. XXII, fig. 8) the proportions are somewhat similar, but the terminal joint of the palp is shorter, more rounded apically and armed with curious sensillae, and the suture between galea and lacinia is apparent—which is exceptional in local species. *Ameletopsis* (Pl. XIX, fig. 5) shows extraordinarily aberrant features—again, only comparable to Eaton's nameless Chilian nymph. The palp is much reduced in size and multiarticulate, the galea-lacinia ends in a number of formidable, long, spine-

like teeth; together with the mandibles, these maxillae form an effective, carnivorous armament.

The maxillae of species of LEPTOPHLEBIIDAE (Pl. XVIII, fig. 4) are very uniform. The galea-lacinia ends in a broad brush of brown hairs, which is used for brushing food into the mouth-cavity and possibly as a diatom strainer of passing water. Hidden by the brush of hairs is half a row of pectinate rakes (Pl. XVIII, fig. 10), which are inserted, starting from the interior corner, along the margin. What are the functions of these curious rakes? Do they comb the food from stones or perhaps from the other trophi? I have noticed a frequent brushing action between the forelegs (which are usually very spinose) and the maxillae, and it is just possible that the combs are used to convey diatoms and other matter from the forelegs. The palp is three-segmented and projects somewhat beyond the galea-lacinia.

(4) *The Hypopharynx* is an unpaired median structure—possibly a fusion of what were originally two-paired structures—which fits dorsally over the labium. It is a sort of trilobed tongue, usually covered with long hairs anteriorly, and consists of a median and two lateral pieces; the latter are called the superlinguae.

Sometimes the median piece is much reduced as in *Ichthybotus* (Pl. XX, fig. 1), sometimes it is about equal in size to each of the two lateral parts as in *Oniscigaster* (Pl. XVII, fig. 2), and sometimes considerably larger as in *Ameletopsis* (Pl. XIX, fig. 4, where it is shown superimposed on the labium). The superlinguae show their maximum development in the LEPTOPHLEBIIDAE (Pl. XVIII, fig. 9).

(5) *The Labium* or lower lip is composed of a pair of lateral appendages fused together. It sweeps food from below or behind (depending on the angle of the head axis to that of the body) into the mouth-cavity. Situated proximally on this mouth-part are the mentum and submentum, which are often incompletely differentiated. Attached to the mentum laterally are the labial palps, which are somewhat variable in form. In *Ichthybotus* (Pl. XX, fig. 5) they are two-segmented, the distal segment being large, flattened, falcate and very hairy; in *Coloburiscus* (Pl. XXI, fig. 6) these characters are even more pronounced. According to Morgan (18), this type of palp is a characteristic of the nymphs, living in swift currents, which use the blade-like distal segments as scrapers upon stones covered with algae and the hair as a plankton basket. This would certainly apply to *Coloburiscus*, but *Ichthybotus* is a slow-water form. The most characteristic, three-segmented palps are shown by *Oniscigaster* (Pl. XVII, fig. 8), *Ameletus* (Pl. XXII, fig. 7) and *Atalophlebia* (Pl. XVIII, fig. 7). *Ameletopsis* (Pl. XIX, fig. 4) again shows an extraordinary form, the palp being long, thin and multiarticulate. Probably it was originally bi-segmented, the basal joint remaining unchanged, the distal one becoming subdivided into a number of smaller joints and becoming narrowed and elongated in the process.

The distal attachments of the mentum are a pair of inner segments (the glossae) and an outer pair (the paraglossae). These may be considered as the laciniae and galeae respectively of the second maxillae. They are always covered with hairs or spines, particularly in the anterior parts, and in *Ameletus* (Pl. XXII, fig. 7) they bear curious sensillae (Pl. XXII, fig. 9), as do the palps; possibly these are gustatory in function. Pls. XVII, fig. 8; XVIII, fig. 7; XIX, fig. 4; XXI, fig. 6; XXII, fig. 7 show various types of these parts of the labium.

The Thorax.

This part of the body contains three segments of about equal width but varying length. The prothorax is always short, the mesothorax considerably

longer and the metathorax about as long as the prothorax. This latter segment is well differentiated, but the meso- and metathorax are completely covered dorsally by the wing-pads,* so that their dividing line cannot be seen. The wing-pads of the hind-wings, which spring from the metathorax, are concealed by those of the fore-wings, which are mesothoracic in origin and which also cover some of the anterior abdominal segments in older nymphs.

Attached to each thoracic segment is a pair of legs, composed of coxa, trochanter, femur, tibia and tarsus. The femur is by far the largest part of the leg, next is the tibia and after that the tarsus; both coxa and trochanter are very small (these two parts are not shown in the legs figured). The tarsus, like the other parts of the leg, is composed of a single segment (adults have multi-segmented tarsi) and ends in a claw.

The legs of different species of nymphs indicate by their appearance the kind of habitat of the species. Thus, the legs of *Ichthybotus hudsoni* (Pl. XX, fig. 11) show how completely the burrowing habits of that nymph are in accordance, with the development of its legs, and it is only necessary to see the speed with which this insect buries itself to realise their efficiency. Compare these with the poorly-developed, almost bare legs of *Ameletopsis* (Pl. XIX, fig. 6) and *Oniscigaster* (Pl. XVII, fig. 4), the nymphs of which are of the swimming type but still crawl a little, and then with the still further reduced legs of *Ameletus* (Pl. XXII, fig. 2), which is solely a swimmer.

Coloburiscus (Pl. XXI, fig. 2) shows an interesting modification. This nymph lives in the rapids, and in its case the legs are heavily spined to help it maintain its foothold; moreover, the fore-legs are thickly fringed, and, when held in the characteristic position, form with the hair fringes of the mouth-parts a plankton trap, with which this nymph strains the rapid-flowing water of its habitat.

Finally, the LEPTOPHLEBIIDAE (Pl. XVIII, fig. 2) have their femora flattened and covered with spines, and also have spines on the tibiae and tarsi; these features, as well as the serrated tarsal claws, help them to retain their hold on the surfaces of stones and in the crevices, even in the swifter streams. Their legs are longer and far more efficient than those of the SIPHLONURIDAE, and they not only help them to hang on in rapid water but also to travel with great agility forwards, backwards and even sideways. If a submerged stone be picked up from the river and the lower surface inspected, as soon as the stone has been turned over the Leptophlebiid nymphs will dodge like lightning round to the other, unexposed side or lodge themselves in a handy crevice.

The Abdomen.

The abdomen, which is by far the largest part of the body, is made up of ten segments, varying slightly in length and width, but always becoming narrower posteriorly. The first segment is fused with the metathorax. Usually the segments broaden slightly from the front until the middle of the abdomen is reached and then narrow less gradually to the last segment. The ninth segment is usually longer than the others, the tenth being very much shorter and narrower. In most species, the latero-posterior angles of segments (particularly those of the posterior segments) are produced backwards as sharp teeth; this is very marked in *Coloburiscus* (Pl. XXI, fig. 1) and *Atalophlebia* (Pl. XVIII, fig. 1).

* The wing-pads contain the larval wings, and it was upon a study of the tracheation of these structures, in local species of the family SIPHLONURIDAE, that Tillyard based his work concerning the wing-venation of this order (19).

The abdomen may be slightly flattened dorso-ventrally as in *Ameletopsis*, decidedly flattened as in *Atalophlebia*, or pronouncedly flattened as in *Deleatidium*. In the swimming nymphs it is cylindrical, tapering posteriorly. *Ameletus* has a torpedo-shaped abdomen, and *Oniscigaster*, though considerably broader laterally than dorso-ventrally, also pertains to the " stream-line " type.

The tenth segment bears three caudal setae apically, each consisting of a large number of small, cylindrical segments. Tillyard (7) calls the median seta the appendix dorsalis, but, for the sake of convenience, the term caudal seta will be applied, in this paper, to all three of the caudal filaments.

In all cases the two lateral setae are of the same length; in the EPHEMERIDAE and LEPTOPHLEBIIDAE the median seta is very slightly longer, in the SIPHLONURIDAE very slightly shorter than the others. In *Coloburiscus humeralis* (Pl. XXI, fig. 1), which belongs to the last-named family, the median seta has been very greatly reduced and is now rudimentary and made up of a few segments only. It is interesting to note that an undescribed Australian species * of this genus has the median seta normal. Doubtless, in the local species, the seta has become partly atrophied, as it is useless in the habitat that this nymph has adopted.

In the EPHEMERIDAE the caudal setae are short and haired throughout on both sides. Among the SIPHLONURIDAE these appendages are nearly always used—interlocked by their thick fringes—as an oar, and they propel the insect through the water by strong dorso-ventral strokes. The form of seta most favourable to propulsion is seen to be a short, thickly-fringed type (*Ameletus* and *Oniscigaster*). In both these genera, the median seta is thickly fringed on both sides, the outer ones on the inner sides only (Pl. XXII, fig. 4). In *Ameletopsis* all three setae are fringed on both sides. *Coloburiscus* is again an exception; it is a poor swimmer and its setae are not fringed at all, but have a whorl of short, weak hairs at the segmental junctions (not shown in Pl. XXI, fig. 1, as they are too small). This type of seta is also found universally among the LEPTOPHLEBIIDAE. Most of the species of this family have long thin setae, which seem to act as secondary balancing organs and as a mild brake, when spread out, as they settle on a surface after a short—and usually involuntary—swim.

The Gills.

On each of the first seven segments of the abdomen there is a pair of gills. These interesting structures, which do not appear until several days after hatching—the new-born Ephemerid breathes cutaneously—are exceedingly diversiform in the different genera.

They were, originally, incorrectly believed to be homologous with wings, but Heymons [(20) and elsewhere] has shown that they arise as laterally-placed hypodermal thickenings and are not tergal outgrowths. Borner (21) has written a very interesting and intricately-reasoned paper, on the origin of these appendages, from a morphological standpoint.

In all the New Zealand species these organs are paired and occur, placed posteriorly, on each side of the segments. Secondary gills do not occur on either the thorax or the maxillae, as occasionally happens in species from other countries.

The gills are either foliaceous or composed of a number of filaments. Usually they attain their maximum development in the middle pairs, whilst either the

* Specimens of this undescribed species were kindly sent me by Dr. Tillyard, so that I might compare them with N.Z. species.

anterior or the posterior gills, or sometimes both, are less strongly developed or even abortive.

In *Ichthybotus* the anterior gills are aborted and are each in the form of a microscopic bifid lash (Pl. XX, fig. 2), whilst in each of the other pairs each gill is double and resembles a pair of feathers (Pl. XX, fig. 3), the "rachis" of the feather containing the trachea and the long, thin "barbs"—the gill filaments—each contain a tracheal branch. These filaments are minutely serrated on each edge, and from the apex of each serration, a small spine projects forwards and outwards. The gills are held upright over the dorsum. They are held similarly in *Coloburiscus humeralis*, a nymph with very differently shaped gills, which increase in size posteriorly (Pl. XXI, fig. 1); this increase is noticeable in the outer fork of each gill only, but the entire gill is smaller in the anterior pair. Each gill (Pl. XXI, fig. 5) is pedunculate and consists of a divergent fork, united in the basal half by a thin lamella. It is armed with numerous short spines, which occur mainly round the edges and towards the distal part. These spines are jointed at the base and can be made to lie flat along the gill surface, but spring up when pressure is removed. It is probable that the purpose of this stout but elastic armament is to protect the gill from damage by the current-borne debris, which abounds in the swift habitat of this nymph. Under the surface of each lamella lies an extensive ramification of tracheoles, and a tracheal branch runs along the middle of each of the forks.

It is interesting to note that the gills of the allied undescribed Australian species mentioned above, p. 408, have tufts of gill filaments at the base of the gills.

Oniscigaster is the only other New Zealand genus in which the gills are held dorsally. Pl. XVI, fig. 2, shows a typical gill. Eaton [(4) Pl. LI] illustrates these elaborate gills very beautifully but omits the posterior gill; they are diversiform and become smaller posteriorly, the last gill being microscopic and probably functionless. They are either green, marbled with white, or red, marbled with white, and are agitated slowly. The rhythm of this movement combined with the beauty of the gills makes it a delight to watch.

The gills of all the other genera are held laterally. Among the SIPHLONURIDAE there remain *Ameletus* and *Ameletopsis*. Both have single lamellate gills, ovate in outline, with rounded apices. There is a central trachea and many branches, frequently much ramified, in each gill. The gills of *Ameletus* (Pl. XXII, fig. 3) decrease in size both anteriorly and posteriorly; their edges are finely toothed in the upper distal portions and bear minute hairs all round, except in a small, upper proximal portion. Below the main tracheal branch, a thick, chitinised, curved band runs longitudinally throughout the gill, acting as a brace.

In *Ameletopsis* (Pl. XIX, fig. 8) the edges are entire and there is no brace.

The LEPTOPHLEBIIDAE show two types of gills, double and single. In *Atalophlebia* the gills are double and become smaller and narrower posteriorly, the seventh gill often being aborted. They are either each in the form of a pair of ovate-acuminate lamellae, e.g. *A. versicolor* (Pl. XVIII, fig. 8), or lanceolate-acuminate. In most cases they have a prominent central trachea, which is pinnately branched, but in *A. nodularis*, where the gills are lanceolate, the main tracheae are unbranched.

Finally, the genus *Deleatidium* has single, lamelliform gills, those of the second to seventh pairs being usually ovate-acuminate as in *D. vernale* (Pl. XVI, fig. 7), but in one case (*D. myzobranchia*) sub-rotund (Pl. XVI, fig. 6). In all these species, the gills become smaller posteriorly and the shape of the first

gill is similar to the outline of a kidney and therefore different from that of the others (Pl. XVIII, figs. 11 and 12). All the gills have each a main trachea with pinnate branching, sometimes much ramified.

In *D. myzobranchia* the gills frequently appear to be held in such a position that they act as suckers and help to hold the insect to the substratum in swift waters.

It is interesting to speculate as to whether the changes which are occurring in this country—due to comparatively recent settlement by Europeans—will induce the mayfly to evolve new adaptations to meet the altered conditions. Thus, *Oniscigaster* has become comparatively rare, for reasons indicated elsewhere in this paper, and it is probable that it must evolve protective measures to meet the new conditions or become extinct.

The clearing of bush from the stream banks and catchment areas has altered many miles of our freshwaters; their beds often change and frequently become dry in midsummer; much of their course is now strewn with pebbles, which move downstream with each severe freshet. These altered conditions affect the mayfly and may influence it, in many ways, in due course.

Dr. Tillyard recently sent me specimens of an undescribed Siphlonurid from Australia. This nymph showed affinities with both *Ameletus* and *Oniscigaster*. The gills were reduced to four pairs, of which those of the first pair were large and thickened, forming an operculum to protect the three posterior gills. It occurred to me that such an evolution may possibly be due to recurrent dry seasons and be a xerophytic adaptation.

In such pebble beds as have become temporarily dry, in this country, mayfly nymphs may often be found a few inches below the surface of the bed, where it is generally cool and damp.

Classification.

Key to Families and Genera of New Zealand Ephemeroptera.

Nymphs.

A. Mandibles with Tusk-like Extension, protruding in front of Head. (Plate XVI, fig. 9) . . . . . Ephemeridae.

With six pairs of gills, visible to the unaided eye: these are feathery and lie on the dorsum (on 2nd to 7th abdominal segments). (Plate XVI, fig. 1.)

(Note.—There is another pair on the first abdominal segment, but it is microscopic).

B. Mandibles Short, not extending in front of Head.

I. **Caudal setae densely haired throughout their length.*

†*Tarsal claws not toothed underneath* (Plate XVI, fig. 12) Siphlonuridae.

With seven pairs of gills.

1. *Gills held upright over the dorsum.*

(i) Gills forked and with numerous spines (Plate XVI, fig. 3). *Coloburiscus*, Eaton.

(Median caudal seta very short).

(ii) Gills lamellate and recumbent on dorsum (Plate XVI, fig. 2). . . . . *Oniscigaster*, McLachlan.

(7th pair microscopic).

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* Except *Coloburiscus*.

† The claws of *Ameletus ornatus* have a number of very minute serrations underneath, but these are very much smaller than those of a Leptophlebiid claw.

2. *Gills held extended laterally: lamellate* (Plate XVI, figs. 4 & 5).
   (i) Head small (Plate XVI, fig. 10): palps three-jointed: outer caudal setae haired internally . . *Ameletus*, Eaton.
   (ii) Head large and skull-like (Plate XVI, fig. 11): palps many-jointed: outer setae haired on both sides *Ameletopsis*, gen. n.

II. *Caudal setae with whorls of a few thin, short hairs at joints. Tarsal claws toothed underneath* (Plate XVI, fig. 12) . LEPTOPHLEBIIDAE.
   A. *Gills double* (Plate XVI, fig. 8) . . . . . *Atalophlebia*, Eaton.
   B. *Gills single* (Plate XVI, figs. 6 & 7) . . . *Deleatidium*, Eaton.

Family EPHEMERIDAE.

This family is identical with Lestage's (10) family EPHEMERIDAE and Needham's (8) sub-family EPHEMERINAE.

In New Zealand the "diggers" are represented by only one genus, *Ichthybotus*. It very greatly resembles the type *Ephemera* of Eaton (4), having the characteristic digging tusk projecting in front of the head, the modified fore-legs which assist fossorial operations, and the double feathery gills which are held over the dorsum and keep aerated water circulating in the creature's burrow.

It differs from *Ephemera* in that the head does not narrow anteriorly; the tusks are shorter, broader and curve *inwards*, not outwards apically; the clypeus is not deeply incurved anteriorly; the setae are shorter in proportion to the length of body, and the labrum is wider in proportion to its length and has concave lateral margins.

Genus **Ichthybotus,** Eaton (1899).

Mandibles prolonged in front of the head in the form of tusks, which curve inwards apically. Maxillary palp of three segments; labial palp of two segments. Antennae long, filiform. Body elongated, tapering posteriorly, convex dorsally. Legs robust, densely haired: order of length, 3, 1, 2: anterior pair adapted for digging: claws untoothed. Six pairs of double feathery gills held upright over dorsum on the second to seventh abdominal segments and one minute, rudimentary pair, each gill in the form of a bifid lash, on the first abdominal segment. Caudal setae short, densely haired on both sides: median seta slightly longer than the others.

There are two species, *I. hudsoni* (McLachlan), which is well distributed throughout New Zealand and is described below, and *I. bicolor*, Tillyard, which occurs in certain parts of the northern districts of the South Island.

Of this second species, Dr. Tillyard writes in a recent letter. . . .

"This latter larva does not differ very much from the larva of the North Island species, *I. hudsoni*, but is smaller and darker in colour. The specimens which we found were in loose, coarse, mixed shingle and mud in the river bed, not actually tunnelling in clay, though the latter is the usual habit for the North Island species."

Until quite recently I had not had the opportunity of seeing this species, but on Jan. 23rd, 1930, I captured a single specimen in the Gowan river, Nelson Province. This nymph was fully-grown, but unfortunately it died before reaching my aquarium at Wellington. However, it was obviously almost ready to transform to the sub-imaginal stage, so that a dissection of the wing-pads

proved it to be a nymph of *I. bicolor*. Whilst alive, the dorsal aspect of the head, the mandibular tusks and fore-legs all had a reddish tinge.

In the summer of 1929–30 I found similar nymphs in the North Island, not in burrows but among rock and rubble in George's Creek, a small tributary which feeds the headwaters of the Wainui-o-mata, about 15 miles east of Wellington.

Unfortunately I was unsuccessful in rearing them, as they met with an accident in the aquarium.

This suspected change of habitat from tunnels in sand or loose mud to living in loose rubble is most interesting, but requires further confirmation.

Incidentally, the opportunity is taken of pointing out that gills are present on the first *seven* abdominal segments, not on the first *six*, Hudson (1) having apparently mistaken the second abdominal segment for the first, which is fused with the metathorax and which bears very minute, reduced gills.

Moreover, the writer would like to submit the opinion that Lestage (10), in describing the family EPHEMERIDAE, was mistaken in regarding the mandibular tusk as a canine, for both outer and inner canines are present, in addition to the tusk, in our species, as indeed they are in American (see Murphy (12), text-fig. 1, p. 16) and European species (Eaton (4), plates, and Needham (13), plates).

A characteristic nymph of this family, *i.e.* a "digger," burrows in the sandy or muddy banks of streams below water-level. It swims with dorso-ventral, undulating movements of the body.

An Ephemerid nymph (*E. vulgata*) was described in some detail by Vayssière (16), and these are very similar.

There is one peculiarity in the structure of this nymph which is very puzzling. As I have seen no mention of it in descriptions of nymphs from other places, it may be a local characteristic. This is the presence of a few feathered hairs, among the normal type, on the legs of specimens of this genus; these hairs occur mainly along the edges. The only other nymph which has these curious hairs is *Atalophlebia cruentata*, an entirely unrelated species, and, in this case, they appear on the anterior pair of legs only.

A feathered hair is illustrated (Pl. XX, fig. 9), as are various other parts of the nymph of *Ichthybotus hudsoni*, a typical nymph of this family (Pl. XX, figs. 1 to 11).

It is unusual to find large swarms of a species of this family in New Zealand, as in many other countries, for in the swift streams with beds of rock, boulders or shingle, there are only occasional patches of sand or mud suitable for the tunnels of burrowing nymphs.

If a nymph of *I. hudsoni* is dug out of its tunnel it will bury itself in the nearest sandy patch, burrowing with its fore legs and mandibular tusks and digging itself in with remarkable rapidity.

When about to transform, nymphs in the writer's aquarium left their burrows and floated for some time, unmoving, on the surface of the water, rarely agitating their gills.

A quantity of air was noted under the skin of the thorax and of the anterior part of the abdomen.

The actual metamorphosis, which occurred as usual through a longitudinal rent in the dorsum of the thorax, was extraordinarily swift, in marked contrast to the long time (sometimes hours) spent on the surface waiting for the change. This protracted wait may have been due to the unnaturally still condition of the water present in the aquarium.

The winged stages appear in December, January and February, but, as nymphs of various sizes are seen at this time, it is likely that this fly has a two-year or even possibly a three-year life-cycle.

The wings of the sub-imago sometimes show curious variations from the normal type, and it is hoped to deal with this subject at a later date.

Family SIPHLONURIDAE.

The New Zealand genera, which this family contains, are of especial interest as they possess many uncommon features.

Tillyard (7) considers the members of this family to be very archaic types. At least one genus is also represented in Eastern Australia, and the others show affinities to some of the genera in that district or to those of Tasmania; but, so far as present-day investigations have disclosed, similar types have not been found elsewhere, and though two of our species still remain, for the present, in the genus *Ameletus*, it is practically certain that they do not really belong there.

Owing to various structural features of New Zealand Siphlonurids, it is impossible to adopt, in their entirety, the characters for the sub-family BAETINAE proposed by Needham (8), or those of Lestage's sub-family SIPHLONURINAE, with both of which this family (*i.e.* the SIPHLONURIDAE) corresponds to a considerable degree.

Needham in his classification (8) states :—". . . sub-family BAETINAE; a very heterogeneous series, only definable as lacking the characteristics of the other two " (*i.e.* sub-families EPHEMERINAE and HEPTAGENINAE) " and including five fairly distinct groups. . . ." (It should be pointed out that Needham's sub-families would correspond to present-day families, as his work was written before mayflies had been accorded ordinal rank.)

In spite of the wide range which his statement embraces and the small number of sub-family characteristics—

> " Mandibles without projecting tusk-like ramus.
> Gills not as in EPHEMERINAE.
> Eyes lateral : form of body various : claws smooth or toothed below "—

the fact that one genus (*Ameletopsis*) has the eyes placed dorsally would prevent our adopting this classification; moreover, the range of the BAETINAE is so wide that it would include the Australasian family LEPTOPHLEBIIDAE as well.

Lestage (10) is rather more detailed in his keys; for his family BAETIDAE he gives—

> " Branchies externes, dorsales ou latéro-abdominales, mais toujours visibles."
> " Mandibles très courtes sans aucun prolongement antécéphalique : pattes grêles ou dilatées mais inaptes à fouir; branchies jamais plumeuses : "
> " Yeux latéraux; corps peu ou pas aplati dorso-ventralement, généralement cylindrique."

and for the sub-family SIPHLONURINAE—

> " Ongles jamais plus longs que les tibias, parfois bifides . . .; parfois ongles simples et alors branchies simples, bi- ou monolamellaires, mais sans branchies auxiliaires, et les pattes faiblement ciliées."

Here again *Ameletopsis* does not conform to a number of these conditions. The body is rather pronouncedly flattened dorso-ventrally, the eyes are *dorsal*, the lateral tails are haired on *both* sides.

Neither could *Coloburiscus* be included here, for its legs are not thin and the first two pairs carry long fringes of hair; moreover, the gills are not lamellate and the tails have very short hairs in whorls on both sides.

I therefore assign the following nymphal characters to the family SIPHLONURIDAE—

Nymph of the swimming type; body usually somewhat cylindrical. Eyes generally lateral. Mandibles short, not extending in front of head. With seven pairs of single gills, inserted dorsally or latero-abdominally. Legs short. Claws seldom toothed underneath. Caudal setae *either* strongly fringed with long hair throughout, all three sub-equal in length and shorter than the body, *or* with very short hair in whorls, in which case the lateral setae are about equal in length to the body and the median one is very short.

Genus **Coloburiscus,** Eaton (1887).

Head convex dorsally and with fringe of hair anteriorly. Eyes lateral. Maxillary and labial palps two-segmented and greatly enlarged. Thorax very large and prominent. Anterior and middle pairs of legs with long fringe of hair anteriorly; order of length of legs 1, 3, 2. Claws not toothed. Latero-posterior angles of 3rd to 9th segments of abdomen projecting backwards as sharp teeth. Caudal setae with very short hairs in whorls at joints of segments; the outer setae about as long as the body; the middle one very short. With a pair of gills on each of the first seven abdominal segments, held upright over the dorsum. Each gill composed of a divergent fork with connective membrane basally and covered with spines.

Habitat in rapids and the fast-flowing parts of streams.

There is only one species, *C. humeralis* (Walker), which is widely distributed throughout New Zealand.

This is the unknown nymph mentioned and figured by Lillie (17); and Hudson (1) has a short description of it.

It lives among the rapids and swiftly-flowing portions of the streams and will not live in poorly-oxygenated water. Both Lillie and Hudson attempted to rear it, but were unsuccessful. Nevertheless, given an aquarium with a constant stream of well-aerated water running through it, the nymph can be kept for months quite successfully and will eventually transform into the sub-imaginal stage. As in all members of this family, the transformation does not take place from the surface of the water but from some solid support on to which the nymph crawls and leaves its cast nymphal skin.

This species is found attached to stones, rocks or boulders and among the vegetable debris which is often lodged among the boulders in rapids. Here, it will cling with remarkable tenacity despite the force of the current, helped doubtless by the many spines, with which its legs and the ventral surface of its abdomen are armed.

It is a poor swimmer, moving its legs in unison jerkily backwards and forwards, and there is at the same time a slight dorso-ventral movement of the tip of the abdomen; after a few spasmodic jerks, it often stops and curves the hinder part of its abdomen upwards and forwards.

The fringes of hair on its fore legs and mouth-parts (Pl. XXI, figs. 1 and 2) would seem to form a plankton straining apparatus, which enables it to secure

food from the rapidly-passing water without undue exertion, while its peculiar gills—unlike those of other New Zealand mayfly nymphs—are held motionless, as it is unnecessary for the insect to move them to obtain fresh oxygen in the swift currents of its habitat.

No other species of this order in New Zealand has succeeded so well in adapting itself to torrential aquatic conditions, and consequently it is the predominant nymph of the rapids.

Metamorphosis to the sub-imaginal stage occurs at the end of spring and throughout the summer.

Illustrations of details of the structure of this nymph are included. (Pl. XXI, figs. 1 to 6.)

Dr. Tillyard kindly sent me specimens of an undescribed Australian nymph of this genus (see p. 408) in which it was interesting to note that the median caudal seta was as long as the others and that the gills had accessory tufts of fibrils at the base.

Genus **Oniscigaster,** McLachlan (1873).

Oniscoidal in form. Head small. Eyes lateral. Antennae short. Labial and maxillary palps, each of three segments. Thorax broad. Wing-pads small. Legs short, robust, almost smooth: order of length, 3, 2, 1. Claws not toothed underneath. Lateral caudal setae strongly fringed with hair on the inner margins, median seta fringed on both margins. The setae are rather less than half as long as the body, the median one being slightly shorter than the others. Latero-posterior angles of segments one to nine of abdomen are strongly toothed outwards in the shape of flanges with recurved backwardly-directed points. There is a median dorsal crest in the form of longitudinal carinations on the abdominal segments. Those of segments two to nine project backwards like the teeth of a saw, each over the segment posterior to it. Gills in the form of lamellate lobes, diversiform and marbled, their edges irregular, are borne on the first six abdominal segments: they are held lying over the dorsum and almost meet along the median line. There is also a very minute pair of gills attached to the posterior margin of the seventh segment.

There are three species, *O. wakefieldi*, McLachlan, described by Eaton (4) and found in the South Island many years ago, but since reported to be becoming extinct (2), *O. distans*, Eaton, noted by Hudson (1), and *O. intermedius*, a North Island species, the nymph of which has not been described, but which appears to be indistinguishable from *O. distans*.

Oniscigaster nymphs are by no means plentiful; they may be found in a number of places, generally in cold, moderately-flowing, well-bushed streams, very seldom in rivers, the banks of which have been cleared of bush, and this is probably because the birds destroy the winged stages if they have no shelter, for the large handsome sub-imago, emerging from its nymphal exuvia on a boulder, is a conspicuous object, and, moreover, it remains in this stage for three days before the final transformation. Consequently, its chances of achieving maturity are proportionately reduced.

The nymph is very sluggish, but its very inertness saves it from extinction by the trout, for these fish usually prefer moving food-organisms. Its marvellous camouflage makes it very difficult to find; furthermore, it often buries itself in the gravel.

Young specimens may be found in very fine gravel, but more mature nymphs occur in coarse gravel, boulders and rock pools. They prefer pools and slow currents, but not stagnant water.

The colour variation of this nymph is most remarkable: it is sometimes

brown, sometimes greyish-green, sometimes whitish, sometimes reddish (a variety has red gills, but the usual colour is khaki); the legs and venter show two clearly-defined types, shown in the figures as type A and type B. Details of *O. intermedius* are illustrated (Pl. XVII, figs. 1 to 8).

Genus **Ameletus,** Eaton (1899).

Nymph torpedo-shaped. Head small. Antennae short. Eyes lateral. Labial and maxillary palps three-jointed. The canines coalesced. Wing-pads large and conspicuous. Legs, short, robust, sub-equal. Claws minutely toothed underneath. Abdomen tapering posteriorly. Latero-posterior angles of segments sharply toothed backwards. Caudal setae about half as long as body; the median seta is slightly shorter than the others and is plumose; the outer setae are thickly fringed with hair on the inner margins only. Simple lamellate gills are borne on the first seven abdominal segments; they are held laterally. The edge of the lamellae are finely toothed and the venation is pinnate.

It will be noticed that the mouth-parts in the species illustrated (Pl. XXII, figs. 5 to 9) are quite different from those of *Ameletus* spp. in the Northern Hemisphere, and when the adult characters of local species have been thoroughly re-examined, it is very likely that a new genus will have to be established for them.

There are two species, *A. ornatus* (Eaton) and *A. flavitinctus*, Tillyard. Hudson (1) has notes on the nymph of the former species, but that of the latter was only discovered in November 1929 in the river Wainui-o-mata, when a nymph, which I had captured there and which appeared to be a very dark variety of *A. ornatus*, transformed into a female sub-imago, which I was able to identify from Dr. Tillyard's paper (6) as *A. flavitinctus*.

Both nymphs will be described in another paper, but some of the details of the structure of *A. ornatus* are illustrated (Pl. XXII, figs. 1 to 9).

Ameletus nymphs are the best examples of the "swimmer" type of mayfly in New Zealand, their powers in this respect far exceeding those of any other Ephemerid species in this country.

Their distribution is widespread, and they occur in most streams except the very sluggish ones. They can exist either in swift currents or in the pools between rapids; they are found both on the upper and on the lower surfaces of boulders, as well as on their vertical sides; they are also found on vegetation at the edges of streams.

When at rest they have, more than any other mayfly nymphs, the curious habit of swaying their setae and the hinder part of the abdomen gently, at intervals, in a dorso-ventral arc.

The movement of these nymphs is so rapid that to the eye it appears as a swift wriggling dart, of which the component motions cannot be perceived. Careful and prolonged observation, however, shows that the movement is made by rapid dorso-ventral shakes of the "tail" and of the posterior part of the abdomen, through a short arc. The legs appear to be used to assist movement and are not held folded back against the body, as in the case of the American *A. velox*, Dodds (Dodds & Hisaw, 14).

Nymphs in captivity will often turn over on their backs, if disturbed, and appear as if dead; whether this is a simulation of death or an actual disturbance of balance due to unknown conditions is open to question; after an interval —which may vary from a few seconds to some minutes—they recover. When narcotised with chloral hydrate, they assume a similar posture.

The nymphs become full-grown during the summer months—though some do not transform till March, and a few even wait till April—when they leave the water and change to the sub-imaginal stage on a stone or boulder.

Genus **Ameletopsis,** gen. nov.

One other insect has been included hitherto among the New Zealand species of *Ameletus,* but for reasons given below (as regards the nymph) and elsewhere (as regards the winged stages), I have placed it in a new genus.

Description.

Structure adapted partly for swimming, partly for creeping. Body more or less flattened dorso-ventrally: head in much the same plane as body. Caudal setae short, sub-equal, fringed with hair on both sides; three in number. Gills on the first seven abdominal segments, consisting of large, round, entire, single, simple leaflets with central pinnate tracheae. Latero-posterior angles of abdominal segments prolonged backwards as sharp teeth. Eyes of male unlike female. Legs alike and sub-equal. Mouth-parts strongly developed; canines very long; palps multi-articulate.

Particulars of some of the structural features of this nymph are illustrated (Pl. XIX, figs. 1 to 8).

Ameletopsis perscitus, Eaton.

The nymph of this mayfly is unique in many respects. Its structure differs so markedly from that of the genus *Ameletus,* and moreover from that of the family or sub-family to which this genus is assigned by writers in the northern hemisphere, that there is little doubt that it has been incorrectly placed.

Indeed Tillyard (6) in his description of *Ameletus flavitinctus* states :—

"It seems advisable here to point out that *A. perscitus,* Eaton, differs very greatly from both *A. ornatus,* Eaton, and *A. flavitinctus,* n. sp., in the shape of its wings, the density and regularity of their cross-venation and in the remarkable structure of its large-headed larva. These characters, taken together, suggest that it is not really congeneric with them. Further than this, a study of the three New Zealand species shows that they differ considerably from the genotype *A. subnotatus,* Eaton, from North America, and it appears probable that they may have to be placed in two new genera."

Hitherto, the larva does not appear to have been described, studied and compared with other larvae of the same genus, and the only notes on it are a few lines by Eaton (5), p. 291, and by Hudson (1).

Needham (8) considers the mayflies to be a single family and divides them into three sub-families, whereas Lestage (10) ranks them as an order and groups them in five families. However, Needham's sub-family BAETINAE corresponds very closely to Lestage's family BAETIDAE—*not* to be confused with his sub-family BAETINAE, for it is to his sub-family SIPHLURINAE that he assigns the genus *Ameletus.* Needham has no sub-division corresponding to this sub-family.

The species under discussion, *A. perscitus,* cannot be included in Lestage's genus *Ameletus* because the head of this species is not vertical but horizontal, the external edges of the gills are not toothed or haired but smooth, and their

tracheal ramification is considerable, not "little ramified"; moreover the palps are not three-segmented but multi-articulate: this, also, takes it out of Eaton's nymphal group (p. 317 (4)), on which most of the work of Needham and Lestage is based, and puts it in a group with his unknown Chilian nymph, to which alone the mouth-parts of *A. perscitus* bear some resemblance, but the structure of other parts of these two is totally different. It cannot be included even in Lestage's sub-family SIPHLURINAE, to which he assigns the genus *Ameletus*, for this sub-family has the outer caudal setae fringed internally only, whereas those of *A. perscitus* are fringed on both sides.

Needham also groups various genera, among which is *Ameletus*, as having the outer caudal setae fringed only on the inner sides, and further states that in the genus *Ameletus*, the ends of the maxillae are fringed with pectinated hooks. *A. perscitus* does not correspond to this description.

Habits.

This nymph is carnivorous, feeding on small specimens of Leptophlebiid nymphs and other organisms.

Though found under stones in rapid water, its favourite haunt is some dark, still backwater or a shallow, slowly-flowing portion at the edge of a stream. Here it will lie perfectly still on a stone or in a crevice, except for an occasional movement of the gills, its camouflage colouring making it very difficult to detect. At times, it will walk forward with a gliding motion for a few inches, "freeze" for some seconds, and then move forward again. It has a habit of brushing its mouth-parts with its anterior pair of legs. Another characteristic is its trick of peering cautiously round the edge of a stone and stalking slowly forward. Though sluggish, when thoroughly disturbed it can move with considerable rapidity, swimming strongly with quick, somewhat jerky movements of its body.

It becomes full-grown from December to March, when it crawls on to a stone above water-level to transform to the sub-imaginal stage.

This species occurs throughout the Wellington, Hawkes Bay, Nelson and Canterbury provincial districts, and is moderately abundant and evenly distributed.

The adult has been described by Eaton (5). Examination of the imago shows certain differences between it and the general type of *Ameletus*, which are sufficient, when taken in conjunction with those of the nymph, to justify making a new genus for it.

Family LEPTOPHLEBIIDAE.

This family, which contains mainly the smaller mayflies, comprises more than half the species in New Zealand. Some of them are very much alike and hard to distinguish from each other, and it will probably be a considerable time before all the species in this country have been identified and described.

Five species of LEPTOPHLEBIIDAE were known until recently; during the last three years, I have found eight new ones, making a total of thirteen species. They form a heterogeneous group, the species being much alike, in sharp contradistinction to the species of the SIPHLONURIDAE, which are extraordinarily diversiform.

Needham (8) has no equivalent division, for although his sub-family BAETINAE would cover all the genera in our family LEPTOPHLEBIIDAE, it would also embrace most of the SIPHLONURIDAE as well.

Lestage (10) has a sub-family LEPTOPHLEBIINAE of his family BAETIDAE, which would fit, with one modification. He states :—". . . Sept paires de branchies tantôt semblables et, dans ce cas, toutes filamenteuses, tantôt dissemblables et alors la première paire rudimentaire et les six suivantes plus ou loins lamelliformes. . . ."

In the case of New Zealand species, the gills of the first pair (of the latter alternative) are not rudimentary and are kidney-shaped.

Description.

Nymph of the crawling type: body more or less flattened dorso-ventrally. Eyes lateral. Antennae long and filiform. Mandibles short, not extending in front of head. Maxillary and labial palps three-segmented. Galea-lacinia of maxilla terminating apically in a broad brush of brown hair and a number of minute pectinate rakes. Wing-pads generally prominent. Legs long, spinose: femora oval: claws toothed underneath. Posterior-lateral angles of segments of posterior half of abdomen toothed backwards. Caudal setae long, median ones usually slightly the longest: whorled on both sides with very short hairs. Gills borne laterally on the first seven abdominal segments, sometimes alike and then in the form of a bifid lash, sometimes dissimilar and then the gills of the first pair are kidney-shaped, those of the remaining pairs round or ovate.

There are two genera, the one, *Atalophlebia*, with double gills, the other, *Deleatidium*, with single ones.

Genus **Atalophlebia,** Eaton (1881).

Nymph of the crawling type. Body somewhat flattened dorso-ventrally. Eyes lateral. Antennae long and filiform. Maxillary and labial palps three-segmented. Labrum always less than three times as broad as it is long and notched medio-anteriorly. Maxilla with broad terminal brush of long brown hairs and small pectinate rakes. Wing-pads large. Legs, long, spinose: femora usually somewhat dilated: claws toothed underneath. Latero-posterior angles of abdominal segments mostly toothed backwards, pronouncedly so in the posterior half. Caudal setae of varying length, minutely haired at segmental junctions; median one longest. Pairs of gills borne laterally on the first seven abdominal segments: the gills are double and consist of a double lash or pair of lanceolate or ovate-acuminate lamellae: venation pinnate. The gills of the posterior pair are often aborted.

It should be noted that the nymphal characters of our species differ somewhat from those defined as generic characters by Needham and Murphy (9).

For example :—" Posterior-lateral angles of rear abdominal segments not tipped with thin flat lateral spines. . . ." On the contrary, our nymphs have teeth or spines in these segments, notably *A. cruentata.* Again, ". . . Femora regularly tapering from near the base, not dilated. . . ." In our species, the femora *are* dilated and the broadest part is at or near the middle of this segment. Further, the labrum could hardly be described as " narrowly elliptical " and the " acute median notch in front " is sometimes merely a slight curved identation.

On p. 36 *tom. cit.*, however, there is a conflicting description of Atalophlebiid nymphal characters, and the nymphs are described as having lateral spines on abdominal segments 5 to 9 and the femora as dilated.

The other characters specified on this page do not agree with the characters of our species, *i.e.* the distal tooth under the tarsal claw is not minute—compared with the others—but slightly larger, the width of the labrum does not exceed the length three times but is not quite twice as long, and the glossae are not conic-pointed in any of our species.

Some structural features of a typical species, *Atalophlebia versicolor*, are illustrated (Pl. XVIII, figs. 1 to 10).

All the members of this genus are found either among debris in the river bed in slow-flowing parts of streams, e.g. *A. versicolor*, or among stones or shingle in slow (*A. cruentata*) or moderately-flowing parts of streams (*A. nodularis*). They are poor swimmers, moving with a jerky, awkward, undulating motion of the body, agitating the legs rapidly and closing the setae, which are normally held well spread out. They can, however, edge sideways and retreat backwards with great agility, and when pursued do so, seeking shelter in a crevice or under a stone and seldom attempting to escape by swimming away. To try and capture a number of nymphs of this genus (especially *A. cruentata*) is to receive an object lesson in minor tactics and the use of ground and cover.

The nymphs of *A. versicolor* and *A. dentata* are much alike, the latter is figured by Hudson (1) and the former may be distinguished from it by the yellow longitudinal stripe, which it bears, placed medianly, on the dorsum.

A. cruentata is bright orange-red and therefore easily recognisable. *A. nodularis* is like a small edition of *A. cruentata*, but is dull-coloured. Lillie (3) figures it, but his drawing is not much like the nymph and the description is very meagre. Its gills, unlike those of the other species, which are all of the *A. versicolor* type (Pl. XVI, fig. 8), are each composed of a bifid lash, each component of which has a strong, central, unbranched trachea.

Genus **Deleatidium,** Eaton (1899).

Nymph of the crawling type. Body markedly flattened dorso-ventrally. Nymphs generally found under stones. Head square. Eyes lateral. Antennae long and filiform. Maxillary and labial palps three-segmented. Labrum at least three times as broad as it is long and notched medio-anteriorly. Maxilla with broad terminal brush of long brown hairs and small pectinate rakes. Wing-pads large. Legs long, spinose; femora very much dilated; claws toothed underneath. Latero-posterior angles of abdominal segments mostly toothed backwards, pronouncedly so in the posterior half. Caudal setae as long as or longer than the body; median seta longest. Pairs of gills borne laterally on the first seven abdominal segments: the gills are single: those of the first pair are kidney-shaped those of the other pairs are ovate-acuminate or sub-rotund.

There are slight differences in the characters of *Deleatidium* nymphs referred to here and those ascribed to that genus—with reference to neotropical species—by Needham and Murphy (9).

This genus was established by Eaton from preserved specimens of a single species sent to him from New Zealand; he distinguished it from *Atalophlebia*, in that in the latter genus the nymphs had double gills and the adults had claws alike in each tarsus, whereas in *Deleatidium* the nymphs had single gills and the adults had claws dissimilar in each tarsus.

The discovery of several new species during my researches has shown that the classification of the LEPTOPHLEBIIDAE is by no means as simple as it appeared at first. Discussion of this matter will be left to another paper as adult characters are involved, and, for present purposes, *Deleatidium* nymphs will be considered as Leptophlebiids with single gills.

With the exception of the gills, there are no differences of major importance between the nymphs of *Deleatidium* and those of *Atalophlebia*. In the former genus the body is rather more pronouncedly flattened dorso-ventrally, the labrum is perhaps longer and narrower and always has a decided median notch in the anterior border, the femora are always dilated and are flattened

dorso-ventrally, the head is square (in *Atalophlebia* spp. it is more rounded anteriorly), and the caudal setae are never shorter than the body, as they sometimes are in *Atalophlebia*.

Deleatidium nymphs are found mainly on the under surfaces of stones in waters of varying rapidity. They are difficult to dislodge; in fact, *D. myzobranchia*—a species with rounded gills—appears to use its gills sometimes as suckers. Species of this genus are also found buried in the sand and shingle of the river-bed and—especially in winter—among submerged moss and waterside vegetation.

Three of the species, *D. lillii*, *D. vernale* and *D. autumnale*, are so much alike that they can only be differentiated, with certainty, when they transform.

Individuals of *Deleatidium* spp. are more numerous than those of any other genus, perhaps because of their superior adaptability to different conditions, such as the rate of flow of the current and the variation in oxygen content of the water.

In the Wellington district, nymphs of *D. lillii* have been seen to metamorphose almost all the year round, even in midwinter.

It is of interest to note, however, that two specimens (one male and one female), which were secured as nymphs on July 4th, 1929, changing the same day into sub-imagines, failed to reach the imaginal stages. They attempted to do so in the laboratory about thirty-six hours later, but apparently had not the necessary energy and died, partly metamorphosed. Whether this is usually, or perhaps often the case in winter is not known.*

Deleatidium nymphs are extensively eaten by trout and by other fish, as well as by predatory insects such as the nymphs of some stoneflies and the larvae of carnivorous aquatic beetles; they have other enemies, also, for Nematode worms may often be found in their stomachs.

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* In further transformations during June 1930, this experience was repeated.

References.

(1) Hudson, G. V. 1904. New Zealand Neuroptera.

(2) Hutton, F. W. 1898. The Neuroptera of New Zealand. Trans. N.Z. Inst., **31.**

(3) Lillie, C. O. 1898. On New Zealand Ephemeridae. Trans. N.Z. Inst., **31.**

(4) Eaton, A. E. 1883–88. A Revisional Monograph of Recent Ephemeridae. Trans. Linn. Soc. Lond., (2) **3.**

(5) ——. 1899. An annotated list of the Ephemeridae of New Zealand. Trans. Ent. Soc. Lond., **1899.**

(6) Tillyard, R. J. 1923. Description of two new species of mayflies from N.Z. Trans. N.Z. Inst., **54.**

(7) ——. 1926. Insects of Australia and New Zealand.

(8) Needham, J. G. 1904. Mayflies and Midges of New York, Bull. N.Y. State Mus., **86.**

(9) Needham, J. G., and Murphy, H. 1924. Neotropical Mayflies. Bull. Lloyd Libr., **24.**

(10) Lestage, J. A. 1917. Larves des Éphémères Paléarctiques, Ann. Biol. lacustre, **8.**

(11) McLachlan, R. 1894. Some additions to the Neuropterous fauna of New Zealand, with notes on certain described species. Ent. Mon. Mag., **30.**

(12) Murphy, H. 1922. Notes on the Biology of some of our North American Mayflies. Bull. Lloyd Libr., **22.**

(13) Needham, J. G. 1917–18. Burrowing Mayflies of our larger lakes and streams. Bull. U.S. Bur. Fish., **36.**

(14) Dodds, G. S., and Hisaw, F. 1924. Ecological Studies of Aquatic Insects. Ecology, **5.**

(15) —— ——. 1925. Ecological Studies on Aquatic Insects. Ecology, **6.**

(16) Vayssière, A. 1882. Recherches sur l'organisation des Larves des Ephémériens. Ann. Sci. Nat. (Zool.), (6) **13.**

(17) Lillie, C. O. 1900. Notes on New Zealand Ephemeridae. Trans. N.Z. Inst., **33.**

(18) Morgan, A. H. 1913. A Contribution to the Biology of Mayflies. Ann. Ent. Soc. Amer., **6.**

(19) Tillyard, R. J. 1923. The Wing-Venation of the Order Plectoptera or Mayflies. J. Linn. Soc. (Zool.), **35.**

(20) Heymons, R. 1896. Ueber die Lebensweise und Entwickelung von *Ephemera vulgata*, L. SitzBer. Ges. naturf. Fr. Berlin, **1896.**

(21) Boerner, K. 1908. Die Tracheenkeimen der Ephemeriden. Zool. Anz., **33.**

(22) Buchanan, R. O. 1930. Hydro-electric Power Development in New Zealand. Geogr. J., **75.**

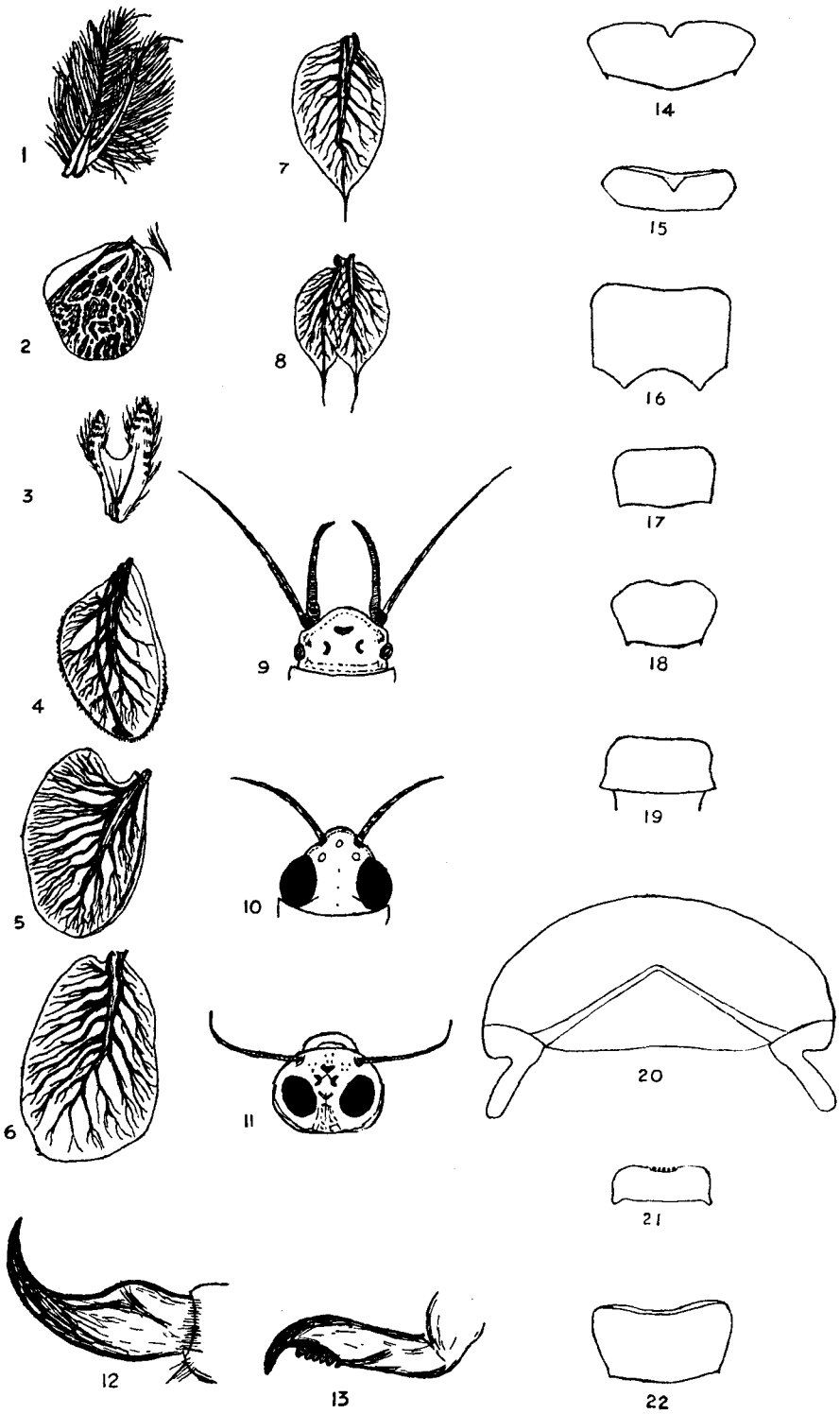
(23) Phillips, J. S. 1929. A Report on the Food of Trout. Fish. Bull. N.Z., **2.**

(24) Tillyard, R. J. 1921. Neuropteroid Insects of the Hot Springs Region, New Zealand, in Relation to the Problem of Trout-food. N.Z.J. Sci. Tech., **3.**

(25) Phillips, J. S. 1931. A Further Report on Conditions Affecting the Well-being of Trout in New Zealand. Fish. Bull. N.Z., **3.**

(26) ——. 1930. A Revision of New Zealand Ephemeroptera. Pt. I. Trans. N.Z. Inst., **61.**

(27) ——. 1930. A Revision of New Zealand Ephemeroptera. Pt. II. Trans. N.Z. Inst., **61.**



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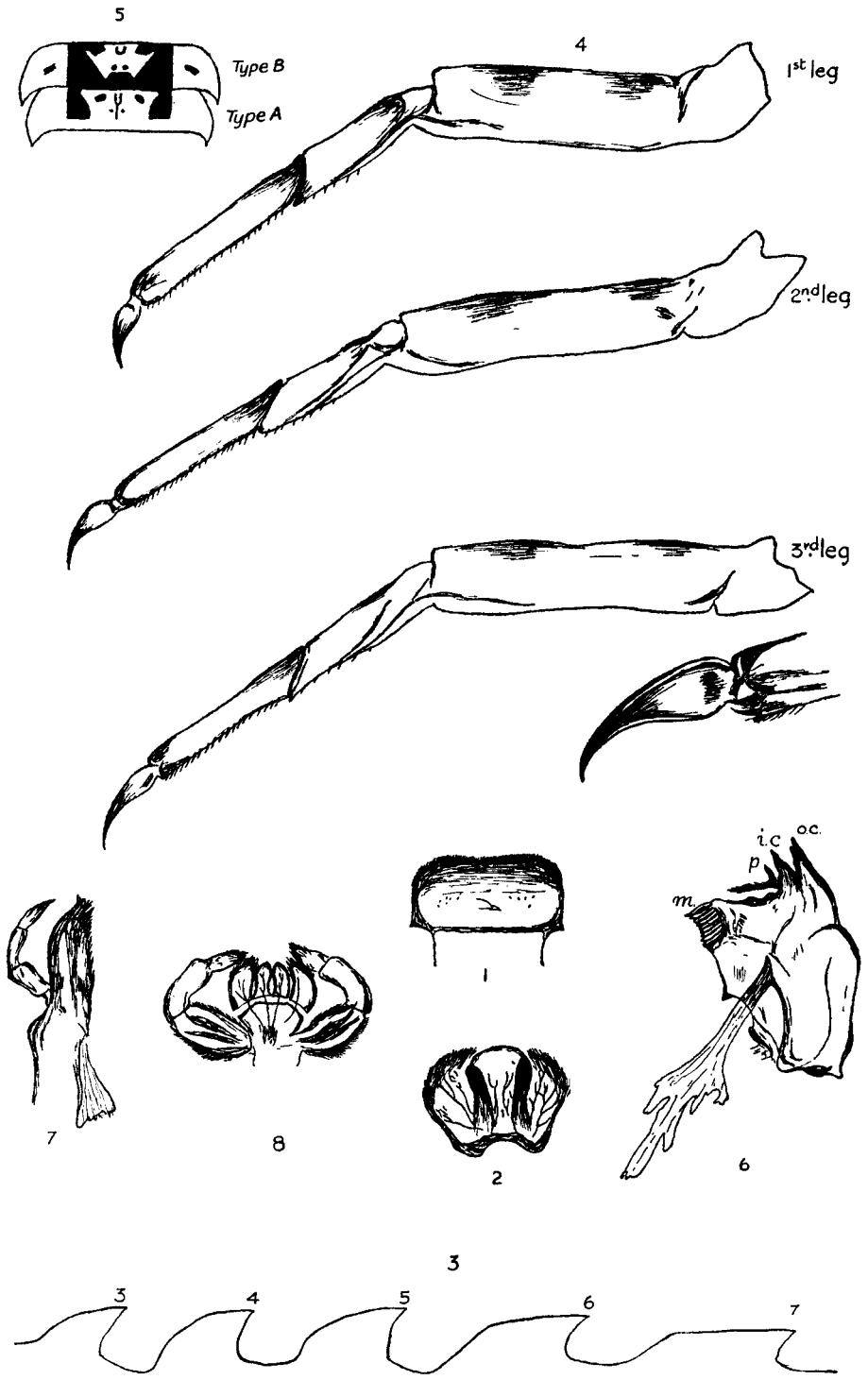

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Explanation of Plates XVI–XXII.

Plate XVI.

Gills.

Fig. 1. *Ichthybotus hudsoni.*
2. *Oniscigaster intermedius.*
3. *Coloburiscus humeralis.*
4. *Ameletus ornatus.*
5. *Ameletopsis perscitus.*
6. *Deleatidium myzobranchia.*
7. *Deleatidium vernale.*
8. *Atalophlebia versicolor.*

Heads.

9. *Ichthybotus hudsoni.*
10. *Ameletus ornatus.*
11. *Ameletopsis perscitus.*

Claws.

12. Family Siphlonuridae.
13. Family Leptophlebiidae.

Labrum of Nymphs.

14. *Deleatidium vernale.*
15. *Deleatidium myzobranchia.*
16. *Ameletus ornatus.*
17. *Coloburiscus humeralis.*
18. *Ichthybotus hudsoni.*
19. *Oniscigaster intermedius.*
20. *Ameletopsis perscitus.*
21. *Atalophlebia cruentata.*
22. *Atalophlebia versicolor.*

Note.—The different figures are not drawn to the same scale.

Plate XVII.

Oniscigaster intermedius (Eaton).

Fig. 1. Labrum, × about 20.
2. Hypopharynx, × about 20.
3. Dorsal crest (3rd to 7th segments), × about 14.
4. Legs, × about 14; claw, × about 30.
5. Types of ventral abdominal segment (diagrammatic).
6. Left mandible, × about 20.
7. Right maxilla, × about 20.
8. Labium, × about 20.

Plate XVIII.

Family Leptophlebiidae.

Fig. 1. *Atalophlebia versicolor:* thorax and abdomen (dorsal view), × 12½.
2. do. do. legs, × 12½.
3. do. do. tarsal claw, × 60.
4. do. do. right maxilla, × 12½.
5. do. do. left mandible, × 12½.
6. do. do. labrum, × 12½.
7. do. do. labium, × 12½.
8. do. do. gills, *ca.* × 12½.
9. do. do. superlinguae, *ca.* × 25.
10. do. do. maxillary rake, much enlarged.
11. do. do. anterior gill, *ca.* × 12½.
12. *Deleatidium vernale*, gills, *ca.* × 7½.

Plate XIX.

Ameletopsis perscitus (Eaton).

Fig. 1. Nymph. Head.
2. do. Labrum, × about 11.
3. do. Left mandible, × about 11.
4. do. Labium and Hypopharynx, × about 11.
5. do. Left maxilla, × about 11.
6. do. Dorsum of 6th abdominal segment.
7. do. Legs.
8. do. Gills.

Plate XX.

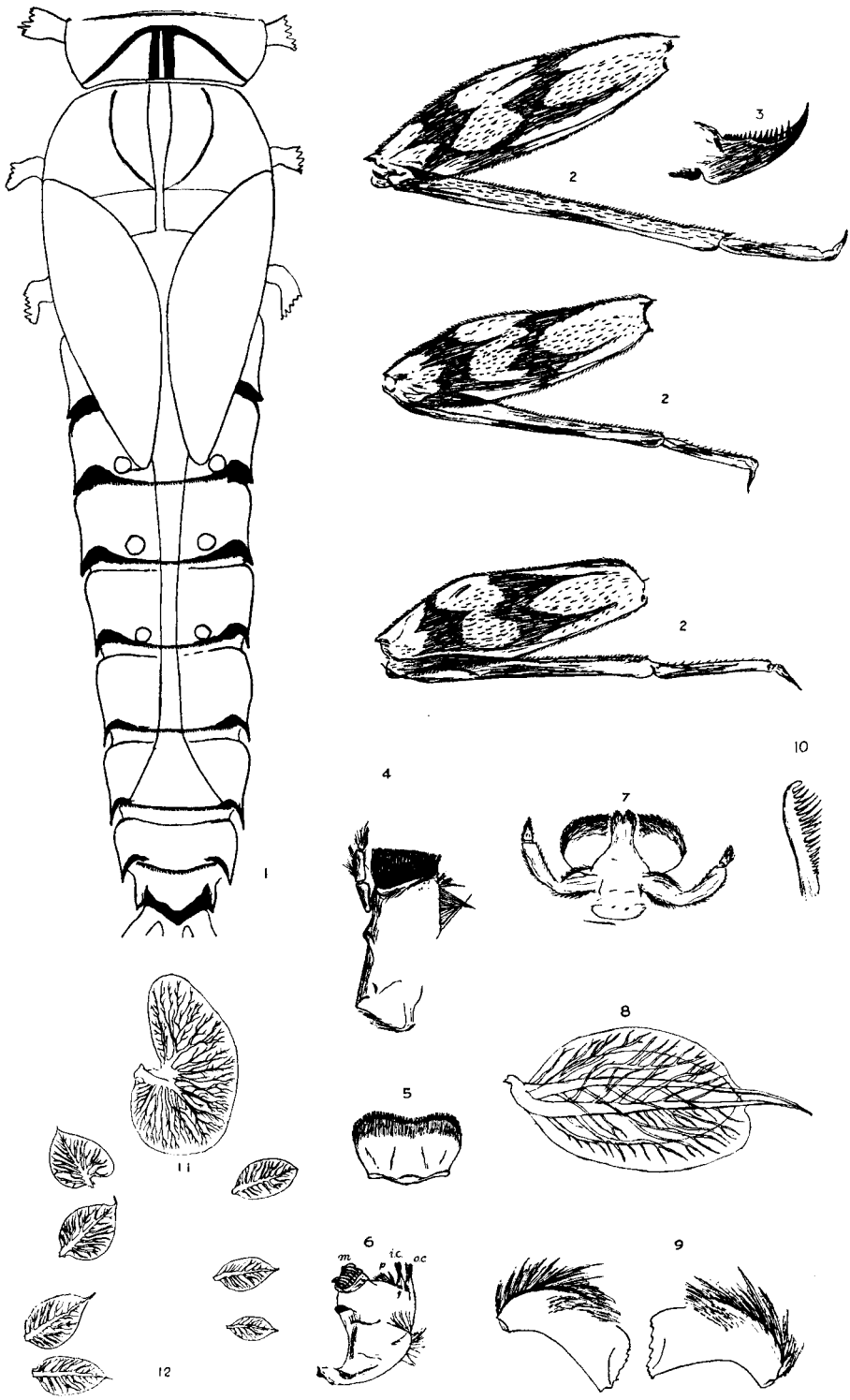
Ichthybotus hudsoni.

Fig. 1. Hypopharynx, × about 30.
2. First pair of gills.
3. Second pair of gills, × about 12.
4. Head (dorsal view), × about 12.
5. Labium, × about 30.
6. Mandible, × about 30.
7. Maxilla, × about 30.
8. Labrum, × about 30.
9. Feathered hair from leg, much enlarged.
10. Claw of third leg, much enlarged.
11. Legs, × about 12.

Plate XXI.

Coloburiscus humeralis (Walker).

Fig. 1. Immature nymph, × about 12.
(In order to show the lateral edges of abdominal segments, the gills on the left are omitted.)
2. Legs, × about 12; tarsal claw, much enlarged.
3. Maxilla, *ca.* × about 25.
4. Labrum, × about 25.
5. Gill, × about 12.
6. Labium, *ca.* × about 25.
7. Mandible, *ca.* × about 25.
8. Canine region of mandible, enlarged.



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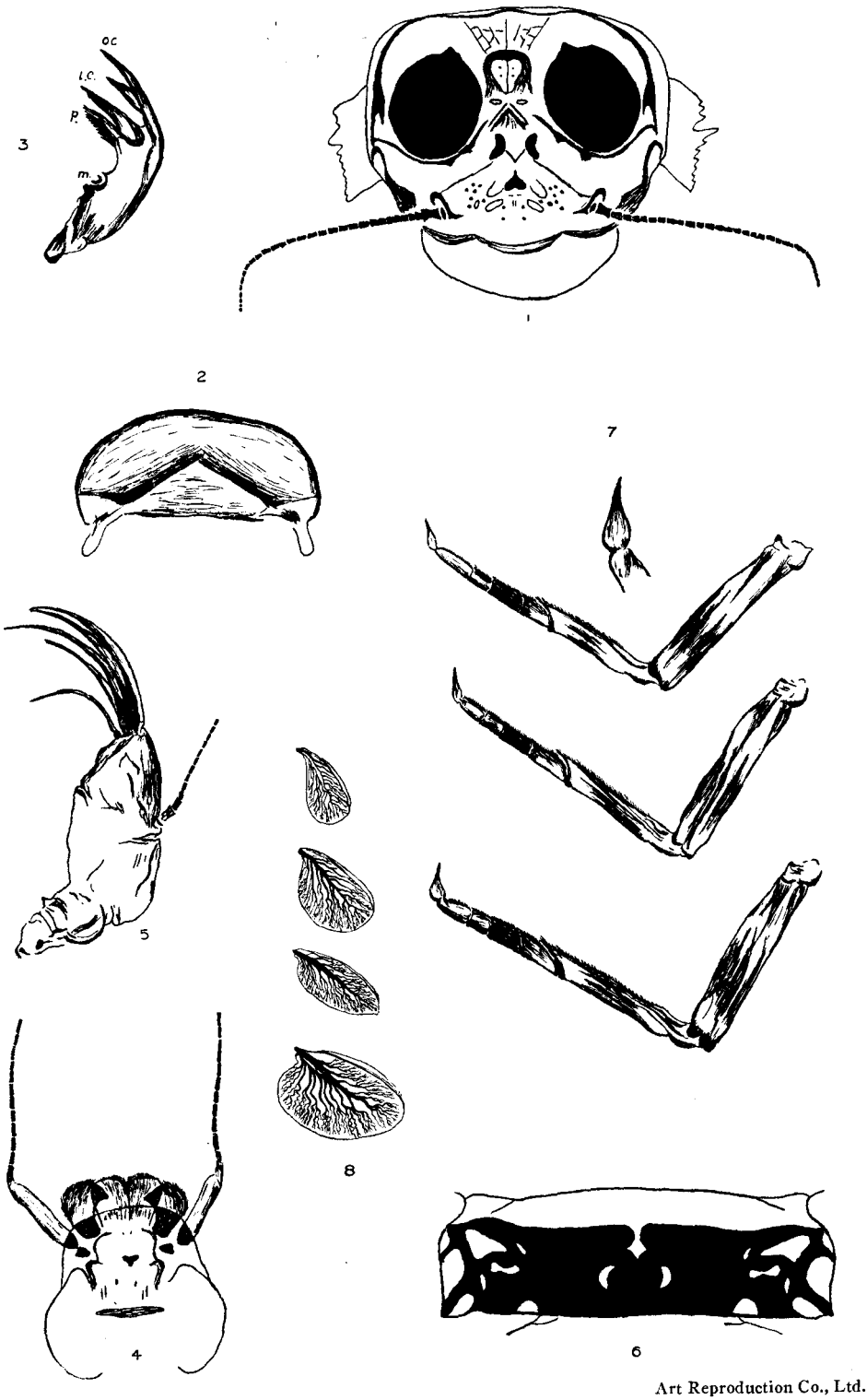

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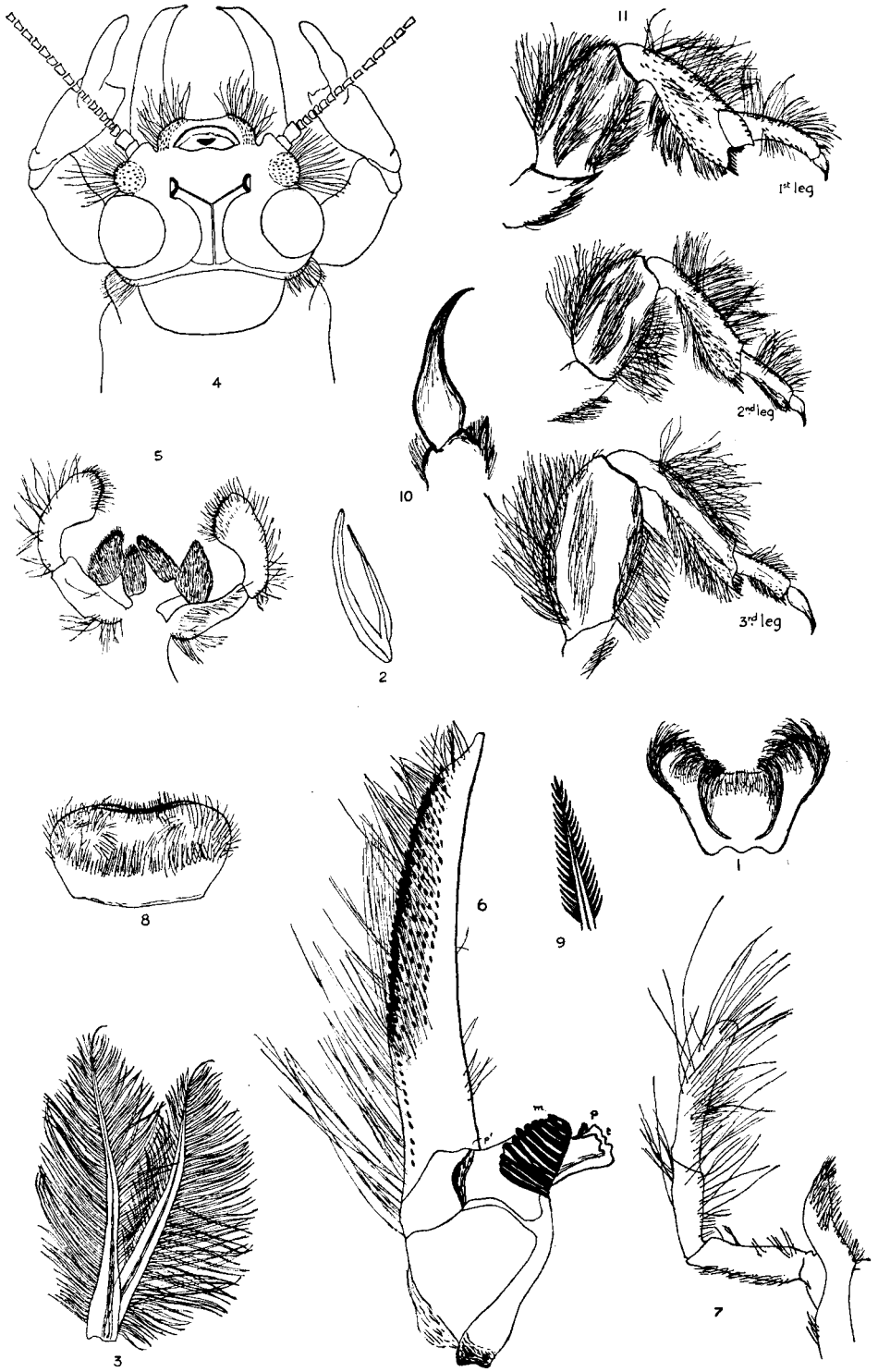

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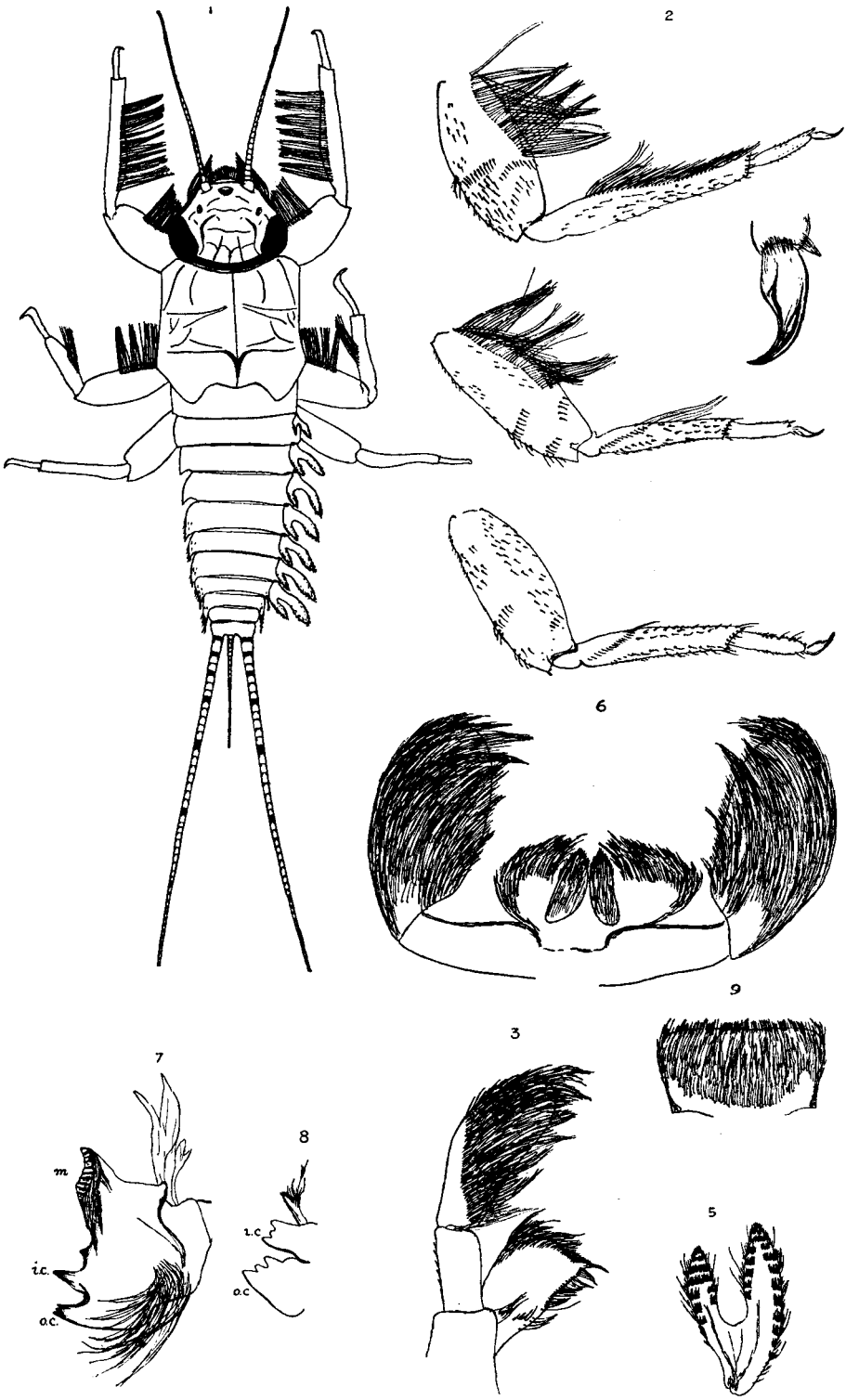

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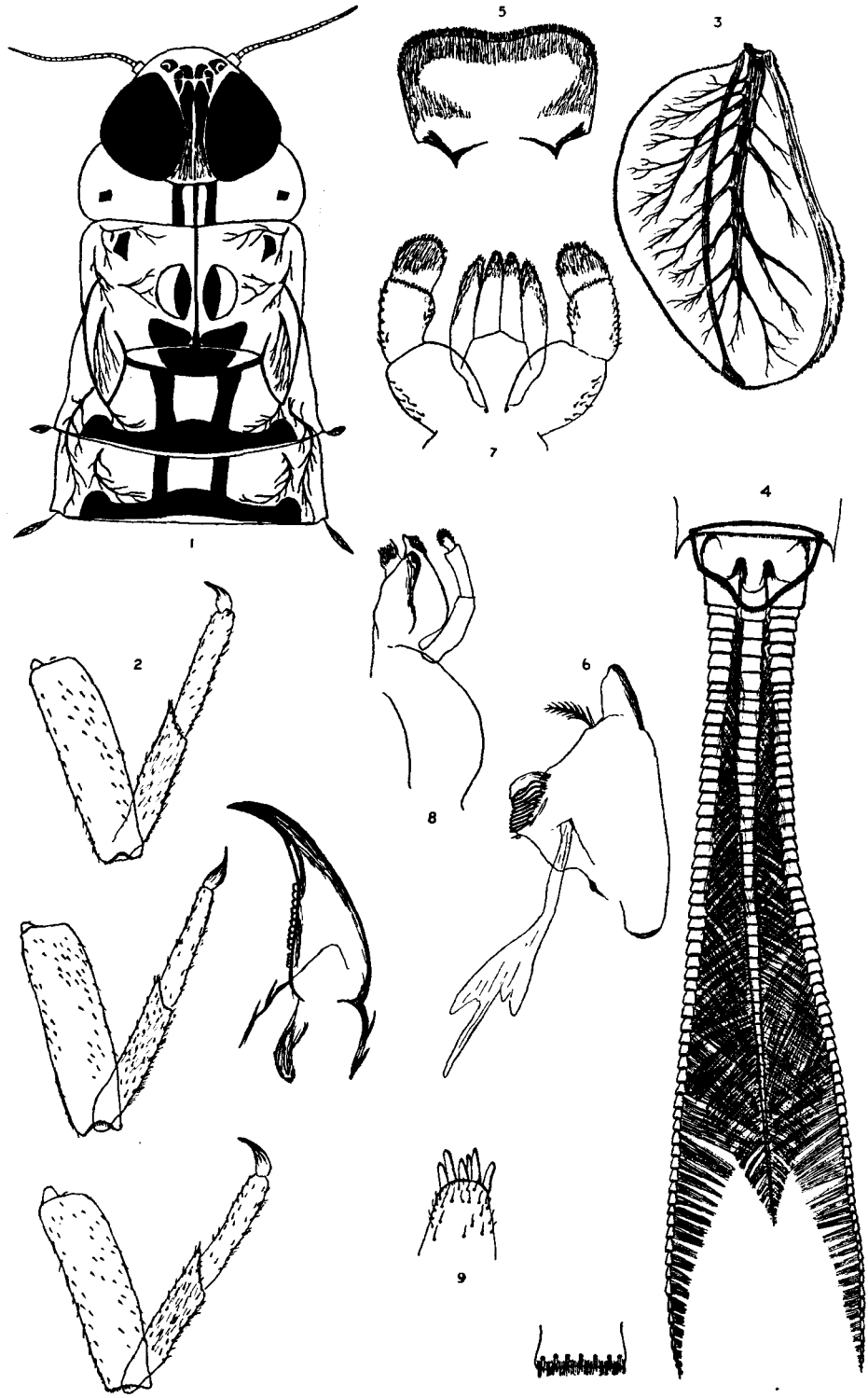

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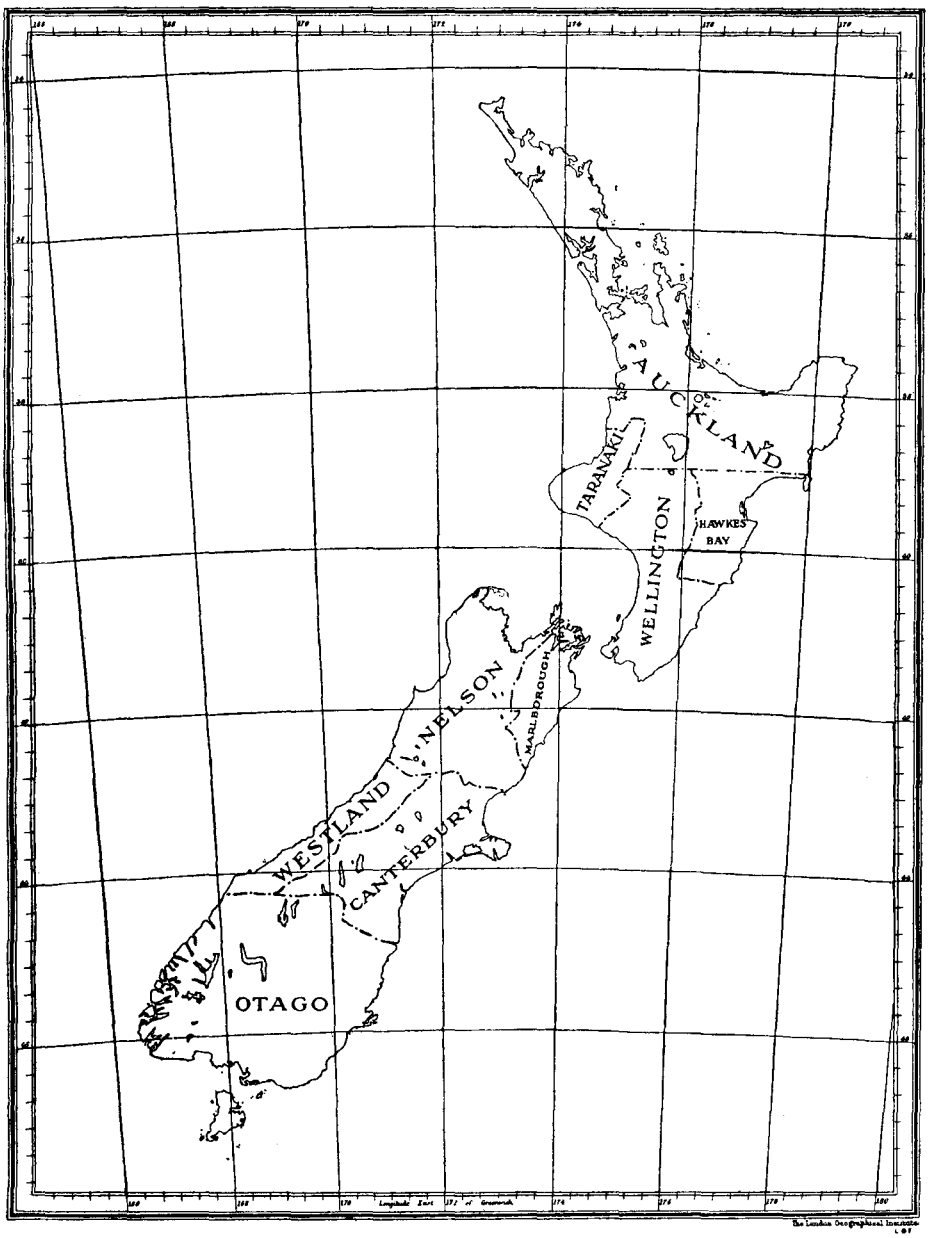
Plate XXII.

Ameletus ornatus (Eaton).

Fig. 1. Thorax and first two abdominal segments, × about 14.
(Immature nymph; wing-pads undeveloped.)
2. Legs, × about 14; tarsal claw, much enlarged.
3. Gill, × about 14.
4. Caudal setae, × about 14, and segment of one, much enlarged.
5. Labrum, × about 25.
6. Mandible, × about 25.
7. Labium, × about 25.
8. Maxilla, × about 25.
9. Tip of glossa, much enlarged.



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Map of New Zealand.