THE INSECTS
OF
AUSTRALIA AND NEW ZEALAND

BY

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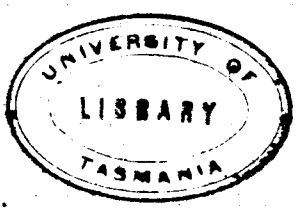

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CHAPTER VIII

Order PLECTOPTERA

(or EPHEMEROPTERA)

(May-flies)

THE May-flies are delicately formed, aërial insects, which can be at once recognized by their short, filiform antennae, aborted mouth-parts, greatly reduced hindwings and long caudal filaments, usually three in number; they are only found in the neighbourhood of water, and are mostly crepuscular in their habits, dancing or drifting in the air, sometimes in large swarms. They are unique in possessing two winged stages, the subimago and imago; the former has opaque wings, and flies but little; the latter has transparent wings, and is active in flight.

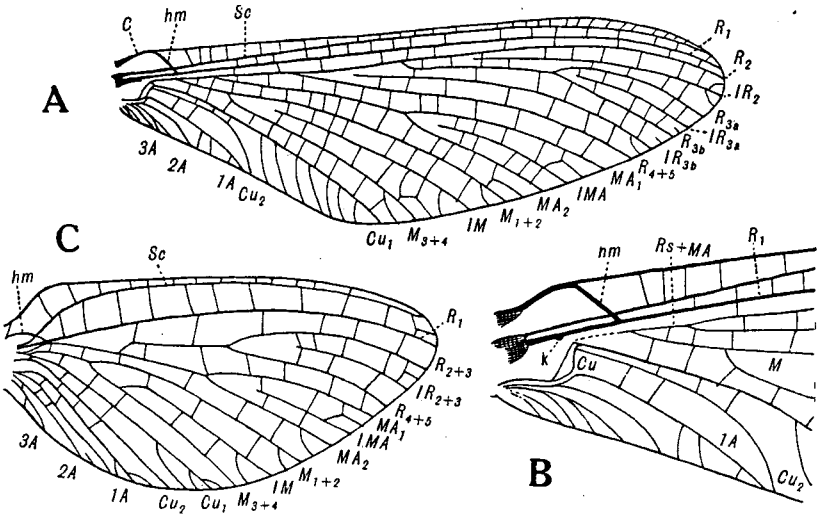


FIG. E1. *Ameletus ornatus* Eat., New Zealand. Fam. *Siphlonuridae*. A, fore-wing, length 17 mm; B, base of same, enlarged to show humeral brace-vein (*hm*) and stump of original base of *Rs* (*k*); C, hind-wing of same, length 6 mm. Lettering as in fig. A8, p. 22, and table on p. 59; note the triadic arrangement of the veins and the numerous branches of *Rs*.
[*R. J. T. del.*

Characters. Head short, transverse; *compound eyes* always present, much larger in male than in female; sometimes each eye in the male is divided into two parts, the upper being the larger; this upper part may be raised upon a projecting cylindrical base, and is then called a *turban-eye;* three *ocelli* always present; *antennae* short, subulicorn, with two distinct basal segments and an indistinctly segmented flagellum. *Mouth-parts* aborted.

Thorax with *prothorax* of variable size, *mesothorax* always the largest, much larger than *metathorax*. *Legs* weak and short, except forelegs of male, which are elongated and held out in front of the head almost like a pair of antennae; *tarsi* with a variable number of segments, from five to one; tarsal claws often modified.

Wings attached to thorax by a single axillary only, and held vertically above the body, pressed close together, back to back. Hindwing always much smaller than forewing, never (in recent forms) more than one-third of it in size, sometimes entirely absent. *Venation* of a very primitive type, with the branches all arranged in complete triads (fig. E1), except sometimes on Cu_1, where a pectinate series may be developed. In recent May-flies, the middle member of each triad generally has its base detached from the other two members of the triad, so that it appears to be an interpolated vein of later origin. The Lower Permian May-flies, however, have exactly the same triads as in recent May-flies, but the middle member of each triad is normally attached to one or other of the outer veins enclosing it. The venation of this Order agrees with that of the Palaeozoic Palaeodictyoptera and related Orders in the possession of a complete archaic media, composed of an anterior, convex branch, MA, and a posterior, concave branch, M; as both of these carry a simple triad, we use the notation MA_1, MA_2 for the convex branches of the former, with IMA as the interpolated concave vein, and the notation M_{1+2}, M_{3+4} for the concave branches of M (these being strictly homologous with the veins so denoted by Comstock in most other Orders), with IM for the interpolated convex vein. *Forewing* with Rs detached from its original base (represented by the stump *k* in fig. E1) and connected with MA; an oblique humeral brace-vein present (fig. E1, *hm*), preceded by a short basal thickening of the costa; this latter formation is the remains of an original, separate, short, costal vein, with descending distal branch, present in the Permian fossils. Owing to the complete system of triads, convex and concave veins alternate with one another regularly along the margin of the wing, which is thus thrown into marked folds formed by the alternating grooves and ridges. Sc simple, running nearly to apex; R_1 also simple, running to apex or nearly so; Rs with three primary, concave branches, viz., R_2, R_3 and R_{4+5}, but R_3 itself with a terminal triad, viz., R_{3a}, IR_{3a} and R_{3b}; two convex veins interpolated between the original three branches, viz., IR_2 and IR_{3b}, making seven branches in all; sometimes a definite chitinized spot, or bulla (fig. E6, *b*) is present on R_{2a} about half-way; M and Cu always more or less bent upwards at base; Cu_1 often connecting with M near its bend by a very short M_5; MA and M simple triads; Cu_1 with a number of descending branches either arranged as modified triads or in a single pectinate series; Cu_2 a simple concave vein bounding the small convex anal area, on which three short anal veins, all convex, branched or simple, are developed. *Hindwing* often with costa much arched near base, sometimes strongly angulated, the wing-coupling being of the amplexiform type, similar to that found in Butterflies (p. 402). Rs, MA and M either simple triads or single veins. Cross-veins usually abundant, irregular, always at right-angles to main veins, sometimes much reduced in number, or absent.

Until recently, the venation of May-flies has not been correctly understood, and several diverse systems of notation were in vogue. Eaton, whose fine work on the Order is acknowledged by everyone,

had his own system, antedating that of Comstock and Needham, which need not be considered here. Comstock and Needham provided a new notation, originally with the branches of *Rs* and *M* arranged in logical sequence. There followed an exhaustive study of the larval wings by Miss Morgan, who, in a thesis evidently inspired by the idea that *Rs* would be found crossing *M* as in Odonata, actually set forth that extraordinary interpretation, although she only succeeded in finding one such tracheal crossing (in *Heptagenia*) in the numerous larval wings examined. As the theory of a crossing of *Rs* in Odonata is no longer tenable, her system falls with it. The new system here given has been derived from a combined study of the Lower Permian fossils and the larval wings of archaic New Zealand Siphlonuridae, both methods of study giving similar results. The New Notation here given differs from that originally proposed by me (1922) in that it takes into account the presence of Lameere's anterior median *MA*, which I originally considered to be R_{4+5}. The following Table exhibits the three systems:—

New Notation	Convex (+) or concave (−)	Comstock-Needham Notation	Morgan's Notation
C	+	*C*	*C*
Sc	−	*Sc*	*Sc*
R_1	+	R_1	R_1
R_2	−	R_2	M_1
IR_2	+	(omitted)	(omitted)
R_{3a}	−	(omitted)	(omitted)
IR_{3a}	+	(omitted)	(omitted)
R_{3b}	−	R_3	*Rs*
IR_{3b}	+	R_4	Interpolated vein 1
R_{4+5}	−	R_5	M_2
MA_1	+	M_1	M_3
IMA	−	M_2	(omitted)
MA_2	+	M_3	M_4
M_{1+2}	−	Cu_1	Cu_1
IM	+	Interpolated vein	Interpolated vein
M_{3+4}	−	Cu_2	Cu_2
Cu_1	+	*1A*	*1A*
Cu_2	−	*2A*	*2A*
1A	+	*3A*	*3A*
2A	+	*3A*	*3A*
3A	+	*3A*	*3A*

A b d o m e n slender, usually cylindrical, with ten complete segments; tenth segment ending in an *appendix dorsalis* and two *cerci*, forming three usually similar, elongated *caudal filaments*, each with numerous segments; sometimes the appendix dorsalis is reduced or absent. *Spiracles* eight pairs, on segs. 1-8. Alimentary canal receiving no food, but inflated with air in imago. Male (fig. A11) with ninth sternite bearing well developed gonocoxites and long, segmented styles; aedeagus consisting of a double symmetrical penis with or without parameres; tenth sternite complete. Female without an ovipositor, but having a wide vulva, *opening between the seventh and eighth sternites*, the two oviducts opening separately into it; seventh sternite often developed as a strong *subgenital plate*; eighth sternite short; ninth sternite sometimes prolonged as a *ventral plate*. *Malpighian tubules* numerous in larvae.

Life History. The early stages are passed entirely in the water, the *eggs* being protruded in two large masses, and washed out of the body of the female, falling freely on the bed of the stream. The larvae (figs. E2, 3, 4) are either vegetarian or carnivorous, and mostly roam freely on the stream-bed (fig. E2) or hide under rocks (fig. E3); some, however, burrow into the banks (fig. E4), and thus avoid becoming a prey to fishes until they emerge; they are elongate,

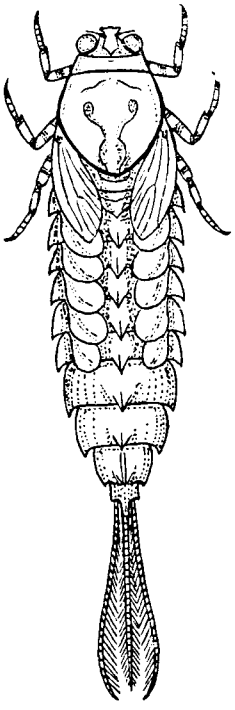


FIG. E2. Free-swimming larva of *Oniscigaster distans* McL., New Zealand. Fam. Siphlonuridae. Length of of body 24 mm. [*R. J. T. del.*

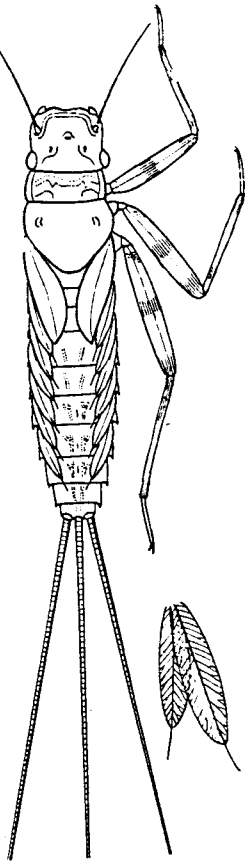


FIG. E3. Rock-dwelling larva of *Atalophlebia costalis* Burm., Australia. Fam. Leptophlebiidae. Length of body 12 mm. At side, one pair of gills from fifth abdominal segment, enlarged. (The long tail-filaments are only partially figured.) [*R. J. T. del.*

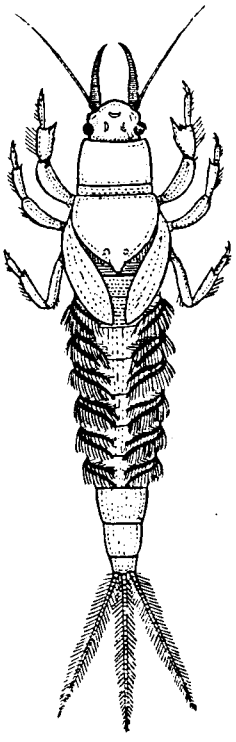


FIG. E4. Burrowing larva of *Ichthybotus hudsoni* Eat., New Zealand. Fam. Ephemeridae. Length of body 27 mm. [*R. J. T. del.*

with strong legs, three caudal filaments, and a more or less complete system of paired segmental gills on the abdomen. In most cases these gills are double, more or less leaf-like, with numerous tracheal branches ramifying in them; they are generally thrown over the back of the larva, the abdomen being pressed flatly down against the surface on which it rests. The number of larval instars is large, twelve or more, wing-buds appearing when the larva is less than half-grown,

and increasing in size through the last five or six instars. The newly-hatched larva has no gills; they arise as slender filaments, a pair or two at a time, from the second instar onwards. When full-grown, the larva swims or climbs to the surface of the water, and there discloses the winged *subimago,* which flies straight up from the water to find a refuge in some near-by foliage or on a rock. This stage lasts three or four days in the older forms, only a few minutes in the highest types; from it there emerges the true *imago,* with transparent wings and mature reproductive organs. This also lives only a few days, and takes no food, the mouth-parts being aborted. Pairing takes place in the air, during the evening flights or dances, and is of short duration, the female at once descending to the water to wash off the eggs, which extrude in a sticky, yellowish mass from the abdomen.

Distribution. Only four families of May-flies are represented in Australia, and one of these, the Baëtidae, is not found in New Zealand. In the other three families, the Australian and New Zealand genera are either the same or very closely allied, and all appear to have had a common origin, probably from Antarctica. The New Zealand species are larger, more brightly-coloured, and much more abundant in individuals than the Australian, as might be expected, owing to the much greater number of fast running rivers, in which these insects live. But the introduced trout have greatly diminished this once abundant fauna, and some species are extinct, or nearly so.

Economics. This Order is entirely beneficial, both the larvae and adults forming one of the best foods for freshwater fishes. Indeed, the art of Fly-fishing is based chiefly upon the keen desire of the trout for the winged May-fly. Unfortunately the May-fly fauna of Australia and New Zealand is not specialized to hold its own against the introduced Brown and Rainbow Trout, and is rapidly being reduced to a minimum, none of the larvae except those of *Ichthybotus* being burrowers.

Fossil History. No fossil May-flies have so far been found in Australia, and it is probable that the Order was never really abundant there, and only became established fairly late in Mesozoic times. True May-flies occur in the Lower Permian of Kansas, but differ from those of the present day in having both fore and hindwings large and almost equal. Some of these forms were even larger than the New Zealand Siphlonuridae existing to-day. Jurassic May-flies are also known, having the hindwings reduced, but considerably larger than at the present day.

CLASSIFICATION

SCHEME OF CLASSIFICATION AND CENSUS OF SPECIES

Order PLECTOPTERA 20 (20)

1. SIPHLONURIDAE 4 (7)
2. EPHEMERIDAE 1 (2)
3. LEPTOPHLEBIIDAE 12 (11)
4. BAETIDAE 3 (0)

The four families represented in our faunas are only a small fraction of the numerous diverse types of May-flies occurring throughout the world; they stand so far apart from each other that each

may be taken as belonging to a separate superfamily, if so desired. They may be distinguished by the following Key:—

1. Hindwings well developed, from one-half to one-third as long as forewings 2
   Hindwings very small or absent, at most less than one fourth as long as forewings 3
2. Prothorax well developed, usually about as long as wide; forewing with *Cu* bent at an acute angle near where it forks basally, and attached to *M*; Cu_1 sigmoidally curved. Fam. 2. EPHEMERIDAE
   Prothorax much shorter than wide; forewing with *Cu* bent at right-angles where it forks basally, not attached to *M*; Cu_1 an almost straight vein ending up about half-way along the wing, just beyond tornus. Fam. 1. SIPHLONURIDAE
3. Forewing with numerous cross-veins; hindwing from about one-fifth to one-seventh of forewing in length; male without turban eyes. Fam. 3. LEPTOPHLEBIIDAE
   Forewing with very few cross-veins; hindwing minute or absent; male with turban eyes and very iridescent wings. Fam. 4. BAETIDAE

Family 1. **Siphlonuridae** [Aus. 4, N.Z. 7]. Forewing with tornus well developed at from two-fifths to nearly one-half the wing-length from base, the nearly straight Cu_1 ending up just beyond it, and having a descending series of pectinate branches; Cu_2 curved concavely to Cu_1. Larvae either active, free-swimming and carnivorous, or torpid, clinging to rocks in fast running streams.

This fine and undoubtedly very archaic family is well represented in New Zealand by the genera *Ameletus, Oniscigaster* and *Coloburiscus*; the first two genera have free-swimming, somewhat shrimp-like larvae with double lamellate gills, the last-named a highly specialized larval type with swollen thorax and peculiar bifid gills which give it a protective resemblance to a piece of aquatic vegetable growth on the rock to which it clings. *Ameletus ornatus* Eat. (fig. E1 and pl. 10, fig. 1) expands from one to one and a half inches, the subimago having the wings variably mottled in brownish or olive-green, the imago with hyaline wings. The shrimp-like larva often rests exposed on damp rocks close to the spray of cascades and waterfalls; when threatened with danger, it jumps vigorously back into the water, the action being very suggestive of that of a Machilid, which it superficially resembles. *A. perscitus* Eat. (pl. 2, fig. 1) is a much larger species of more robust build, lemon-yellow in both winged instars; its larva has a very large head, and is highly carnivorous. Larvae of the *Ameletus* type, but with fewer gills, occur in small streams on the Blue Mountains, New South Wales, but the imagines are not yet known. *Coloburiscus humeralis* Walk. is much the commonest of the large New Zealand May-flies; it can be recognized by the shaded costa of forewings, the sharply angulated costa of the hindwings, and the aborted appendix dorsalis; the imago is not unlike that of *A. ornatus* Eat., but the subimago has dull, greyish, unornamented wings. This genus is also represented by two fine species in Australia, *C. halcuticus* Eat. in Victoria and a very large, undescribed species on Mt. Kosciusko. *Oniscigaster wakefieldi* McL., now almost extinct, is remarkable for its broad abdomen with lateral dilatations of abdominal segs. 7-9. *O. distans* Eat. (pl. 10, fig. 2) is a larger species, the females expanding up to 2 inches, without lateral dilatations. The beautiful subimago, with purplish-black wings, has been kept alive for three days before disclosing the very different, hyaline-winged imago. The larva (fig. E2) is dorso-ventrally flattened, living freely on the fine, gravelly beds of small mountain streams; it cannot dart forward like the larvae of *Ameletus*, and has little chance of survival against the introduced trout. *Tasmanophlebia lacustris* Till. (pl. 10, fig. 3) is a small, lake-dwelling species allied to *Oniscigaster*, found in Tasmania.

Family 2. **Ephemeridae** [Aus. 1, N.Z. 2]. Prothorax well developed, as long as wide. Forewing with well developed tornus at one-third to two-fifths of wing-length from base, with Cu_1 ending beyond it; Cu_1 acute-angled at its basal fork and fused for a short space with *M*. Larvae (fig. E4) burrowers, with short, feathery gills kept continually in motion so as to ensure a flow of water through the burrows. The New Zealand species are the fine *Ichthybotus hudsoni* McL., expanding 1½ to over 2 inches, in the North Island, and *I. bicolor* Till., a smaller and rarer species with dark hindwings in imago, found in the South Island. Both sexes agree in having the costa strongly shaded with reddish-brown, but the females in both species have yellowish wings, those of the male

being hyaline; the subimagines have in addition dark blotches or complete fasciae on the wings. Larvae resembling those of *Ichthybotus* occur also in the Fish River in New South Wales, but the imago is not known.

The Great Papuan May-fly, *Plethogenesia papuana* Eat., belongs to this family; though its rich, creamy-yellow subimago has been seen in count'ess numbers on the Fly River, not a single imago has ever been observed, and it is believed that this species mates and dies in the subimaginal stage.

Family 3. **Leptophlebiidae** [Aus. 12, N.Z. 11]. Forewing with tornus more or less well marked, always close to base (at one-fourth of wing-length from base or less) in correlation with the greatly reduced hindwings. Cu_1 attached to M at a point just beyond its origin and very strongly angulated there; branches of Cu_1 few; Cu_2 sigmoidally curved, ending not far short of tornus; anal veins much reduced. A bulla (fig E6, *b*) usually present on R_{2+3} about half-way along the wing. Larvae (fig. E3) active, carnivorous, hiding under rocks or stones in still or running waters; gills lanceolate.

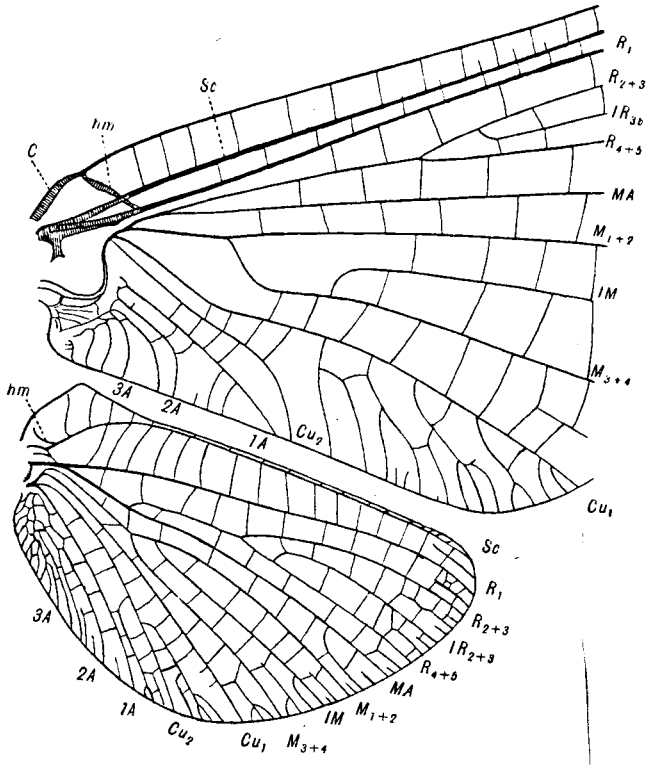


FIG. E5. *Ichthybotus hudsoni* McL., New Zealand. Fam. Ephemeridae. Hindwing and basal portion of forewing. Length of hindwing 6.5 mm. Lettering as in fig. E1, p. 57. Note *IM* of forewing switched on to M_{3+4}. [*R. J. T. del.*

This is the dominant family of May-flies in both countries, the principal genus being *Atalophlebia* with numerous species. *A. costalis* Burm. (pl. 10, fig. 5), the commonest May-fly in Australia, is a rich brown species remarkable for the enormous length of the cerci in the males; the appendix dorsalis is usually aborted. The larva (fig. E3) is handsomely variegated in fuscous and olive-green. Of several fine New Zealand species, the reddish-brown *A. dentata* Eat. (pl. 2, fig. 2) and *A. cruentata* Huds. are barely distinguishable in the winged stages, though the larvae are distinct both in colour and shape. *A. versicolor* Eat. (pl. 10, fig. 4) has a subimago with richly variegated wings. Of a number of very small species, the New Zealand *Deleatidium lillii*

Eat. occurs in great swarms in many localities; this genus, *Thraulus* and *Euphyurus* are all represented in Australia.

Family 4. **Baetidae** [Aus. 3, N.Z. 0]. This family is only represented in Australia by three species of tropical origin; they are of very small size,

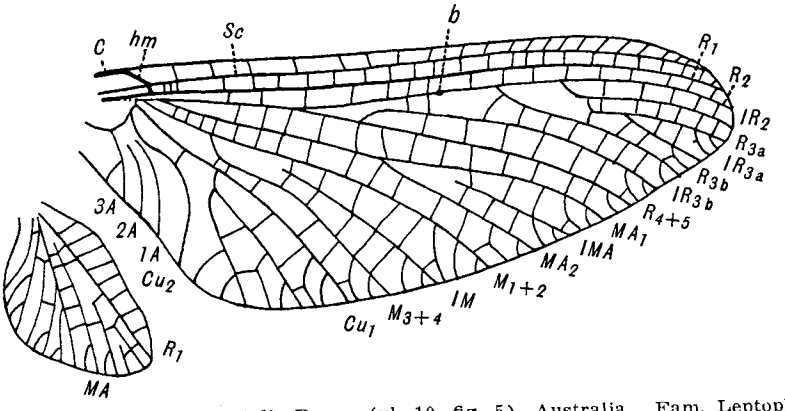


FIG. E6. *Atalophlebia costalis* Burm. (pl. 10, fig. 5), Australia. Fam. Leptophlebiidae. Wing-venation. Length of forewing 10 mm. Lettering as in fig. E1, p. 57, except *b*, bulla. [*R. J. T. del.*

with few cross-veins, the hindwings minute or absent, the males with turban eyes. The larvae inhabit slow or stagnant waters. *Baëtis soror* Ulm. reaches as far south as Sydney. The male of *Chloeon viridis* Klap. has the forewings a brilliantly iridescent green; the hindwings are absent.

REFERENCES.

EATON, A. E., 1883-7. "Revisional Monograph of Recent Ephemeridae or May-flies". *Trans. Linn. Soc. London*, 3 parts. 1899, "An annotated list of the Ephemeridae of New Zealand", *Trans. Ent. Soc. London*, pp.285-293.

HUDSON, G. V., 1904. *New Zealand Neuroptera*, pp.23-44.

MORGAN, ANNA H., 1912. "Homologies in the Wing-veins of May-flies". *Ann. Ent. Soc. Amer.*, ii, pp.89-106.

SELLARDS, E. H., 1907. "Types of Permian Insects: Part ii, Plectoptera." *Amer. Journ. Sci.*, xxiii, pp.345-355.

TILLYARD, R. J., 1922. "The Wing-venation of the Order Plectoptera". *Journ. Linn. Soc. London*, pp.143-162. 1923, *Trans. N.Z. Inst.*, liv, pp.226-230.

ULMER, G., 1916. "Ephemeroptera" in "Results Mjoberg's Swedish Sci. Exped. to Australia", No. 6, *Arkiv. f. Zool.*, x, No. 4, pp.1-18.

PLATE 10

PLECTOPTERA AND PERLARIA

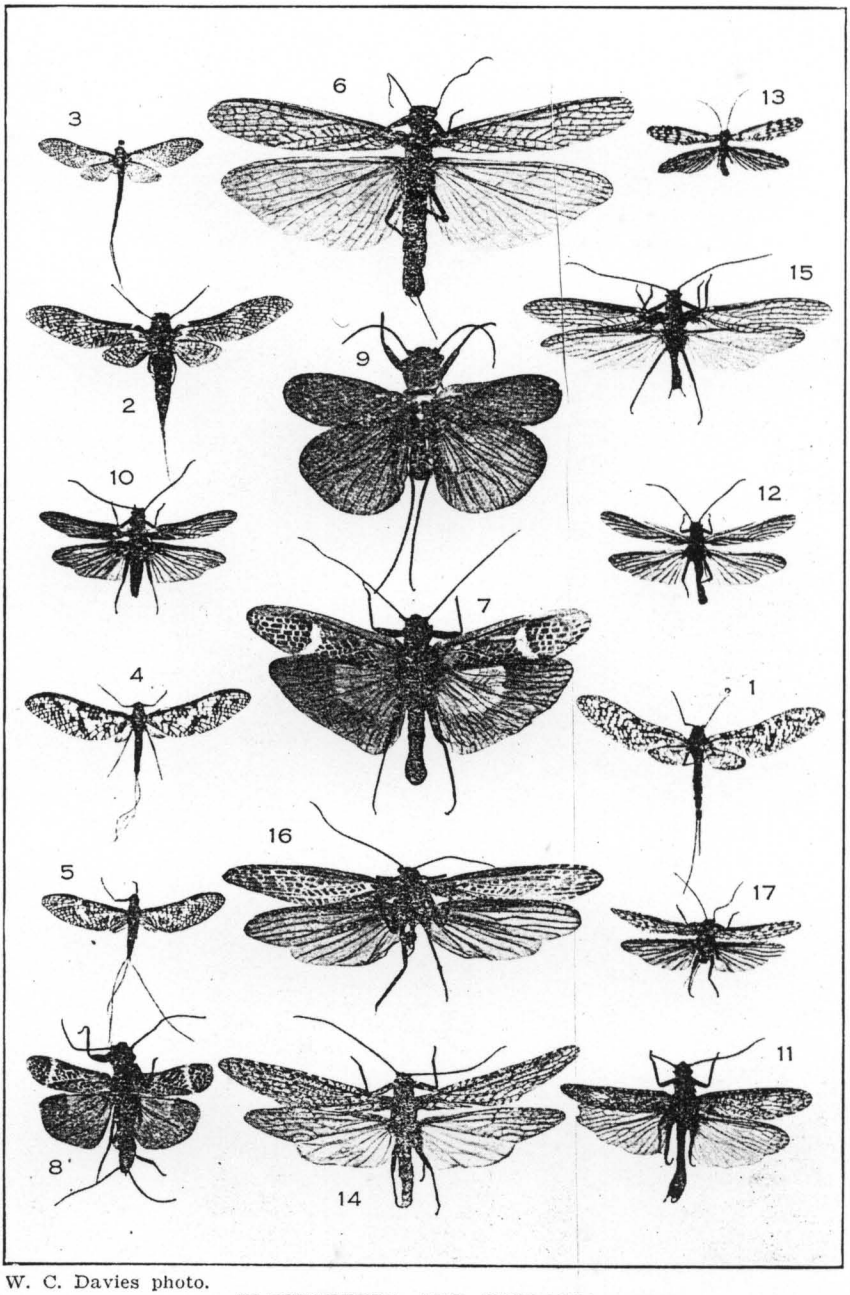
All figures natural size

Order PLECTOPTERA

1. *Ameletus ornatus* Eat. (Fam. SIPHLONURIDAE), male subimago, N.Z.
2. *Oniscigaster distans* Eat. (Fam. SIPHLONURIDAE), female subimago, N.Z.
3. *Tasmanophlebia lacustris* Till. (Fam. SIPHLONURIDAE), male subimago, Aus.
4. *Atalophlebia versicolor* Eat. (Fam. LEPTOPHLEBIIDAE), female subimago, N.Z.
5. *Atalophlebia costalis* Burm. (Fam. LEPTOPHLEBIIDAE), female subimago, Aus.

Order PERLARIA

6. *Stenoperla australis* Till. (Fam. EUSTHENIIDAE), female, Aus.
7. *Eusthenia lunulata* Till. (Fam. EUSTHENIIDAE), female, Aus.
8. *Eustheniopsis venosa* Till., form *brachyptera* Till. (Fam. EUSTHENIIDAE), Aus.
9. *Thaumatoperla robusta* Till. (Fam. EUSTHENIIDAE), male, Aus.
10. *Austroperla cyrene* Newm. (Fam. AUSTROPERLIDAE), N.Z.
11. *Tasmanoperla diversipes* Walk. (Fam. AUSTROPERLIDAE), Aus.
12. *Tasmanoperla ruficosta* Till. (Fam. AUSTROPERLIDAE), Aus.
13. *Dinotoperla fasciata* Till. (Fam. LEPTOPERLIDAE), Aus.
14. *Trinotoperla irrorata* Till. (Fam. LEPTOPERLIDAE), Aus.
15. *Trinotoperla australis* Till. (Fam. LEPTOPERLIDAE), Aus.
16. *Eunotoperla kershawi* Till. (Fam. LEPTOPERLIDAE), N.Z.
17. *Zelandoperla decorata* Till. (Fam. LEPTOPERLIDAE), N.Z.



W. C. Davies photo.

PLECTOPTERA AND PERLARIA